Weaning age variation in beluga whales (*Delphinapterus leucas*)

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Beluga whales (*Delphinapterus leucas*) have a protracted nursing period estimated to last from 6–32 months, although current estimates of beluga nursing duration are derived using approaches subject to capture bias. Recent studies have shown stable isotope profiles of dentin growth layer groups (GLGs) in marine mammal teeth serve as a reliable nursing proxy and can be used to assess individual weaning patterns. We measured stable isotope ratios of nitrogen (δ^{15}N) and carbon (δ^{13}C) of dentin GLGs in teeth from eastern Canadian Arctic belugas to estimate weaning age and assess relative contributions of milk and solid food during the nursing period. δ^{15}N declines of ~1‰ over the first 3 GLGs of most individuals were interpreted as evidence of weaning. Individual δ^{15}N profiles indicated 15 of 27 whales were completely weaned by the end of their 2nd year, although a number of whales were weaned by the end of their 1st or 3rd year (9 and 3, respectively). Intermediate GLG2 δ^{15}N values relative to GLGs 1 and 3 indicated most whales consumed a mixture of milk and solid food during their 2nd year, consistent with gradual weaning. Contrary to predictions based on parental care theory, nursing duration was not related to relative GLG width (used as a proxy for somatic growth) and did not differ for females and males, or among populations. δ^{13}C variation was not a reliable indicator of nursing duration, as approximately half of the whales showed no ontogenetic δ^{13}C patterns across GLGs deposited over the nursing period. This study provides novel life history information, which may inform beluga conservation and management decisions, and indicates belugas share prolonged nursing duration marked by individual variation observed in other odontocetes.

Key words: Arctic, dentin, growth layer groups (GLGs), marine mammal, nursing, stable isotopes, teeth

Parental investment is defined by Trivers (1972) as expenditure of parental resources to increase an offspring's chances of survival that diminishes ability to invest in other offspring. One of the defining mammalian characteristics is the provision of milk to dependent young, when transfer of maternal nutrients and energy supports offspring until they can forage independently (Pond 1977). Lactation is the most energetically costly stage of female mammalian reproductive effort (Gittleman and Thompson 1988), when allocation of maternal resources to offspring comes at the expense of self-maintenance and future reproductive success of the mother (Clutton-Brock et al. 1989). Maternal provisioning strategies therefore balance investment in offspring growth and survival against condition and reproductive costs incurred by mothers (Lee et al. 1991; Fairbanks and McGuire 1995; Rogowitz 1996).

Cetacean calves are weaned when they reach a threshold length relative to maternal size (Huang et al. 2009), similar to other large-bodied mammals (Lee et al. 1991). Capital breeding mysticetes have brief, but intensive, nursing periods during which more than 30% of maternal body fat is converted into high fat milks until calves are weaned at 6 months to 1 year (Tyack 1986; Oftedal 1997, 2000). Odontocetes, by comparison, are income breeders that nurse their calves over prolonged periods ranging up to several years (Tyack 1986; Oftedal 1997). Continual food consumption throughout the nursing period, along with lower rates of energy transfer (odontocete milks have less fat than mysticete milks), allow energetic demands of lactation to be distributed over a longer period (Oftedal 1997). Nevertheless, odontocete mothers must increase their daily food consumption by 32–63% over nonlactating requirements to fuel milk production (Lockyer 1981). These energetic costs translate into fitness returns, as the extended nursing period provides time for development of sensorimotor systems used to pursue highly mobile prey (as opposed to grazing by baleen whales—Brodie 1969; Hayssen 1993). Prolonged periods of maternal dependence may also facilitate social learning in complex groups characteristic of odontocetes (Brodie 1969; Mann and Smuts 1999; Colbeck et al. 2013).

Beluga whales (*Delphinapterus leucas*—Pallas 1776) are a mid-sized odontocete that occupy a discontinuous circumpolar

distribution in Arctic and sub-Arctic waters (Stewart and Stewart 1989). Mating occurs seasonally in late winter to early spring (Brodie 1971; Burns and Seaman 1985), and reproductive tract morphologies suggest belugas have a promiscuous rather than polygynous mating system (Kelley et al. 2014). Females give birth to a single calf following a gestation of 12–14.5 months (Brodie 1971; Sergeant 1973; Seaman and Burns 1981; Doidge 1990). Calving varies geographically, but generally peaks from June to mid-August in the eastern Canadian Arctic (Brodie 1971; Sergeant 1973; Cosens and Dueck 1990; Kilabuk 1998). The calving interval is largely accepted to be 3 years (Sergeant 1973; Doidge 1990; Heide-Jørgensen and Teilmann 1994), although a biennial breeding cycle is suggested in some females (Seaman and Burns 1981), and some observers believe belugas give birth annually (Kleinenberg et al. 1964; Kilabuk 1998; Stewart 2001). Female belugas are reproductively active throughout their adult life, but birth rate declines gradually with age (Burns and Seaman 1985).

Beluga whales have a protracted nursing period typical of odontocetes, although estimates of nursing duration vary considerably. Brodie (1971) captured 2-year-old calves alongside lactating females in Cumberland Sound (CS), Baffin Island and concluded beluga calves are nursed for at least 2 years. Sergeant (1973) calculated a lactation period of 21 months in Western Hudson Bay (WHB) belugas based on the ratio of lactating to pregnant animals captured in nets, multiplied by a gestation period that was based on fetus length and calf length at birth. Using the same "ratio method," lactation duration estimates were about 32 months for beluga whales off northern Quebec (Doidge 1990) and 6–12 months for belugas off northwest Alaska (Burns and Seaman 1985), while Kleinenberg et al. (1964) cite a lactation period of just 5–6 months for belugas in the Sea of Okhotsk. Milk is considered the only form of nutrition during the 1st year (Brodie 1971), but studies reporting a mixture of milk, fish, and squid in stomachs of 2-year-old calves (Heide-Jørgensen and Teilmann 1994) indicate diet is supplemented with solid food in the 2nd year.

Current estimates of beluga nursing duration based on the ratio and cow–calf methods are subject to harvest or capture bias (Perrin and Reilly 1984). For example, slowed movements of lactating females accompanied by calves may make them more susceptible to harvest than pregnant females, or to capture in nets if they return to assist an entangled calf (Doidge 1990). Stomach contents can be similarly misleading for species that consume solid food before deriving much nutritional value from it (see Heyning 1988; Lee 1997), or engage in nonnutritive suckling (e.g., Best et al. 1984). Isotopic analysis has shown $\delta^{15}N$ values in tissues of suckling mammals are higher than those of their mothers (Jenkins et al. 2001; Polischuk et al. 2001), which has been attributed to consumption of milk, a maternally derived tissue enriched in ^{15}N relative to the trophic level at which the mother feeds (Jenkins et al. 2001). Nursing has also been associated with lower stable carbon isotope ratios ($\delta^{13}C$), which presumably reflect incorporation of carbon derived from relatively ^{13}C-depleted milk lipids (Hobson and Sease 1998). However, this nursing effect on offspring $\delta^{13}C$

values is not consistently observed (Jenkins et al. 2001; Habran et al. 2010). Newsome et al. (2006) suggest tissue $\delta^{13}C$ patterns over the nursing period reflect the degree of preferential routing of carbon from milk lipids versus proteins to tissue synthesis.

Isotopic profiling of dentin growth layers in teeth spanning the nursing period has documented chronological $\delta^{15}N$ declines that are consistent with weaning in several marine mammal species (Hobson and Sease 1998; Hobson et al. 2004; Newsome et al. 2006; Knoff et al. 2008; Newsome et al. 2009; Matthews and Ferguson 2014a). Conversely, weaning-associated ontogenetic $\delta^{15}N$ shifts are absent or dampened in teeth of pinnipeds that abruptly wean their pups after a brief nursing period because the bulk of the 1st year spent foraging attenuates any nursing signal (e.g., Newsome et al. 2006). $\delta^{15}N$ patterns in teeth can therefore be used as a nursing proxy, offering an alternative to other methods that have been used to estimate lactation duration in cetaceans (e.g., Brodie 1971; Sergeant 1973). This approach is ideal for belugas because they are born with a full set of teeth that are retained throughout their lifetime (Stewart 2012). The pulp cavity of each tooth gradually fills with dentin that undergoes little postdepositional modification (Bloom and Fawcett 1975). A neonatal line formed just after birth marks the beginning of postnatal dentine deposition (Stewart 2012), and alternating broad and narrow bands define annually deposited growth layer groups (GLGs) from then on (Stewart et al. 2006; Luque et al. 2007; Campana and Stewart 2014; Matthews and Ferguson 2014b).

Here, we use isotopic profiles across dentin GLGs of beluga whales from the eastern Canadian Arctic to determine whether belugas have prolonged nursing periods typical of toothed whales. Further, we examine individual isotope profiles to infer whether beluga whales have variable nursing periods, which has been reported in other odontocetes (e.g. Mann et al. 2000). In accordance with parental care theory, which posits that mothers should invest in their offspring in a manner that maximizes their own fitness (Clutton-Brock 1991), we predicted nursing duration may vary 1) with relative GLG width, which we considered a proxy for growth, since faster growing individuals attain size required for independence quicker and should be weaned earlier (see Lee et al. 1991; Huang et al. 2009); 2) by sex, since beluga are sexually dimorphic (Sergeant and Brodie 1969) and male calves may have greater lactational requirements than females, and investment in males potentially confers greater fitness to the mother if larger males are more likely to successfully reproduce (e.g., Clutton-Brock et al. 1985); and 3) by population, since whales at different latitudes with varying migration patterns may experience different environmentally imposed energetic constraints on nursing (e.g., Trillmich 1990; Luque and Ferguson 2010). We also consider the influence of additional factors (e.g., maternal age—Clutton-Brock 1984) on beluga nursing duration.

MATERIALS AND METHODS

Tooth collection and micromilling.—Teeth were extracted from mandibles of beluga whales ($n = 30$) harvested in subsistence hunts

throughout the eastern Canadian Arctic during the 1980s–2000s. Our sample included equal numbers of females and males from 3 geographically separated and genetically distinct populations (Brown Gladden et al. 1997; Brennin et al. 1997): Western Hudson Bay (WHB; $n = 7$), Cumberland Sound (CS; $n = 11$), and Eastern High Arctic-Baffin Bay (EHA-BB; $n = 12$; Fig. 1). Teeth were extracted from the standard aging positions 2 and 5 (Stewart 2012), except when noticeably less wear occurred in adjacent teeth.

Teeth were air-dried and sectioned longitudinally along the midline using a water-cooled diamond-encrusted saw blade. Beluga dentin is deposited in a series of stacked cones, which appear in longitudinal section as GLGs comprising 1 thick and 1 thin annulus (Stewart 2012). Tooth sections were polished using 30- and 9-μm aluminum oxide lapping film to accentuate GLG definition. GLGs were counted under reflected light and aged assuming annual deposition, using the neonatal line separating prenatal and postnatal dentin as a reference (Stewart 2012). GLG widths (micrometre) were measured from digital micrographs using the image analysis software Image-Pro Plus (Media Cybernetics, Bethesda, Maryland). Although the relationship between dentinal GLG width and somatic growth has not been studied in detail in belugas, Sergeant (1973) speculated the width of growth bands was related to skeletal growth because thicker GLGs in males corresponded to body size differences between the sexes. Dentin deposition varies with overall somatic growth in other species (Klevezal 1980; York et al. 2008); GLG width was therefore assumed to reflect growth during the nursing period.
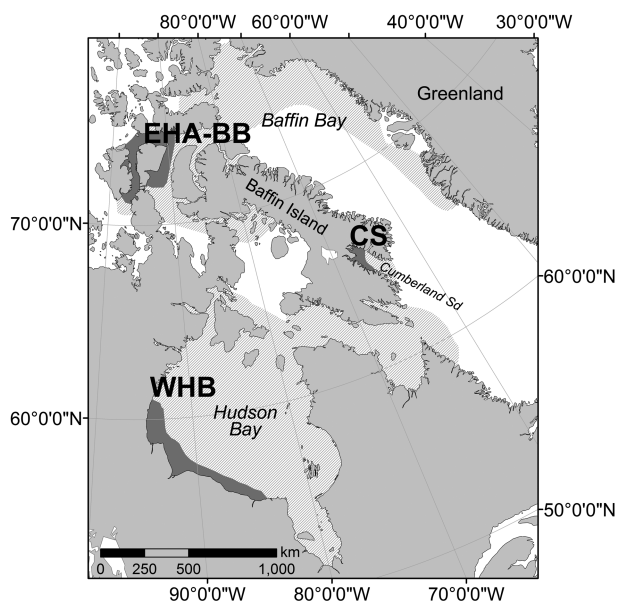

Fig. 1.—Teeth were collected from 3 beluga (*Delphinapterus leucas*) populations in the eastern Canadian Arctic: the Western Hudson Bay (WHB) population, the Cumberland Sound (CS) population, and the Eastern High Arctic-Baffin Bay (EHA-BB) population. Distributions (gray hatch lines) and areas of summer occupancy (dark gray) of each population were reproduced from COSEWIC (2004), with modifications to WHB distribution after Smith et al. (2007).

Dentin GLGs were sampled using a high-resolution micro-mill (New Wave Research, Freemont, California) fitted with a 300-μm-diameter drill bit at a depth of 150 μm to minimize sampling of adjacent layers. Only teeth with a very clear neonatal line demarcating the 1st GLG from prenatal dentin were chosen for analysis, and only GLGs of sufficient clarity and width to allow discrete sample collection were micromilled.

Stable isotope analysis.—The organic, mainly collagen, component of dentin is typically isolated from its mineral matrix prior to isotopic analysis (e.g., Hobson and Sease 1998), since both fractions contain carbon (in protein and carbonates, respectively) routed from biomolecules with differing $\delta^{13}C$ values (Ambrose and Norr 1993). Removal of inorganic carbon from dentin using acidification prior to analysis was not feasible due to small sample amounts, so bulk dentin was analyzed instead. Recent studies (e.g., Martin et al. 2011; Matthews and Ferguson 2014b) have shown little difference between $\delta^{13}C$ values of bulk versus acidified dentin.

Powdered dentin was weighed (~1 mg) into tin cups for isotopic analysis on a Vario EL III elemental analyzer (Elementar, Hanau, Germany) connected to a Finnigan DELTAplus XP isotope ratio mass spectrometer (Thermo Fisher Scientific, Waltham, Massachusetts). Isotope ratios are reported as per mil (‰) deviation from the isotope ratios of atmospheric N_2 and Vienna Pee-Dee Belemnite limestone for nitrogen and carbon, respectively, defined as $\delta^{15}N$ or $\delta^{13}C = (R_{sample} - R_{standard})/R_{standard}) * 1,000$, where R is $^{15}N/^{14}N$ or $^{13}C/^{12}C$. Values were normalized using reference materials whose isotopic composition spanned the sample range (nicotinamide, ammonium sulfate + sucrose, and caffeine; $\delta^{15}N$ −16.61 to 16.58‰, $\delta^{13}C$ −34.46 to −11.94‰), calibrated to international standards IAEA-N1, IAEA-N2, USGS-40, and USGS-41 for $\delta^{15}N$ and IAEA-CH6, NBS-22, USGS-40, and USGS-41 for $\delta^{13}C$. Analytical precision based on repeated measures of laboratory reference materials not used in calibrations was 0.09 and 0.06‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively, and that based on duplicate measures of ~10% of samples was 0.14 and 0.06‰. Atomic C:N of bulk dentin (2.98 ± 0.06; mean ± *SD*) was within the range of unaltered collagen (DeNiro 1985).

Data analysis.—Individual $\delta^{15}N$ and $\delta^{13}C$ profiles were restricted to the first 5 GLGs, which encompassed previous estimates of lactation duration in beluga whales. As a proxy for *complete* weaning, the point at which $\delta^{15}N$ values stopped decreasing relative to GLG1 was determined visually for each individual. Visual assessment was followed with single-detection changepoint analysis on individual profiles using the "changepoint" package (Killick and Haynes 2014) available for R software (R Core Team 2014). Single-detection changepoint analysis detects changes in mean (or variance) along a measurement series by comparing the difference between maximum log likelihoods of the null (1 mean provides best fit to all data points) and alternative (single changepoint) models against a threshold penalty value, which we set to be sensitive to changes in mean $\delta^{15}N$ values of ~1‰ (a signal consistent with weaning; see Jenkins et al. 2001). Changepoints were used to classify intermediate $\delta^{15}N$ values during the nursing period as being more similar to GLG1 (i.e., representative of milk-derived $\delta^{15}N$ values) versus

subsequent GLGs in each profile, which were assumed to reflect the postweaning diet. This process was repeated on $\delta^{13}C$ profiles.

Assessments of weaning differences between sexes, among populations, and against GLG width were based on $\delta^{15}N$ patterns ($\delta^{13}C$ patterns varied considerably among individuals and could not be used to infer weaning; see "Results"). "Weaning age" was summarized by sex and population in contingency tables. To increase cell counts, weaning ages were grouped as GLG1 or GLG2+ to create a binary variable. Weaning differences between females and males and among populations were assessed using Fisher's exact tests recommended for small sample sizes (Agresti 1992). A logistic regression model implementing Firth's penalized likelihood approach to deal with small sample size (Firth 1993) was fit to pooled data (there was no evidence of sex or population differences in weaning age; see "Results") to examine how weaning age varied with relative GLG1 width. Relative GLG1 width was used as a measure of a whale's growth in its 1st versus subsequent years and was calculated by dividing GLG1 width by the total width of the first 5 GLGs. The model was fit using the R package "logistf" (Heinze et al. 2013).

RESULTS

Complete isotopic profiles (GLGs 1–5) were available for 25 of the 30 whales. GLGs 4 and 5 were too thin or obscure to be milled in the remaining 5 whales, resulting in profiles from GLGs 1–4 for 3 whales and GLGs 1–3 of 2 whales (Figs. 2 and 3). $\delta^{15}N$ declines of 0.4 to 2.79‰ ($\overline{X} = 1.26‰$) were obvious over the 1st several GLGs of all whales, with the exception of whale ARGFxx1042 (Fig. 2). $\delta^{15}N$ values appeared to decline up to GLGs 4 or 5 in whales B95-24, B95-547, and ARGFxx1024, so entire available profiles (up to GLGs 7–10) of these whales were examined to derive weaning age estimates (Fig. 2). Although $\delta^{15}N$ values declined in teeth with profiles comprising just 3 GLGs (ARGF87-11 and ARPG86-16; Fig. 2), they are not considered in further analyses because weaning ages could not be confirmed. Changepoints were detected along all but 1 of the 28 $\delta^{15}N$ profiles comprising 4 or more GLGs (Fig. 2).

Of the 27 whales for which $\delta^{15}N$ declines over the first 4 to 5 GLGs could be reliably characterized, $\delta^{15}N$ values declined between GLGs 1–2 in 9 whales and changepoint detections for 6 of these individuals also occurred at GLG1. Changepoint detections in the 3 whales with increasing $\delta^{15}N$ values beyond GLG2 (ARARxx1057, ARGFxx1035, and ARPGxx 1281) are not considered representative of weaning since they were influenced by high $\delta^{15}N$ values in older GLGs (Table 1; Fig. 2). These 9 whales were therefore interpreted as having been weaned in their 1st year (Table 1).

$\delta^{15}N$ values declined across the first 2 GLGs of 15 whales (Fig. 2), indicating they were weaned during their 2nd year. Of these 15 whales, GLG2 $\delta^{15}N$ values were grouped with GLG1 in 6 whales and with the remaining GLGs in 9 whales (Table 1; Fig. 2), indicating solid food was more important than milk in the 2nd year diet of most animals. $\delta^{15}N$ values declined over

the first 3 GLGs of 2 whales and over the first 4 GLGs of 1 whale, which were judged to have been weaned in their 3rd and 4th years, respectively (Table 1; Fig. 2). As with the whales that were nursed for 2 years, changepoint detections in these 3 whales indicated solid food contributed more to the diet than milk during the final year of nursing.

Inferred weaning age did not differ between females and males or among populations (Fisher's exact $P = 1$ for all tests), nor with relative GLG1 width (logistic regression; $\chi^2 = 0.15$, $d.f. = 1$, $P > 0.6$; Table 1).

Visual inspection and changepoint analysis of $\delta^{13}C$ profiles revealed no consistent patterns in $\delta^{13}C$ values across GLGs 1 through 5 (Fig. 3).

DISCUSSION

$\delta15N$ profiles and beluga nursing duration.—$\delta^{15}N$ profiles over the 1st several GLGs in the majority of teeth are consistent with weaning, when the transition from milk to solid prey was predicted to cause a commensurate decline in dentin $\delta^{15}N$ values. $\delta^{15}N$ declines are similar to $\delta^{15}N$ differences between tissues of nursing offspring–mother pairs across a range of mammal species (1–3‰—Hobson et al. 2000; Jenkins et al. 2001; Polischuk et al. 2001; Ducatez 2008; Habran et al. 2010), and chronological $\delta^{15}N$ declines (1–3‰) in dentin spanning the nursing period of pinnipeds (Hobson and Sease 1998; Hobson et al. 2004; Newsome et al. 2006; Riofrío-Lazo et al. 2012), bottlenose dolphins (*Tursiops truncatus*—Knoff et al. 2008), and killer whales (*Orcinus orca*—Newsome et al. 2009; Matthews and Ferguson 2014a).

$\delta^{15}N$-derived estimates of beluga nursing duration are similar to previous estimates of weaning age and lactation duration for eastern Canadian Arctic beluga using the cow–calf or ratio approaches (21–24 months—Brodie 1971; Sergeant 1973), but are shorter (in the majority of whales) than the 32-month estimate for belugas off northern Quebec (Doidge 1990). Some discrepancy between the approaches is expected (harvest bias of the cow–calf and ratio methods notwithstanding) because isotope-derived estimates of nursing duration are based on whales that survived to weaning age, while estimation of lactation duration using the ratio method takes into account differential calf mortality (the deaths of calves prior to weaning, which decreases the proportion of lactating females in the population—see Perrin and Reilly 1984). Additional discrepancy can be expected since the majority of our sample comprised whales aged 5+ years, and isotope-derived estimates could be biased toward the high side if a longer nursing period conveys increased survival, or, conversely, on the low side if early weaning reflects good foraging conditions conducive to higher survival (York et al. 2008). We also acknowledge selection of teeth with clearly defined neonatal lines and annuli could bias estimates if these factors are related to health or growth.

Accuracy of isotope-derived estimates of nursing duration is also limited by several factors, including: 1) uncertainty in the timing of formation of the broad and narrow bands comprising individual GLGs; 2) the spatial scale, and therefore temporal
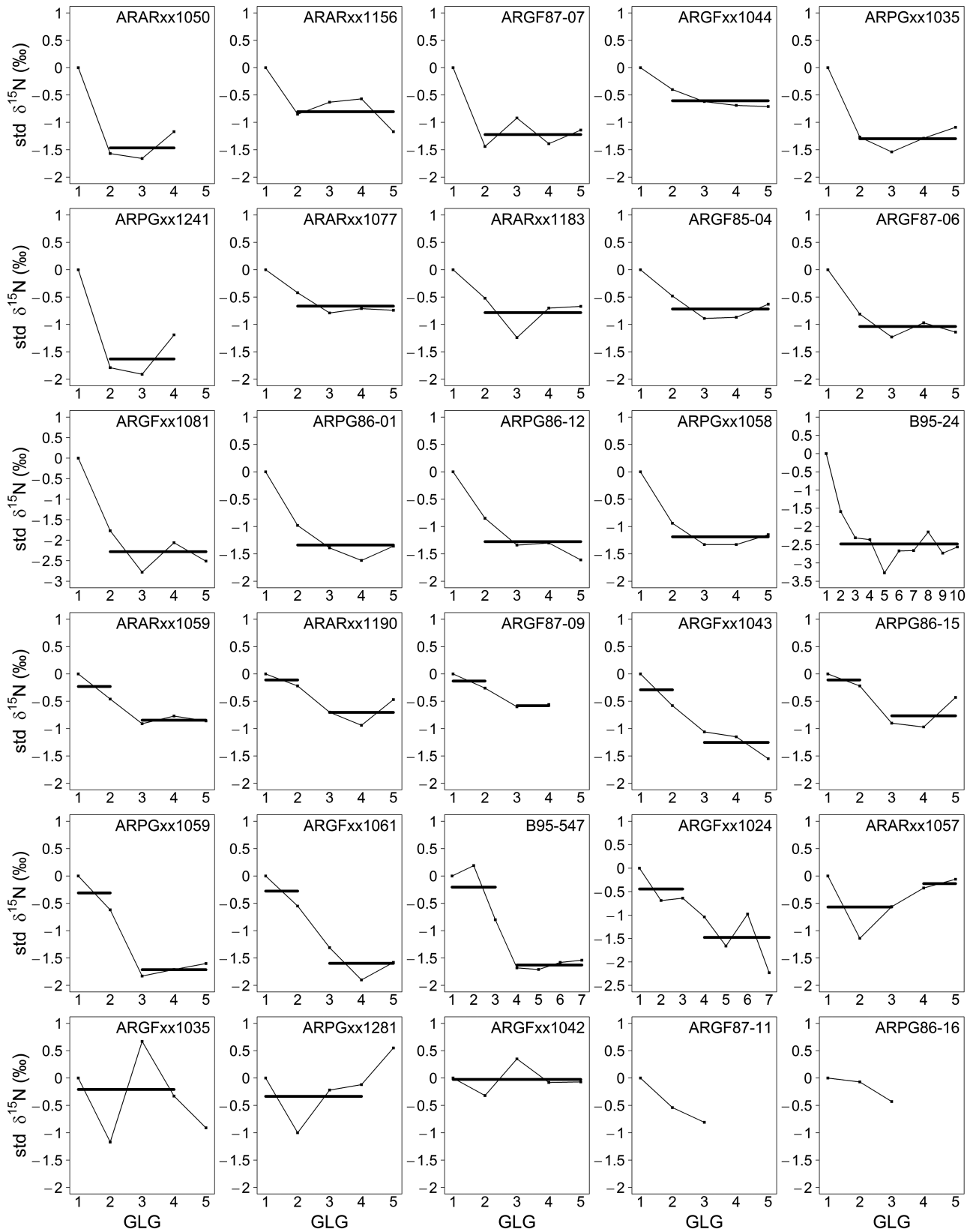
Fig. 2.—Standardized δ15N values across the first 5 growth layer groups (GLGs) of eastern Canadian Arctic beluga (*Delphinapterus leucas*). Most individuals show δ15N declines over GLGs 1–4 that are consistent with weaning. Changepoints are indicated by breaks in black horizontal lines, which represent the mean value of that segment. δ15N values in each series were standardized by subtracting GLG1 δ15N values from each GLG within a given tooth to control for potential extrinsic factors that influence offspring isotope values such as maternal trophic level and regional and temporal baseline isotopic variation. The 5 whales with incomplete profiles were aged 5 years or greater, but thin or obscure GLGs prevented milling of GLGs 4 and/or 5. Note different y-axis scales for whales ARGFxx1081, B95-24, and ARGFxx1024.
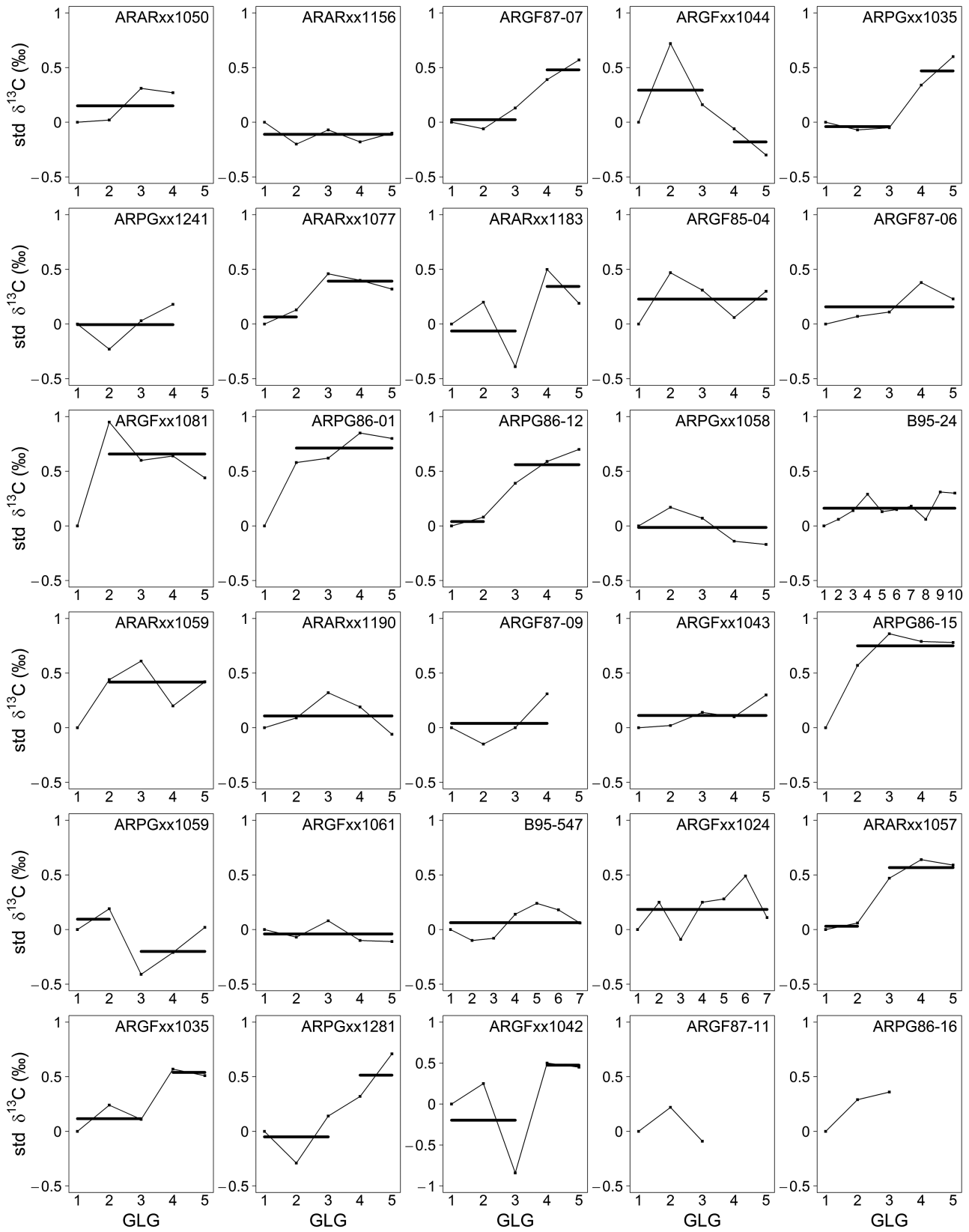
Fig. 3.—Unlike δ¹⁵N profiles, standardized δ¹³C values showed no consistent patterns across the first 5 growth layer groups (GLGs) of eastern Canadian Arctic beluga (*Delphinapterus leucas*). δ¹³C increases relative to GLG1 values occurred in less than half the whales, while many individuals had relatively constant δ¹³C values. Changepoints are indicated by breaks in black horizontal lines, which represent the mean value of that segment. δ¹³C values in each series were standardized as per δ¹⁵N values (see Fig. 2). The 5 whales with incomplete profiles were aged 5 years or greater, but thin or obscure GLGs prevented milling of GLGs 4 and/or 5. Note different y-axis scale for whale ARGFxx1042.

Table 1.—Weaning interpretations of δ¹⁵N profiles in teeth of 30 eastern Canadian Arctic beluga (*Delphinapterus leucas*) from the Western Hudson Bay (WHB), Cumberland Sound (CS), and Eastern High Arctic-Baffin Bay (EHA-BB) populations.

Whale	Population	Sex	Relative GLG1 width	Visual	Changepoint	Interpretation
ARARxx1050	WHB	F	0.229	GLG1	GLG1	Weaned in 1st year
ARARxx1156	WHB	M	0.226	GLG1	GLG1	
ARGF87-07	EHA-BB	M	0.213	GLG1	GLG1	
ARGFxx1044	EHA-BB	F	0.182	GLG1	GLG1	
ARPGxx1035	CS	F	0.195	GLG1	GLG1	
ARPGxx1241	CS	M	0.178	GLG1	GLG1	
ARARxx1077	WHB	F	0.240	GLG2	GLG1	Weaned in 2nd year; solid food > milk in 2nd year
ARARxx1183	WHB	F	0.195	GLG2	GLG1	
ARGF85-04	EHA-BB	F	0.275	GLG2	GLG1	
ARGF87-06	EHA-BB	M	0.225	GLG2	GLG1	
ARGFxx1081	EHA-BB	M	0.219	GLG2	GLG1	
ARPG86-01	CS	M	0.190	GLG2	GLG1	
ARPG86-12	CS	M	0.179	GLG2	GLG1	
ARPGxx1058	CS	F	0.203	GLG2	GLG1	
B95-24	CS	F	0.204	GLG2	GLG1	
ARARxx1059	WHB	F	0.222	GLG2	GLG2	Weaned in 2nd year; milk ≈ solid food in 2nd year
ARARxx1190	WHB	M	0.208	GLG2	GLG2	
ARGF87-09	EHA-BB	M	0.275	GLG2	GLG2	
ARGFxx1043	EHA-BB	F	0.166	GLG2	GLG2	
ARPG86-15	CS	M	0.144	GLG2	GLG2	
ARPGxx1059	CS	F	0.224	GLG2	GLG2	
ARGFxx1061	EHA-BB	F	0.261	GLG3	GLG2	Weaned in 3rd year; solid food > milk in 2nd year
B95-547	CS	F	0.152	GLG3	GLG2	
ARGFxx1024	EHA-BB	M	0.187	GLG4	GLG3	Weaned in 4th year; solid food > milk in 3rd year
ARARxx1057	WHB	F	0.204	GLG1		Weaned in 1st year; possible trophic or baseline δ¹⁵N variation postweaning
ARGFxx1035	EHA-BB	F	0.219	GLG1		
ARPGxx1281	CS	M	0.188	GLG1		
ARGFxx1042	EHA-BB	M	0.214	None	None	No nursing or weaning signal detected
ARGF87-11	EHA-BB	F				Not assessed; profile consisted of 3 GLGs
ARPG86-16	CS	F				

resolution, of GLG sampling; and 3) delays in isotopic equilibration between diet and dentin. Alternating broad and narrow bands in marine mammal teeth are assumed to reflect physiological responses to seasonality, mediated perhaps through seasonal food availability or endocrine responses to environmental variation (Myrick 1980; Klevezal 1980). In a meta-analysis of the timing of dentin growth layer formation in marine mammals, Klevezal (1996) found the broad band formed during spring-fall in the majority of species examined, while the narrow band corresponded to fall-early spring. As the broad band constitutes the bulk of each sampled GLG, δ¹⁵N values of individual GLGs are weighted towards diet integrated over the period of its formation. Although seasonality of dentin growth layers in beluga teeth has not been studied in detail, the majority of whales included in this study had been forming a broad band at the time of death (June–September; data not shown), indicating the broad band of each GLG forms during summer (but does not inform the period over which the narrow band forms).

More complete understanding of growth layer seasonality coupled with subsampling GLGs over a finer spatial scale to increase temporal resolution would improve

accuracy of estimates currently constrained to yearly integers. However, delayed isotopic equilibration of dentin with diet of ~2–3 months (Zazzo et al. 2006), coupled with a 2–3-month birthing period, such that the 1st GLG represents a different amount of time for whales born earlier versus later, ultimately restricts accuracy of isotope-derived estimates. Owing to these limitations, it cannot be ruled out that whales weaned by the end of GLG1 were not weaned as early as 5–6 months, as suggested by Kleinenberg et al. (1964) or Burns and Seaman (1985). However, although population differences in weaning age among beluga populations in Canada (this study) and Russia (Kleinenberg et al. 1964) or Alaska (Burns and Seaman 1985) cannot be discounted (see Lee 1997 for examples with primates), the range in previous estimates of beluga lactation using the ratio method likely reflects biases affecting the ratio of lactating to pregnant females, such as the season of capture or differential capture success of females accompanied by young (Perrin and Reilly 1984; Doidge 1990). The low weaning ages cited by Kleinenberg et al. (1964) in particular appear to stem from unreliable age assignments to calves based on body size. The authors estimated 280-cm belugas to be 5–6 months old, while published growth curves for several beluga populations

indicate they would have been considerably older (Heide-Jørgensen and Teilmann 1994; Stewart 1994; Suydam 2009).

Intermediate GLG2 δ^{15}N values in whales that were nursed beyond their 1st year likely reflect diets comprising milk and solid prey, indicating weaning was gradual. This is consistent with previous reports of 2-year-old beluga calves having a mixture of milk, fish, and invertebrates in their stomachs (Brodie 1971; Sergeant 1973; Heide-Jørgensen and Teilmann 1994), and yearling calves suckling throughout their 2nd summer (Smith et al. 1992). Smith et al. (1994) observed calves judged to be 2+ years old based on body size in suckling position, but could not verify that nursing had occurred. GLG2 δ^{15}N values were more similar to those of GLGs 3–5 (assumed to represent the postweaning diet) in a majority of whales, indicating either that milk supplemented solid prey over the 2nd half of the nursing period, or that those whales were weaned relatively early during their 2nd year compared to whales with GLG2 δ^{15}N values that were more similar to GLG1 values (i.e., reflecting milk diet). The former interpretation is more consistent with the gradual weaning typical of odontocetes, when milk becomes a nutritional supplement to prey after the 1st year (Kasuya and Marsh 1984; Lockyer 1993).

Brodie (1969) and Tyack (1986) hypothesized the extended nursing period of odontocetes allows sufficient time for development of sensorimotor systems used in pursuit of prey, as well as learning communication during coordinated group hunting tactics. Belugas consume a range of fish and invertebrate prey, which may vary seasonally (COSEWIC 2004; Kelley 2014), and may require specialized foraging techniques (CJDM and SHF, pers. obs.) that could be learned during prolonged mother–calf associations. Belugas also undertake long seasonal migrations between offshore regions in winter to shallow coastal areas in summer, to which they exhibit site fidelity (Smith and Hammill 1986; Caron and Smith 1990). Colbeck et al. (2013) found beluga offspring travelled with their mothers, as well as siblings and other relatives, during seasonal migrations, indicating young beluga learn migration routes from their mothers and other family members. Similar social learning has been linked with prolonged nursing and mother–offspring associations in other species that live in complex social groups (e.g., dolphins—Mann and Smuts 1999; primates—Pusey 1983; elephants—Lee and Moss 1986).

Strong seasonality is expected to influence reproductive parameters such as the timing and duration of lactation (Trillmich 1990; Whitehead and Mann 2000). The seasonal environment of belugas may therefore have imposed selective pressures (e.g., seasonal food availability, the calf's need to accumulate a thick blubber layer) on belugas to evolve traits somewhat similar to the capital breeding strategy of mysticetes. Reduced foraging may be part of the reproductive strategy of beluga mothers while summering in protected estuaries with their calves (Sergeant 1973), although the importance of summer feeding appears to vary with population (Martineau et al. 1987; Lydersen et al. 2001; Loseto et al. 2009). Female, but not male, belugas have seasonal oscillations in blubber thickness that Sergeant and Brodie (1969) linked with reproductive state,

with females being particularly fat during late pregnancy and early lactation. The few measurements of beluga milk indicate its fat content (27%—Lauer and Baker 1969) falls towards the high end of the odontocete range (10–30%) and approaches the lower end of the mysticete range (30–50%—Lockyer 1984; Oftedal and Iverson 1995). However, milk composition varies considerably over the course of lactation (West et al. 2007) and within species (Oftedal 1997), necessitating more measurements on beluga milk for a valid comparison. In an analysis of a range of life history traits (not including lactation duration) in over 80 cetacean species, Ferguson and Higdon (2013) found that belugas were grouped with whales the authors termed "bet-hedgers." Bet-hedgers were characterized by long lifespans and reduced maternal investment, perhaps as an adaptation to environmental variability. Belugas that were weaned by age 1 would be in line with this characterization, although the 2-year nursing period observed in most individuals is on par with average nursing durations of similar-sized odontocetes (Perrin and Reilly 1984; Oftedal 1997; Whitehead and Mann 2000).

$\delta 13$C values over the nursing period.—Unlike other studies that have attributed δ^{13}C increases across dentin annuli to weaning (e.g., Hobson and Sease 1998; Hobson et al. 2004), δ^{13}C values across beluga GLGs spanning the nursing period showed no consistent pattern. We assume analysis of bulk dentin, as opposed to isolated collagen, was not a factor, since δ^{13}C measurements of bulk dentin largely reflect that of collagen (Martin et al. 2011, Matthews and Ferguson 2014b). Other studies have found either no δ^{13}C differences between dentin deposited preweaning and postweaning (e.g., Knoff et al. 2008), or no consistent δ^{13}C pattern associated with weaning (e.g., Newsome et al. 2006). Newsome et al. (2006) suggest that offspring δ^{13}C values over the nursing period vary with the fat content of milk. That lower δ^{13}C values have been noted in nursing otariids (Hobson and Sease 1998; Hobson et al. 2004), which have milk fat content around 30–50% (Oftedal and Iverson 1995), but not in belugas (this study), bottlenose dolphins (Knoff et al. 2008), or killer whales (Newsome et al. 2009), which collectively have lower fat milks than otariids (10–30%—Lauer and Baker 1969; Oftedal 1997), offers some support to this hypothesis. However, δ^{13}C values did not vary with weaning in northern elephant seals (*Mirounga angustirostris*—Riofrío-Lazo et al. 2012), despite the higher fat content of their milk than both otariids and odontocetes (Oftedal and Iverson 1995). This was likely unrelated to the abrupt weaning of northern elephant seals, since a clear decline in δ^{15}N values was noted between dentin layers corresponding to pup and adult female age classes. The lack of δ^{13}C signal may have more to do with the fact that the majority of milk fat is routed directly to the blubber layer of phocid seals (Oftedal 2000), such that little lipid-derived carbon is diverted to protein synthesis. Although blubber development in beluga calves has not been quantified, belugas have thick blubber relative to other odontocetes (~40% body weight—Sergeant and Brodie 1969). As such, we hypothesize that the lack of nursing effect on δ^{13}C values in beluga whales reflects the direct incorporation of dietary lipids into the developing blubber layer of calves.

Variation in nursing duration.—$\delta^{15}N$ profiles varied among whales, indicating the majority (> 50%) were weaned by the end of their 2nd year, a 3rd by the end of their 1st year, and about 10% beyond their 2nd year. Variation in nursing duration has been reported in a variety of other odontocetes. For example, bottlenose dolphins (*Tursiops* sp.) are nursed for 3–6 years and occasionally for up to 8 years (Mann et al. 2000). Sperm whales (*Physeter macrocephalus*) and short-finned pilot whales (*Globicephala macrorhynchus*) are reportedly nursed beyond 10 years of age (e.g., Best et al. 1984; Kasuya and Marsh 1984), although the mean nursing duration is just several years in both species (alternative explanations for these extreme reports are provided by Oftedal 1997). Given a gestation period of about 12–14.5 months, nursing duration estimates derived here are consistent with a full female beluga reproductive cycle of about 3 years (i.e., 1-year gestation + 2-years lactation). The smaller proportion of whales weaned during their 1st year would also be consistent with a 2-year calving interval suggested in some females (Seaman and Burns 1981; Suydam 2009).

Irregular GLG deposition over the nursing period, if it occurred, would lead to variation in $\delta^{15}N$ patterns among individuals. The onset of permanent tooth eruption in belugas ranges from 3 to 10 years (Stewart 2012), indicating the age at which teeth erupt varies among individuals, or that GLG deposition is irregular in young belugas. Assuming previous estimates of lactation duration in belugas are reasonable, similar $\delta^{15}N$-derived weaning age estimates of 1–2 years allows us to rule out multiple GLG deposition in beluga calves, which would instead draw out $\delta^{15}N$ declines over more GLGs than observed. Interpretation of dentin growth layers, on the other hand, involves a degree of subjectivity due to accessory layers (Hohn et al. 1989; Lockyer 1995), which may be difficult to assess in some beluga teeth (Stewart 2012). For this study, error due to incorrect aging of GLGs was minimized by selecting only teeth with very clearly defined neonatal lines and GLGs. Thus, while inaccurate age assignments cannot be completely discounted, we do not believe isotopic variation among individuals to be an artefact of age assignment errors.

Lee et al. (1991) found the primary factor determining nursing duration in large-bodied mammals (primates, ungulates, and pinnipeds) was offspring size. Weaning occurred when offspring attained a threshold mass required for nutritional independence, typically 4 times the birth weight. Similarly, cetacean calves are weaned when they reach a threshold size relative to that of adult females (Huang et al. 2009). Lee et al. (1991) therefore proposed lactation duration is a function of maternal condition, which influences milk yield/nutrient transfer and concomitant offspring growth rates. Nutritional limitations of poor-quality habitat or stressful conditions have been associated with both reduced and extended nursing (e.g., Lee and Moss 1986), while abundant food resources have been linked to early weaning (Ramsay and Stirling 1988; Trillmich 1990). Another factor that probably influences the size attained by a beluga calf over its 1st year is its birthdate. Although the calving season is generally restricted to June–August (Brodie 1971; Sergeant 1973), newborn belugas have been observed throughout much of the Canadian Arctic from March–September (Braham 1984) and in the EHA-BB population from February–October (Stewart 2001). Belugas born early in the calving season would have more time to nurse during their 1st year relative to calves born later, which could allow them to attain critical weaning size earlier.

The lack of relationship between relative GLG1 width and inferred weaning age does not support hypotheses linking weaning age and growth, although the constant proportions of dentin deposition represented by each GLG (0.21, 0.19, 0.21, 0.20, and 0.19 for GLGs 1 through 5, respectively), despite a gradual decline in overall growth rate over the same period (Burns and Seaman 1985), suggests beluga GLG deposition rate is independent of overall growth. In contrast, York et al. (2008) showed relative GLG1 width was greater in Steller sea lions (*Eumetopias jubatus*) that were weaned during their 1st year than in animals that continued to be nursed into their 2nd year, indicating faster growing pups were weaned earlier. Considerable interannual variation in Arctic marine ecosystems (e.g., sea ice cover—Parkinson and Cavalieri 1989; Parkinson 2000) may have influenced beluga nursing duration, especially since birth years spanned several decades. Unfortunately, our restricted sample size did not allow for comparison of nursing duration among calves from specific birth years, which may expose impacts of environmental variation on weaning age. Similar variation in weaning age among populations (although sample size is small) likely means each experiences relatively similar environmental conditions such that there is no population-specific selection on weaning age.

Among sexually dimorphic species, the greater growth rate of male offspring is sustained through greater lactational transfers relative to females (Clutton-Brock et al. 1985). Additionally, among polygynous species, sex-biased maternal investment favoring male offspring confers size advantages that provide greater fitness returns later in life (Clutton-Brock et al. 1981; Kovacs and Lavigne 1986). Immature belugas of both sexes have similar growth rates (at least in terms of length) spanning the nursing period, and relative increases in male versus female size do not occur until age 7–10 years (Sergeant 1973; Heide-Jørgensen and Teilmann 1994). The energetic demands of female and male calves over the nursing period may therefore be similar, and postweaning growth rates and foraging dynamics may be more relevant for adult male size and condition than maternal investment during lactation. Recent evidence also suggests that, although they are sexually dimorphic, belugas lie more closely to a promiscuous mating system along the promiscuous-polygynous continuum (Kelley 2014). The absence of either a polygynous mating system or maternal effects on male adult size is not conducive to sex-biased maternal investment (Trivers and Willard 1973). That being said, our failure to detect differences in nursing duration between the sexes could be a sample size limitation, which did not allow for proper control of potential confounding variables (e.g., environmental factors), as well as sampling resolution, since measurements integrated timespans that would have obscured differences in weaning age of less than several months. Nursing duration

may also not be the best measure of maternal investment, as suckling frequency or milk quality are common manifestations of differential maternal investment (e.g., Anderson and Fedak 1987; Landete-Castillejos et al. 2005).

Nursing duration also varies with maternal age, as older females may compensate for declines in fecundity towards the end of their lifespan with increased reproductive effort in current offspring (Pianka and Parker 1975; Clutton-Brock 1984). Additionally, larger mature mothers can afford to allocate more resources to reproduction while incurring less body condition costs than primiparous mothers, which must often bear the energetic demands of growth and lactation simultaneously (Lockyer 1981; Gomendio 1989). Among cetaceans, sperm whale mothers > 20 years old nursed their young for 67% longer than mothers < 20 years old (Best et al. 1984). Kasuya and Marsh (1984) found associations between older suckling calves and older lactating female short-finned pilot whales, indicating older mothers nurse their calves for longer than younger ones. Similarly, long-finned pilot whale (*Globicephala melas*) mothers over 40 years old lactate about 3 times longer than mothers at the beginning or middle of their reproductive lifespan (Martin and Rothery 1993). Diminishing birth rates with age in belugas (Burns and Seaman 1985) may therefore reflect increasing interbirth intervals caused by increasing reproductive effort by older females. Allonursing (nursing offspring of other females) could also be a factor, especially in the longer nursing durations (> 2 years) inferred for several individuals. Although not reported in wild belugas, allonursing is exhibited by captive belugas (Leung et al. 2010). Given that belugas live in matrilineal groups comprising closely related females (Colbeck et al. 2013), allonursing could be an adaptive behavior via kin selection that promotes calf survival.

Of the components that make up the calving cycle, the lactation period is the most variable, and understanding factors affecting its duration is important for models of reproductive rates in a population (Perrin and Reilly 1984). An isotopic approach was used to derive nursing duration estimates that are similar to previous estimates of lactation duration in eastern Canadian Arctic belugas, but revealed individual variation in weaning age previously unreported in belugas. Future study could assess environmental influences on weaning age by including multiple whales from each of a range of birth years spanning periods of environmental variation (e.g., York et al. 2008), or belugas from the more southern St. Lawrence Estuary population to examine weaning age along a latitudinal gradient spanning temperate and Arctic regions (e.g., Trillmich 1990). Unfortunately, the retrospective isotopic approach employed here provides no direct information about maternal condition and age, important determinants of lactation duration in a range of mammal species. Nevertheless, this study, like previous ones, indicates $\delta^{15}N$ profiles of sequentially sampled dentin growth layers deposited over the nursing period can provide estimates of nursing duration, revealing individual variation in weaning age that cannot be detected using other currently available approaches for odontocetes.

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