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Spatial segregation and similar trophic-level diet among eastern Canadian Arctic/ north-west Atlantic killer whales inferred from bulk and compound specific isotopic analysis

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Killer whales in the Eastern Canadian Arctic (ECA) prey on narwhal, beluga, bowhead whales and seals, while further south in the north-west Atlantic (NWA), killer whales off the coast of Newfoundland and Labrador prey on both marine mammals and fish. Bulk and amino acid (AA) specific isotopic composition of dentinal collagen in teeth of 13 ECA/NWA killer whales were analysed to assess the degree, if any, of dietary specialization of killer whales across the region. Dentine was sampled from within annual growth layer groups (GLGs) to construct chronological profiles of stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopic compositions for individual whales spanning 3–25 years. Interannual isotopic variation across GLGs was less than that among individuals, and median bulk $\delta^{15}N$ values differed by up to 5‰ among individuals. Significant correlation between bulk $\delta^{15}N$ values and baseline (source AA) $\delta^{15}N$ values indicates much of the observed isotopic variation among individuals reflects foraging within isotopically distinct food webs, rather than diet differences. This interpretation is supported by consistent differences in bulk $\delta^{13}C$ values between the two individuals with lowest source AA $\delta^{15}N$ values and the remaining whales. After accounting for baseline isotopic variation, comparable $\delta^{15}N$ values among individuals indicates similar trophic-level diet, although uncertainties in relative trophic ^{15}N enrichment of individual AAs currently limits trophic position estimates for top consumers. Further research is required to clarify seasonal movement patterns and possible diet shifts of ECA/NWA killer whales to better define their role in marine ecosystems across the region.

Keywords: *Orcinus orca*, dentine, growth layer groups, stable isotope analysis, nitrogen, carbon, amino acids, marine mammals, distribution

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INTRODUCTION

Killer whales (*Orcinus orcus*, Linnaeus 1758) occupy high trophic levels in marine ecosystems (Jefferson *et al.*, 1991), preying on a diverse range of species including fish, cephalopods, sea turtles, seabirds and marine mammals (Forney & Wade, 2006). While this broad prey range is reflected in generalist diets of some killer whales, for example, in waters off Hawaii (Baird *et al.*, 2006), New Zealand (Visser, 2000) and South Africa (Best *et al.*, 2010), several killer whale populations worldwide comprise distinct ecotypes or forms with more restricted prey preferences (Ford *et al.*, 1998; Saulitis *et al.*, 2000; Pitman & Ensor, 2003; Burdin *et al.*, 2004; Foote *et al.*, 2009; Ford *et al.*, 2011). As apex predators, killer whales can potentially exert important top-down regulation on prey populations (e.g. Estes *et al.*, 1998, but see Kuker & Barrett-Lennard, 2010), and conversely, highly specialized foraging leading to dependence on a narrow range of prey can introduce bottom-up control on killer whale population dynamics (Ford *et al.*, 2010). Understanding killer whale foraging behaviour is, therefore, essential to understanding structure and function of marine ecosystems in which they occur.

In the Eastern Canadian Arctic (ECA), where killer whales occur seasonally during the open-water period from July to September, killer whales have been documented feeding on narwhal (*Monodon monoceros*), beluga (*Delphinapterus leucas*) and bowhead (*Balaena mysticetus*) whales, as well as several seal species (Reeves & Mitchell, 1988; Higdon *et al.*, 2011). Although marine mammals have been the only confirmed prey of killer whales in the ECA (Higdon *et al.*, 2011; Ferguson *et al.*, 2012a), evidence suggests killer whales in Davis Strait off western Greenland also forage on fish (Heide-Jorgensen, 1988; Laidre *et al.*, 2006). In adjacent regions of the north-west Atlantic (NWA), killer whales off the coast of Newfoundland and Labrador have been documented pursuing or feeding on both marine mammals and fish, including humpback (*Megaptera novaeangliae*) and minke whales (*Balaenoptera acutorostrata*), beluga, white-beaked

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dolphins (*Lagenorhynchus albirostris*), seals, seabirds and herring and tuna (Sergeant & Fisher, 1957; Whitehead & Glass, 1985; Lawson *et al.*, 2008).

Although the broad prey range taken by whales across the ECA and NWA suggests they may be generalist predators, assessment of the degree of individual diet specialization within this population(s) is impeded by a lack of individual foraging records over time. Increasingly, stable isotope (SI) analysis of dentine layers in marine mammal teeth is being used to reconstruct chronological diet records over periods not possible through direct observation. Dentine is laid down in discrete annual growth layer groups (GLGs) consisting of inorganic (hydroxyapatite) and organic (mainly collagen) components derived from diet (Hobson & Sease, 1998; Walker & Macko, 1999). Post-depositional alteration of dentine does not occur (Bloom & Fawcett, 1975), so dentine GLGs represent a lifelong chronological archive along the axis of tooth growth.

Isotopic analysis of sequentially sampled dentine GLGs in marine mammal teeth has revealed ontogenetic distribution and diet patterns (e.g. Hobson & Sease, 1998; Mendes *et al.*, 2007a, b; Martin *et al.*, 2011; Riofrío-Lazo *et al.*, 2012), as well as individual diet preferences (e.g. Newsome *et al.*, 2009). Trophic position can be inferred from nitrogen isotope composition ($\delta^{15}N$), owing to metabolic fractionation causing consistent ^{15}N enrichment in consumer tissue relative to prey (DeNiro & Epstein, 1981). Incorporation of dietary carbon into consumer tissue occurs with less isotopic fractionation (DeNiro & Epstein, 1978), such that more conservative carbon isotope composition ($\delta^{13}C$) across trophic levels primarily reflects underlying biogeochemical processes at the base of the food web. Foraging patterns of marine predators over several spatial scales have been inferred from tissue $\delta^{13}C$ values (Cherel & Hobson, 2007; Mendes *et al.*, 2007a), which can reflect differences between benthic vs pelagic (France, 1995) and coastal vs offshore (Walker *et al.*, 1999) environments, as well as latitudinal $\delta^{13}C$ gradients (e.g. Rau *et al.*, 1982).

Isotopic composition across dentine GLGs of wide-ranging marine mammals also integrates $\delta^{15}N$ variation at the base of the food web during movements among regions with isotopically distinct source nitrogen, which can confound trophic interpretations of $\delta^{15}N$ values. Bulk tissue $\delta^{15}N$ measurements cannot differentiate between baseline $\delta^{15}N$ variation, which can exceed 5–10‰ across ocean basins (Montoya *et al.*, 2002; Graham *et al.*, 2010), and that due to trophic ^{15}N enrichment, which typically ranges from 3–5‰ with each trophic transfer (Minagawa & Wada, 1984; McCutchan *et al.*, 2003). While the two sources of tissue $\delta^{15}N$ variation can be decoupled by characterizing primary producer or consumer $\delta^{15}N$ values, baseline isotopic variation cannot be independently and retroactively resolved across the considerable spatial and temporal scales over which dentine deposition occurs in highly mobile, long-lived species.

Recent studies have shown that compound specific isotope analysis of individual amino acids (AA-CSIA) can be used to constrain baseline influences on bulk tissue $\delta^{15}N$ values. Certain amino acids ('source' AAs, *sensu* Popp *et al.*, 2007) undergo little consumer modification and retain the isotopic value of source nitrogen, while kinetic isotope fractionation during transamination and deamination reactions causes consistent ^{15}N enrichment in other AAs ('trophic' AAs, *sensu* Popp *et al.*, 2007) (Gaebler *et al.*, 1966; McClelland & Montoya, 2002; Chikaraishi *et al.*, 2007, 2009). AA-CSIA can, therefore, be used to constrain baseline $\delta^{15}N$ variation of a consumer's foraging habitat via source AA $\delta^{15}N$, and subsequent comparison against trophic AA $\delta^{15}N$ allows for internal calibration of trophic position (e.g. McClelland & Montoya, 2002; Popp *et al.*, 2007; Chikaraishi *et al.*, 2009). AA-CSIA has been applied in foraging studies of a growing number of marine consumer taxa, including invertebrates (Schmidt *et al.*, 2004; Hannides *et al.*, 2009; O'Malley *et al.*, 2012), teleost fish and elasmobranchs (Popp *et al.*, 2007; Dale *et al.*, 2011; Choy *et al.*, 2012), sea turtles (Seminoff *et al.*, 2012) and seabirds (Lorrain *et al.*, 2009), but has not been rigorously validated for marine mammals (e.g. Germain *et al.*, 2013).

Increases in killer whale sightings in both the ECA and NWA over the past several decades (Higdon & Ferguson, 2009; Lawson & Stevens, 2013), along with anticipated range expansions accompanying reductions in sea ice extent (Higdon & Ferguson, 2009), have underscored the need for a better understanding of killer whale predation in these regions (e.g. Ferguson *et al.*, 2012b). To that end, we measured bulk dentine isotopic composition across GLGs of ECA/NWA killer whales ($N = 13$), followed by AA-CSIA to constrain potential baseline isotope influences on bulk $\delta^{15}N$ values. Our combined bulk and AA-specific isotope analyses allowed us to assess individual isotopic profiles over periods up to 25 yr, and evaluate relative foraging behaviour among individuals and between regions.

MATERIALS AND METHODS

Killer whale tooth specimens

Teeth were collected opportunistically from stranded killer whales across the ECA ($N = 6$) and NWA ($N = 7$) over several decades (1948–2011), including Cumberland Sound, Hudson Bay/Foxe Basin, Admiralty Inlet, south-western and south-eastern Newfoundland and Sable Island, Nova Scotia (Figure 1). When possible, large teeth with minimal occlusal wear were selected to maximize the number of GLGs available for sampling. All teeth had been stored dry since collection. Although sex and body size measures were available for some individuals, relevant biological information was not available for all (Table 1). Killer whale population structure across the ECA and NWA remains unknown, and reference to individuals from either area solely reflects collection location without inference of broad population structure across the region.

Tooth sectioning and ageing

Teeth were sectioned longitudinally to remove an approximately 2 mm thick section following the midline of each tooth. Sections were polished using 30 and 9 μm AlOx lapping film, then placed in 10% formic acid for 12 h to etch the polished surface and accentuate GLG definition. Sections were rinsed thoroughly with distilled water for several hours following formic acid treatment and air dried. Acid etching at the tooth's surface has been assumed not to influence isotope values of underlying dentinal collagen (Hobson & Sease, 1998; Newsome *et al.*, 2009).

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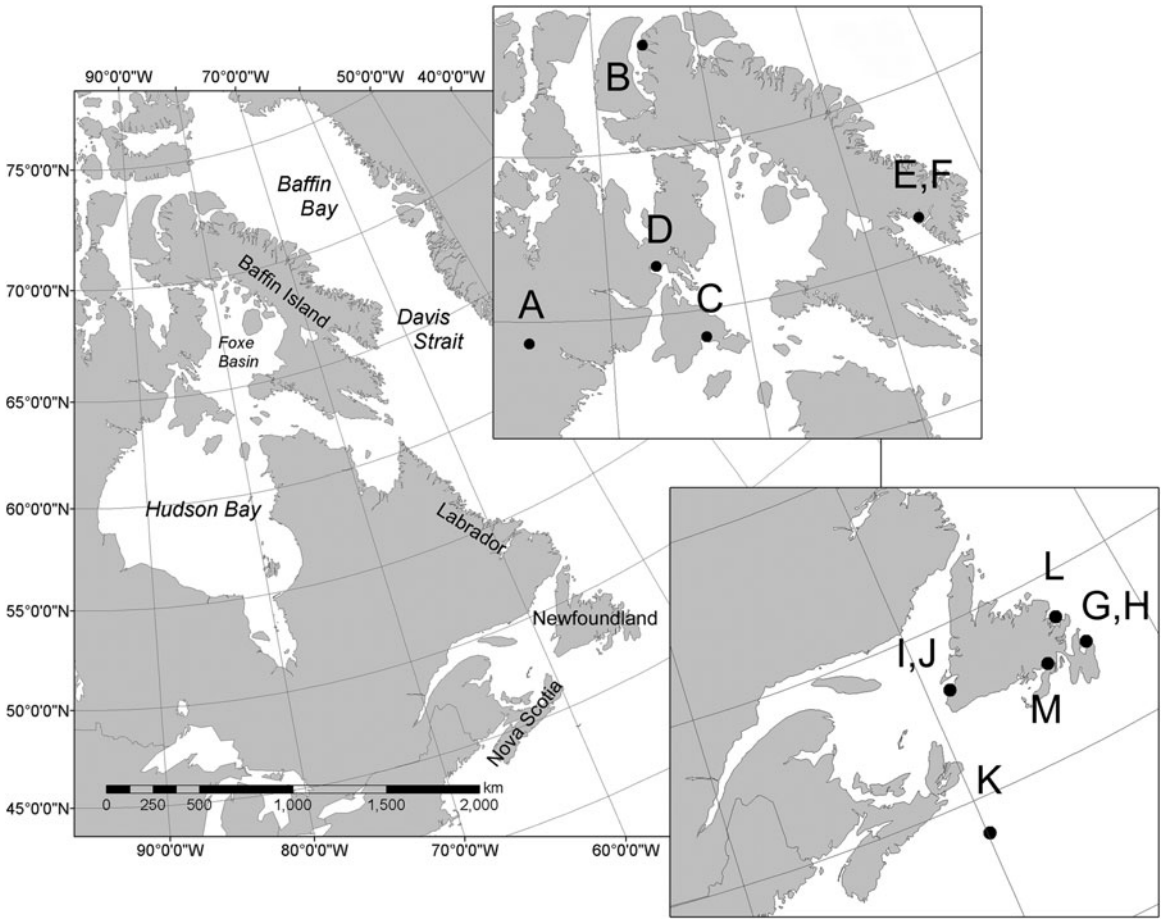

Fig. 1. Teeth used in this study were collected from killer whale specimens in various locations throughout the eastern Canadian Arctic (ECA) and north-west Atlantic (NWA) off the coasts of Newfoundland and Nova Scotia. Letters correspond to specimens listed in Table 1.

Annual dentine GLG deposition has been confirmed in killer whales through calibration of tetracycline labelled teeth with treatment history of captive individuals (Myrick *et al.*, 1988), as well as comparisons of GLG counts with corpora counts in sexually mature females (Amano *et al.*, 2011) and GLG count with estimated age of a well-known wild killer whale (Mitchell & Baker, 1980). Growth layers were observed under reflected light and counted three times by one reader over several weeks to estimate the age of each specimen. Successive readings typically differed by 1–3 GLGs, and the median of these measurements was recorded as the age (Table 1). Calendar year of GLG deposition was calculated from whale age and year of death to examine longitudinal isotopic trends.

Table 1. Estimated age and number of growth layer groups (GLGs) sampled for each Eastern Canadian Arctic (ECA) and north-west Atlantic (NWA) killer whale tooth, along with location and year sampled.

Individual	Museum ID	Location collected	Year collected	Age	Sex*	# GLGs sampled
A. ECA-BL-1978	5754-26	Baker Lake, NU	1978	17	M	13
B. ECA-AB-1948	MM406	Arctic Bay, NU	1948	31	U	15
C. ECA-RB-2009		Repulse Bay, NU	2009	28	F	16
D. ECA-CH-2011		Coral Harbor, NU	2011	35	M	23
E. ECA-CS-1997-1		Cumberland Sound, NU	1977	4	U	4
F. ECA-CS-1977-2		Cumberland Sound, NU	1977	18	U	13
G. NWA-CB-1971-1	D119-71	Conception Bay, NF	1971	31	M	15
H. NWA-CB-1971-2	D118-71	Conception Bay, NF	1971	29	F	25
I. NWA-SC-1975-1	VMK5	Ship Cove, NF	1975	20	M	19
J. NWA-SC-1975-2	VMK6	Ship Cove, NF	1975	23	M	12
K. NWA-SI-1977	10783	Sable Island, NS	1977	13	U	12
L. NWA-BB-2002		Bonavista Bay, NF	2002	3	M	3
M. NWA-BP-1998		Burin Peninsula, NF	1998	5	F	5

*, U, sex undetermined.

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Dentine collection and preparation

A high-resolution micromill (Merchantek) was used to collect dentine from within individual GLGs for bulk isotopic analysis. GLGs were milled using a 500 μm diameter carbide dental drill bit at a depth of 400–500 μm to prevent drilling into adjacent layers. Sampling started at the first visible GLG adjacent to the enamel/dentine interface and continued until GLG definition became uncertain or layers adjacent to the pulp cavity became too thin to mill (i.e. <500 μm wide), resulting in 3–25 GLGs sampled per tooth (Table 1). Myrick *et al.* (1988) measured relatively constant dentinal deposition across all months in teeth of captive killer whales, so each sampled GLG is assumed to represent diet integrated over each year of the animal's life from birth year (first GLG sampled) to the final sampled GLG.

Given considerable spatial heterogeneity in $\delta^{15}N$ values across the North Atlantic Ocean basin (Waser *et al.*, 2000; Graham *et al.*, 2010) and the potentially large range of ECA/NWA killer whales (Matthews *et al.*, 2011), AA-CSIA was performed to constrain baseline isotope influences on bulk $\delta^{15}N$ values. Consistent bulk collagen $\delta^{15}N$ values across GLGs within individuals (see Results) allowed us to collect representative 'whole-tooth' dentine samples to provide sufficient material for AA-CSIA. Dentine was milled perpendicular to the axis of GLG growth using a 1 mm diameter drill bit, encompassing all GLGs except for the youngest three, which showed isotopic variation related to weaning (see Results).

Collagen was isolated from powdered dentine samples using repeated rinses (12 h each) of 0.25 N HCl at 4°C. Dentine was demineralized after two to three acid rinses, and remaining collagen was washed using successive rinses of deionized water. Samples were centrifuged between each rinse to minimize sample loss, and freeze-dried for 48 h after the final rinse. Collagen atomic C:N (mean ± sd = 2.9 ± 0.1; range = 2.8–3.3) was within the range of unaltered collagen (DeNiro, 1985), indicating adequate removal of inorganic carbon during acid rinses.

Stable isotope analysis

BULK STABLE ISOTOPE ANALYSIS

Growth layer group collagen samples (~0.5 mg) were weighed into tin cups for isotopic analysis on a Vario EL III elemental analyser (Elementar, Germany) interfaced with a DELTAplus XP isotope ratio mass spectrometer (Thermo, Germany) at the G.G. Hatch Stable Isotope Laboratory, University of Ottawa. Isotope ratios are reported in delta notation (δ; units are per mil, ‰), defined as $\delta^{15}N$ or $\delta^{13}C = (R_{sample} - R_{standard}) / R_{standard}) \times 1000$, where R is $^{15}N/^{14}N$ or $^{13}C/^{12}C$. All isotope values are normalized to international standards (atmospheric N_2 for $\delta^{15}N$ and Vienna Pee-Dee Belemnite limestone for $\delta^{13}C$) calibrated through repeated measures of laboratory reference materials. Analytical precision based on repeated measures of reference material not used in calibrations was 0.05‰ for $\delta^{15}N$ and 0.06‰ for $\delta^{13}C$, and that based on duplicate measures of ~15% of samples was 0.11 and 0.07‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively.

AMINO ACID COMPOUND SPECIFIC ISOTOPE ANALYSIS

Approximately 2.5–5.5 mg of each whole-tooth collagen sample was acid hydrolysed and derivitized to produce trifluoroacetic AA esters following procedures described in Dale *et al.* (2011). $\delta^{15}N$ values of derivitized AAs were measured on a Thermo Scientific Delta V Plus mass spectrometer interfaced with Thermo Finnigan Trace GC gas chromatograph via a Thermo Finnigan GC-C III combustion/reduction system at the Stable Isotope Biogeochemistry Laboratory, University of Hawaii. All samples were analysed in triplicate and normalized relative to co-injected reference compounds of known isotopic composition (L-2-aminoadipic acid and L-(+)-norleucine). Co-elution and interference prevented measurement of some AAs, but reliable measurements were obtained for 13 individual AAs. Mean analytical precision based on repeated measures of the two reference compounds was 0.46‰, while that based on triplicate measures of each sample was 0.32‰ (range: 0.02–1.21‰). AA-specific $\delta^{15}N$ values are reported relative to isotopic composition of atmospheric N_2.

Data analysis

TEMPORAL ISOTOPIC TRENDS ACROSS GLGS

Potential sources of temporal SI variation across dentine GLGs include whale age, in terms of ontogenetic diet shifts (e.g. Newsome *et al.*, 2009) and growth-related variation in diet–tissue SI discrimination (e.g. Trueman *et al.*, 2005), as well as variation in baseline SI over the broad timeframe represented by sampled GLGs. Generalized linear mixed effects models with random intercepts were used to assess bulk $\delta^{15}N$ and $\delta^{13}C$ profiles across GLGs with respect to these variables. The variable 'decade' (1920s–2000s) was constructed from calendar year of GLG formation and treated as a fixed effect, along with GLG (age). Whale identity was included as a random effect, allowing models to account for correlation of repeated measures within individuals. Models were run using the maximum likelihood method, and the best-fit model was selected based on ANOVA results comparing full and reduced models. Statistical significance was assessed at $P < 0.05$, and analyses were performed using the nlme package (Pinheiro *et al.*, 2012) available for R software (R Core Team, 2012).

BULK ISOTOPIC VARIATION AMONG INDIVIDUALS

Differences in bulk $\delta^{15}N$ and $\delta^{13}C$ among individuals were assessed using one-way repeated measures ANOVA on rank-transformed data (Conover & Iman, 1981) using the nlme package in R (Pinheiro *et al.*, 2012), followed by Tukey's HSD *post-hoc* tests using the multcomp package in R (Hothorn *et al.*, 2008). The systematic decrease in $\delta^{15}N$ values over the first three GLGs (see Results) was interpreted as a weaning signal (e.g. Newsome *et al.*, 2009) and removed from each profile before further analysis to ensure comparison of diet after completion of nursing. This decision resulted in two individuals (ECA-CS-1977-1 and NWA-BB-2002) being dropped from the dataset due to their young age. The number of remaining GLGs for a third individual (NWA-BP-1998) was insufficient for statistical comparisons. Although killer whales show other ontogenetic SI patterns across dentine GLGs which may not be entirely diet-related (Newsome *et al.*, 2009), we did not observe any clear age-related patterns beyond the first three GLGs. Comparisons among individuals, therefore, included entire profiles beyond the third GLG. We applied a *post-hoc*

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correction of 0.019‰ yr^{-1} to $\delta^{13}C$ values ($\delta^{13}C_{cor}$) to account for the oceanic ^{13}C Suess effect in the North Atlantic (Quay *et al.*, 2003) over the period of GLG deposition.

AA-specific $\delta^{15}N$–baseline $\delta^{15}N$ and trophic position indices

Because bulk and AA-specific isotopic measurements were conducted at different laboratories on differently sampled material (i.e. individual GLGs vs whole-tooth), we compared bulk collagen $\delta^{15}N$ values with those calculated from individual AA $\delta^{15}N$ values using a mass balance approach. The $\delta^{15}N$ value of each individual AA was multiplied by its percentage contribution to total dentinal collagen nitrogen, which was determined from AA % composition of dentinal collagen (Eastoe, 1963) multiplied by weight % N of each individual AA. Contributions of each individual AA, which together represented ~80.4% of total collagen N, were then summed. Correlation between calculated and measured bulk collagen $\delta^{15}N$ values was determined using linear regression.

Source AAs phenylalanine, glycine, and serine, and trophic AAs alanine, leucine, proline, aspartic acid and glutamic acid were used to assess baseline and trophic contributions to bulk collagen $\delta^{15}N$ patterns. To clarify baseline SI influences on bulk $\delta^{15}N$ values, linear regression of mean bulk GLG $\delta^{15}N$ values against mean source AA $\delta^{15}N$ values was performed. Generalized linear mixed effects models with random intercepts and slopes were also fitted to rank-transformed source AA $\delta^{15}N$ values (dependent variable) along groupings identified in Figure 3 (fixed effect), with whale identity set as a random effect to account for multiple AA measures from each individual. Tukey's HSD *post-hoc* tests were performed to identify pairwise differences. AA-CSIA also provided an additional check on temporal baseline $\delta^{15}N$ variation over the timeframe of the study through linear regression of mean source AA $\delta^{15}N$ values against calendar year. Regression analyses were performed using the R Stats Package (R Core Team, 2012).

Differences in trophic AA $\delta^{15}N$ values among individuals were investigated using ANOVA as per source AA. Trophic position of marine consumers has been estimated using the difference in $\delta^{15}N$ values of glutamic acid ($\delta^{15}N_{Glu}$) and phenylalanine ($\delta^{15}N_{Phe}$) using

$$\text{Trophic position} = \frac{\left(\delta^{15}N_{Glu-}\delta^{15}N_{phe}\right) - 3.4}{7.6} + 1 \quad (1)$$

to account for the isotopic difference between the two AAs in primary producers (β, 3.4‰) and trophic enrichment ($TEF_{Glu\text{-}Phe}$, 7.6‰) (Chikaraishi *et al.*, 2009). This calculation was derived largely from experimental studies on invertebrates and fish, and recent studies have suggested that a $TEF_{Glu\text{-}Phe}$ of 7.6‰ results in lower than anticipated trophic position estimates of higher marine consumers (Lorrain *et al.*, 2009; Dale *et al.*, 2011), including marine mammals (Germain *et al.*, 2013). Given equation (1) also results in trophic position estimates too low for killer whales (see Results), we used simpler 'trophic indices' to compare relative trophic level differences among individual killer whales. We estimated relative trophic position using the difference in $\delta^{15}N$ values of the primary trophic (glutamic acid) and source (phenylalanine) AAs ($\Delta\delta^{15}N_{Glu\text{-}Phe}$) (McLelland & Montoya, 2002; Chikaraishi *et al.*, 2009), as well the difference in mean $\delta^{15}N$ values of multiple trophic and source AAs ($\Delta\delta^{15}N_{\Sigma trophic\ AA\text{-}\Sigma source\ AA}$) (e.g. McCarthy *et al.*, 2007; Popp *et al.*, 2007; Hannides *et al.*, 2009; Seminoff *et al.*, 2012), which can compensate for uncertainty in any single AA measurement.

RESULTS

Temporal isotopic trends across GLGs

Decade of GLG formation was not retained as a significant predictor of $\delta^{15}N$ values in generalized linear mixed effects models ($P > 0.1$), and there was no temporal trend in source AA $\delta^{15}N$ values over the study period (linear regression, adj R^2 −0.030, $P > 0.4$). $\delta^{13}C$ values, on the other hand, showed a clear linear decline over the same period (data not shown), and decade of GLG formation was a significant predictor of $\delta^{13}C$ values ($P < 0.001$). However, models did not retain decade as a significant explanatory variable of $\delta^{13}C_{cor}$ ($P > 0.2$).

Best-fit generalized linear mixed effects models indicated GLG (age) was a significant predictor of $\delta^{15}N$ values ($P < 0.005$), but not $\delta^{13}C_{cor}$ values ($P > 0.6$). Teeth of most individuals showed a decrease in $\delta^{15}N$ values over the first 1–3 GLGs of ~1 to 2‰ (Figure 2). Although adjacent GLGs differed by up to 2.1‰, no clear $\delta^{15}N$ patterns were observed beyond the first three GLGs in most teeth. There were no discernible ontogenetic $\delta^{13}C_{cor}$ patterns, although values differed by up to 1.1‰ between adjacent GLGs (Figure 2).

Bulk isotopic variation among individuals

Bulk $\delta^{15}N$ values differed among individuals ($F = 29.91$, $P < 0.0001$, df = 9). Tukey's *post-hoc* comparisons indicated significant differences among whales within and between collection regions (Figure 3). Four ECA individuals had significantly higher $\delta^{15}N$ values than all other individuals (median $\delta^{15}N$ range: 17.7–18.4‰, adj $P < 0.01$), but did not differ among each other (adj $P > 0.7$). $\delta^{15}N$ values were similar among five individuals collected in the NWA (median $\delta^{15}N$ range: 16.3–17.1‰) (adj $P > 0.2$). $\delta^{15}N$ values of one ECA individual (median: 15.2‰) were significantly less than all but one of the individuals of the previous 'groups' (adj $P < 0.01$) (Figure 3). The remaining NWA individual (NWA-BP-1998) had lower $\delta^{15}N$ (13.1‰) than all other individuals (Figure 3).

While $\delta^{13}C_{cor}$ values differed among individual whales ($F = 15.62$, $P < 0.0001$, df = 9), *post-hoc* analyses indicated this result was driven primarily by individual ECA-RB-2009. This whale had significantly lower $\delta^{13}C_{cor}$ values than all individuals (adj $P < 0.01$) except ECA-CS-1977-2 (adj $P > 0.3$) and NWA-SI-1977 (adj $P > 0.5$). While significant differences in $\delta^{13}C_{cor}$ values occurred between several of the remaining whales, for the most part, similar $\delta^{13}C_{cor}$ values among most individuals (adj $P > 0.25$) did not reflect the clear distinctions among individuals and between regions noted for $\delta^{15}N$ (Figure 3). $\delta^{13}C_{cor}$ of whale NWA-BP-1998 was lower than that of most other whales, as it was for $\delta^{15}N$.

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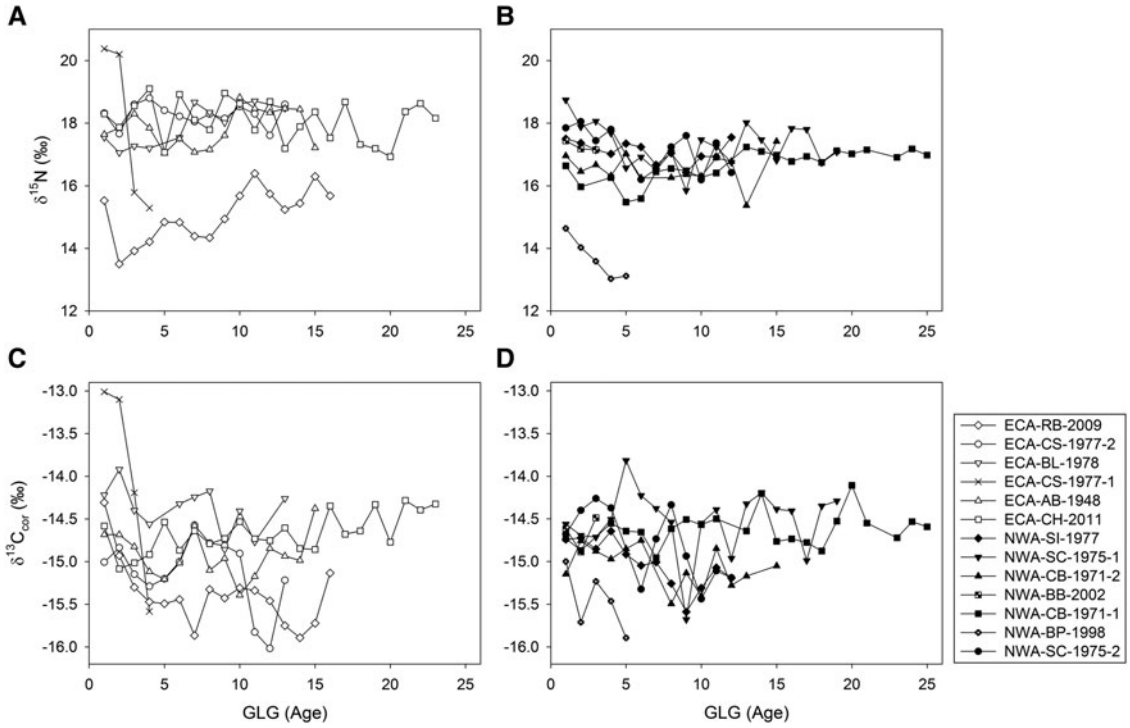

Fig. 2. $\delta^{15}N$ values of individual dentinal growth layer groups (GLGs) in teeth of eastern Canadian Arctic (ECA) (A) and north-west Atlantic (NWA) (B) killer whales show consistent long-term separation of individuals. Similar profiles for $\delta^{13}C_{cor}$ values (*post-hoc* adjustment of 0.019‰ yr^{-1} to account for oceanic Suess effect; panels (C) and (D) show less distinction among individuals.

Source AA and trophic position indices

Individual AA $\delta^{15}N$ values spanned a range of ~25‰ (Table 2). Trophic AAs (alanine, leucine, proline, aspartic acid, and glutamic acid) had higher $\delta^{15}N$ values (mean 23.92 ± 2.0, range 17.80–27.46‰) than source AAs phenylalanine, glycine, and serine (mean 11.13 ± 0.98, range 3.00–15.59‰) (Table 2; Figure 4). Bulk collagen $\delta^{15}N$ values calculated from mass balance of individual AA $\delta^{15}N$ values correlated strongly with mean bulk collagen $\delta^{15}N$ values measured across GLGs (adj R^2 0.89, $P < 0.001$), although with a consistent offset of −1 to −2‰.

Mean bulk GLG $\delta^{15}N$ values and mean source AA $\delta^{15}N$ values were significantly correlated (linear regression, adj R^2 0.91, $P < 0.001$, unstandardized regression coefficient (B) 0.64 ±0.06 (SE)) (Figure 5). This relationship remained significant (adj R^2 0.45, $P < 0.05$, B 0.54 ±0.19) after removal of the two whales with the lowest bulk and source AA $\delta^{15}N$ values (Figure 5). Groupings identified by differences in bulk $\delta^{15}N$ values (Figure 3) differed similarly in their source AA $\delta^{15}N$ values (ANOVA, $F = 11.07$, $P < 0.005$, $df = 3$). ECA individuals with high bulk $\delta^{15}N$ values (group 'a', Figure 3) had significantly higher source AA $\delta^{15}N$ values than NWA whales with high bulk $\delta^{15}N$ values (group 'b') ($P < 0.05$), as well as whales ECA-RB-2009 ('c') ($P < 0.001$) and NWA-BP-1998 ($P < 0.001$). Whales ECA-RB-2009 and NWA-BP-1998 had lower source AA $\delta^{15}N$ values than NWA whales (group 'b') ($P = 0.05$ and 0.004, respectively), but did not differ from each other ($P > 0.8$).

Trophic AA $\delta^{15}N$ values differed among individuals (ANOVA, $F = 3.35$, $P < 0.05$, $df = 3$), although *post-hoc* tests indicated this was entirely driven by significant differences between whale NWA-BP-1998 and each of groups 'a', 'b' and 'c' identified in Figure 3 ($P < 0.001$). Trophic AA of the remaining groups did not differ ($P > 0.2$). Variation in trophic indices ($\Delta\delta^{15}N_{Glu\text{-}Phe}$ and $\Delta\delta^{15}N_{\Sigma trophic\ AA\text{-}\Sigma source\ AA}$) among individuals (Table 2) was, therefore, driven by source AA $\delta^{15}N$ rather than trophic AA $\delta^{15}N$. Among ECA whales, ECA-RB-2009 had the greatest $\Delta\delta^{15}N_{Glu\text{-}Phe}$ (17.59 ‰). $\Delta\delta^{15}N_{Glu\text{-}Phe}$ of the remaining ECA whales ranged from 11.37 to 14.57‰ (Table 2). Similar variation was observed among NWA whales, with whales NWA-SC-1975-2, NWA-BP-1998, and NWA-SC-1975-1 having greater $\Delta\delta^{15}N_{Glu\text{-}Phe}$ (18.91, 18.80 and 17.63‰, respectively) than the other NWA whales (range 12.30–14.65‰) (Table 2). Trophic positions calculated using equation (1) ranged from 2.1 ±0.1 to 3.0 ±0.1 (data not shown).

$\Delta\delta^{15}N_{\Sigma trophic\ AA\text{-}\Sigma source\ AA}$ values were more consistent among individuals than $\Delta\delta^{15}N_{Glu\text{-}Phe}$ values (Table 2). Among ECA whales, ECA-RB-2009 had a greater $\Delta\delta^{15}N_{\Sigma trophic\ AA\text{-}\Sigma source\ AA}$ (14.69‰) and ECA-CH-2011 had a lower $\Delta\delta^{15}N_{\Sigma trophic\ AA\text{-}\Sigma source\ AA}$ (9.87 ‰) relative to the other ECA whales (11.35–12.28‰) (Table 2). Among NWA whales, NWA-BP-1998 had a greater $\Delta\delta^{15}N_{\Sigma trophic\ AA\text{-}\Sigma source\ AA}$ (14.82‰) than the remaining whales (11.69–12.79‰) (Table 2).

DISCUSSION

Longitudinal $\delta^{15}N$ and $\delta^{13}C$ profiles across dentinal GLGs indicate consistent isotopic differences between ECA and NWA killer whales at individual and regional levels. While we recognize complex ecosystem-level processes can influence baseline isotope values over the period of GLG deposition

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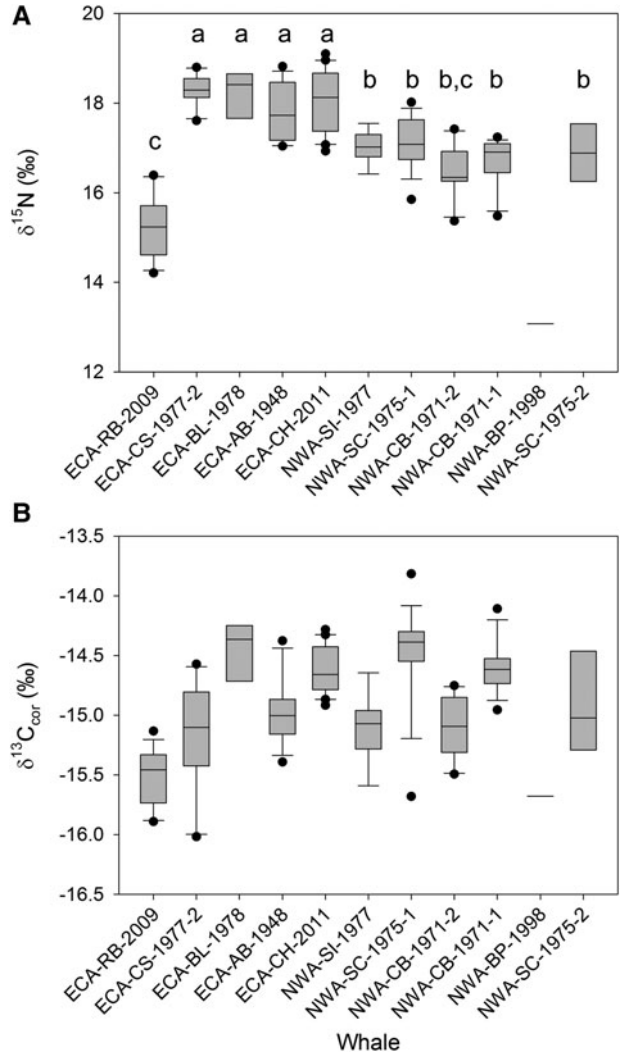

Fig. 3. Box-and-whisker plots of median dentinal growth layer group (GLG) $\delta^{15}N$ (A) and $\delta^{13}C_{cor}$ values (B) (first three GLGs not included) in teeth of eastern Canadian Artic (ECA) and north-west Atlantic (NWA) killer whales. Horizontal lines represent the median, box width represents the interquartile range (IQR), and whiskers mark the 10th and 90th percentiles. Distinct grouping of individuals noted with $\delta^{15}N$ values (indicated by lower case letters) were not reflected in $\delta^{13}C_{cor}$ values.

(1917–2000), the lack of temporal patterns in bulk GLG and source AA $\delta^{15}N$ values over the 80 yr study period indicates isotopic differences among individuals were not related to temporal isotopic variation, and that observed for $\delta^{13}C$ values was attributed to the oceanic ^{13}C Suess effect. Analysis of AA-specific $\delta^{15}N$ values, however, showed as much as 91% of the bulk $\delta^{15}N$ variation among individuals was due to baseline (source AA) $\delta^{15}N$ variation, rather than diet differences. Results therefore indicate killer whales included in our sample foraged consistently at similar trophic levels, but within food webs with distinct baseline isotopic values.

Our assessment of the degree to which bulk isotopic differences among individuals reflect baseline vs trophic-level diet differences depends on interpretations of AA-specific $\delta^{15}N$ values. While its application to marine mammal foraging studies has not been rigorously validated, AA-CSIA has been used successfully to decouple baseline vs trophic influences on bulk $\delta^{15}N$ in a variety of other marine consumers.

Table 2. $\delta^{15}N$ values ± SD (‰) of trophic and source amino acids (AA) in dentinal collagen of Eastern Canadian Arctic (ECA) and north-west Atlantic (NWA) killer whales.

		Eastern Canadian Arctic (ECA)					North-west Atlantic (NWA)				
		ECA-RB-2009	ECA-CS-1977-2	ECA-BL-1978	ECA-AB-1948	ECA-CH-2011	NWA-SI-1977	NWA SC-1975-1	NWA CB-1971-2	NWA CB-1971-1	NWA BP-1998	NWA SC-1975-2
Trophic AA	Alanine	23.97 ± 0.12	25.17 ± 0.03	24.14 ± 0.07	24.32 ± 0.54	22.99 ± 0.24	23.86 ± 0.04	23.60 ± 0.48	24.92 ± 0.10	23.99 ± 0.30	20.51 ± 0.60	23.94 ± 0.17
	Leucine	23.56 ± 0.25	24.24 ± 0.54	23.84 ± 0.30	24.19 ± 0.23	22.98 ± 0.06	22.71 ± 0.64	22.73 ± 0.65	22.85 ± 0.13	23.57 ± 0.14	20.02 ± 0.18	23.00 ± 0.05
	Proline	25.73 ± 0.32	26.41 ± 0.07	25.85 ± 0.25	27.36 ± 0.19	27.44 ± 0.08	24.76 ± 0.06	27.05 ± 0.15	26.48 ± 0.25	25.47 ± 0.13	21.07 ± 0.27	27.01 ± 0.07
	Aspartic acid	21.11 ± 0.24	21.02 ± 0.33	20.26 ± 0.18	21.76 ± 0.55	20.98 ± 0.16	20.63 ± 0.18	20.33 ± 0.42	20.44 ± 0.12	20.67 ± 0.47	17.80 ± 0.35	20.44 ± 0.28
	Glutamic acid	25.64 ± 0.18	25.94 ± 0.25	24.47 ± 0.14	26.88 ± 0.27	25.25 ± 0.37	25.07 ± 0.18	26.19 ± 0.16	24.12 ± 0.36	25.71 ± 0.02	21.80 ± 0.15	26.34 ± 0.23
Source AA	Mean trophic AA	24.00 ± 0.52	24.56 ± 0.72	23.71 ± 0.57	24.90 ± 1.07	23.93 ± 0.69	23.41 ± 0.89	23.98 ± 0.96	23.76 ± 0.49	23.88 ± 0.60	20.24 ± 1.21	24.15 ± 1.28
	Phenylalanine	8.05 ± 0.22	13.85 ± 0.25	11.12 ± 0.35	12.31 ± 0.45	13.89 ± 0.15	12.77 ± 0.40	8.57 ± 0.53	10.02 ± 0.48	11.06 ± 0.30	3.00 ± 0.21	7.44 ± 0.36
	Glycine	8.43 ± 0.23	11.89 ± 0.12	11.10 ± 0.41	12.92 ± 0.20	12.70 ± 0.03	9.81 ± 0.14	12.53 ± 0.09	12.64 ± 0.35	11.63 ± 0.29	6.09 ± 0.37	12.03 ± 0.12
	Serine	11.45 ± 0.30	13.89 ± 0.21	13.03 ± 0.57		15.59 ± 0.16	12.56 ± 0.46	13.68 ± 0.13	12.18 ± 0.56	12.74 ± 0.28	7.16 ± 0.82	14.59 ± 0.31
	Mean source AA	9.31 ± 0.64	13.21 ± 0.53	11.75 ± 0.93	12.62 ± 0.49	14.06 ± 0.43	11.71 ± 0.80	11.59 ± 0.65	11.61 ± 0.96	11.81 ± 0.67	5.422 ± 1.00	11.35 ± 0.67
Trophic index	$\Delta\delta^{15}N_{Glu\text{-}Phe}$	17.59 ± 0.28	12.09 ± 0.35	13.35 ± 0.38	14.57 ± 0.52	11.37 ± 0.40	12.30 ± 0.44	17.63 ± 0.56	14.10 ± 0.61	14.65 ± 0.30	18.80 ± 0.26	18.91 ± 0.43
	$\Delta\delta^{15}N_{\Sigma trophicAA\text{-}\Sigma sourceAA}$	14.69 ± 0.82	11.35 ± 0.90	11.96 ± 1.09	12.28 ± 1.18	9.87 ± 0.81	11.69 ± 1.20	12.39 ± 1.16	12.15 ± 1.07	12.07 ± 0.90	14.82 ± 1.57	12.79 ± 1.44

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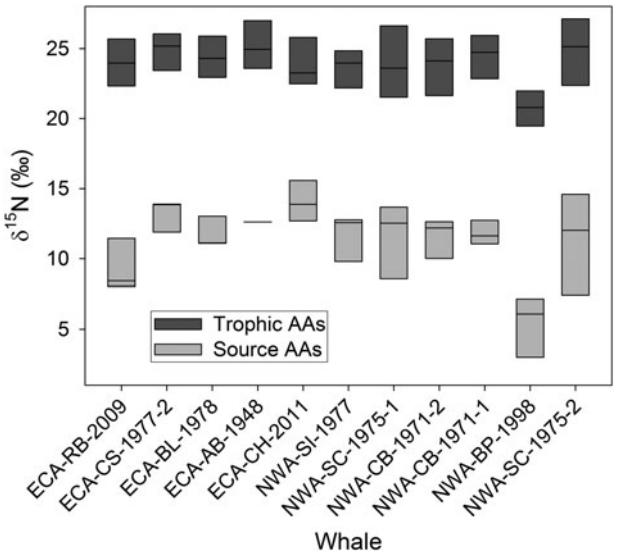

Fig. 4. Box plots of median trophic (alanine, leucine, proline, aspartic acid, and glutamic acid) and source (phenylalanine, glycine, and serine) amino acid (AA) $\delta^{15}N$ values from 'whole-tooth' dentinal collagen of eastern Canadian Arctic (ECA) and north-west Atlantic (NWA) killer whales show typical separation between the two types of AAs, reflecting ^{15}N enrichment of trophic relative to source AAs.

AA-specific $\delta^{15}N$ patterns in this study generally follow that of previous studies on marine birds and mammals. Lorrain *et al.* (2009) reported a $\delta^{15}N$ difference between mean trophic and source AA in penguin blood of ~13‰, while that between trophic and source AAs in harbour seal serum reported in Germain *et al.*'s (2013) study is ~11–12‰ (calculated from values presented in Table 1 using the same trophic and source AAs measured in this study). Relative differences between trophic and source AA $\delta^{15}N$ values in this study

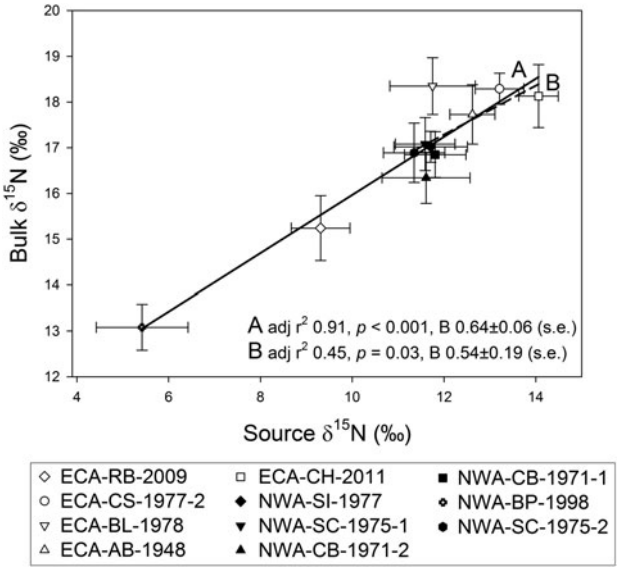

Fig. 5. Simple linear regression of mean bulk growth layer group vs mean source AA $\delta^{15}N$ values shows up to 91% of variation in bulk $\delta^{15}N$ is explained by isotopic variation in source AA among individuals (A, solid line). The relationship holds when whales ECA-RB-2009 and NWA-BP-1998 are not included in the regression (B, dashed line). Regression coefficients (slopes) are similar for both.

are also similar to $\Delta\delta^{15}N_{\Sigma\text{trophic AA-}\Sigma\text{source AA}}$ of bone collagen of an unidentified whale and two cape fur seals (*Arctocephalus pusillis*) (~13‰; Styring *et al.*, 2010). We therefore proceed with interpretation of AA-specific $\delta^{15}N$ results while recognizing this method has not yet been validated in marine mammals, and that further research, especially in terms of trophic position estimation, is required (see below).

While all AA can undergo deamination leading to ^{15}N enrichment of the remaining AA pool (Macko *et al.*, 1986), the negligible trophic fractionation of ~0.4‰ between diet and zooplankton $\delta^{15}N_{Phe}$ values (McClelland & Montoya, 2002) appears to be conserved in higher marine consumers (e.g. Naito *et al.*, 2010; Styring *et al.*, 2010). In the only controlled feeding study on AA-specific trophic ^{15}N enrichment in marine mammals, Germain *et al.* (2013) reported similar $\delta^{15}N_{Phe}$ values between captive harbour seals (*Phoca vitulina*) ($\delta^{15}N_{Phe}$ range: 9.1 ±1.0–12.7 ±0.9‰) and their diet comprising Atlantic herring (*Clupea harengus*) ($\delta^{15}N_{Phe}$ 11.3 ±4.4‰). The strong linear relationship between bulk and source AA $\delta^{15}N$ values in killer whale dentine, therefore, most likely reflects foraging within regions with distinct baseline $\delta^{15}N$ values (e.g. Hannides *et al.*, 2009). Measured source and trophic AAs account for similar amounts of total dentinal collagen nitrogen (Eastoe, 1963), so the correlation between bulk and source AA $\delta^{15}N$ is not simply a reflection of greater contribution of the latter to total collagen nitrogen. While generally poor resolution of baseline isotopic variation across the NWA limits interpretations within a spatial context, Graham *et al.* (2010) reported a gradual decrease in $\delta^{15}N$ values in upper water column plankton from the high Arctic to more southern latitudes in the North Atlantic. The low $\delta^{15}N$ values of ECA-RB-2009 and NWA-BP-1998 relative to the other whales could, therefore, reflect consistent foraging within food webs at lower latitudes in the North Atlantic Ocean, a plausible scenario given the track of a killer whale recently satellite-tagged in the ECA (Matthews *et al.*, 2011) spanned a gradient in $\delta^{15}N$ values similar to the range in source AA $\delta^{15}N$ values among individuals measured in this study.

Mid-latitude foraging in the North Atlantic by these two whales is also supported by their relatively low $\delta^{13}C_{cor}$ values, which indicate they foraged primarily within a region(s) characterized by distinctly lower baseline $\delta^{13}C$ values. Although $\delta^{13}C$ values in the North Atlantic generally increase with decreasing latitude, a large region of relatively lower $\delta^{13}C$ values at ~30–40°N (Graham *et al.*, 2010) also coincides with locations of the satellite-tagged killer whale (Matthews *et al.*, 2011). Other possibilities that could potentially account for relative differences in $\delta^{13}C_{cor}$ values (but may be difficult to reconcile with concurrent $\delta^{15}N$ patterns) include foraging along a coastal–offshore gradient (e.g. Walker *et al.*, 1999), or in north-east Atlantic waters off eastern Greenland, Iceland, and the British Isles, where zooplankton $\delta^{13}C$ values are lower than off Newfoundland and Nova Scotia (but not relative to the ECA) (Graham *et al.*, 2010). Although impossible to narrow potential distributions with certainty, we speculate whales ECA-RB-2009 and NWA-BP-1998 had a different over-wintering range than the other killer whales, or could have been infrequent visitors to the ECA or coastal Newfoundland.

Significant bulk $\delta^{15}N$ differences between remaining ECA and NWA whales (groups 'a' and 'b' in Figure 3) due largely to baseline isotopic variation provides support for separate,

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largely non-overlapping populations of killer whales within the ECA and NWA, at least during some portion of the year. Currently little is known about seasonal movements of ECA and NWA killer whales, and whether they move regularly between the two areas or share a common winter range is not known. Higdon (2007) found little evidence for large-scale migrations from southern latitudes into the ECA during summer months, given killer whale sightings occur along a range of latitudes throughout the ECA and NWA over that period, and to date, no re-sightings of photo-identified killer whales have occurred between the ECA and NWA (Young *et al.*, 2011). Considerable ^{15}N enrichment in ECA marine mammals such as narwhal, beluga, and ringed seal ($\delta^{15}N$ ~16–18‰; Hobson & Welch, 1992) relative to those occupying similar trophic position along the coast of Newfoundland such as common dolphin (*Delphinus delphis*) and harp seals (*Pagophilus groenlandicus*) ($\delta^{15}N$ ~14–15‰; Ostrom *et al.*, 1993; Lawson & Hobson, 2000) suggests baseline $\delta^{15}N$ values are higher in the ECA. Regular seasonal foraging trips into Arctic waters by ECA killer whales would have allowed them to prey on marine mammals with relatively higher $\delta^{15}N$ values (but not higher trophic position), which could account for the observed differences in $\delta^{15}N$ values if residency time within the ECA and foraging intensity was of sufficient duration to be recorded by dentine growth. Energy intake of killer whales can be greater during seasonal periods of prey availability (Baird & Dill, 1995), and this is likely the case for killer whales foraging on seasonally predictable aggregations of marine mammals in the ECA (Ferguson *et al.*, 2012b).

Baseline $\delta^{15}N$ differences could also reflect spatial segregation throughout the year, given each micromilled GLG sample represents diet integrated over an entire year of GLG deposition. Killer whales are not regularly sighted in the ECA during winter months (Higdon *et al.*, 2011), and Reeves & Mitchell (1988) hypothesized their winter range could include the Labrador Sea, the open North Atlantic, and the North American coast as far south as the Caribbean, while winter sightings of killer whales along the west coast of Greenland (Heide-Jørgensen, 1988) suggest it as a possible winter range of ECA killer whales. Lawson & Stevens (2013) reported similar sightings patterns around Newfoundland between summer and winter, and suggested certain locations are important throughout the year. However, it remains to be determined whether winter sightings off Newfoundland comprise individuals that summer in the ECA. Considerable overlap in dentinal $\delta^{13}C_{cor}$ values among ECA and NWA killer whales provides little additional indication of geographical separation. However, since $\delta^{13}C$ values of potential prey show little distinction across these regions (Hobson & Welch, 1992; Ostrom *et al.*, 1993; Lawson & Hobson, 2000; Hobson *et al.*, 2002), foraging within distinct areas across the broader ECA/NWA would not be expected to produce considerable differences in $\delta^{13}C_{cor}$ values. Nonetheless, consistent isotopic values across GLGs within individuals appears to be largely related to spatial foraging patterns, suggesting potential long-term site fidelity and separate killer whale groups/populations across the greater north-west Atlantic. Order of magnitude differences in several classes of persistent organic pollutants (D. Muir, Environment Canada, Burlington, ON, unpublished data) and correlations between genetic and isotopic differences among some of the whales included in this study (Morin *et al.*, 2010; A. Foote, personal communication) support this assertion.

Absolute trophic position estimates derived from AA-specific $\delta^{15}N$ values and equation (1) were too low for ECA/NWA killer whales known to feed at least to some extent on other marine mammals (expected trophic position of 4.5–4.6; Pauly *et al.*, 1998). Recent studies (Lorrain *et al.*, 2009; Dale *et al.*, 2011; Germain *et al.*, 2013) have also produced unexpectedly low trophic level estimates for higher marine consumers using AA specific $\delta^{15}N$ values, suggesting $TEF_{Glu\text{-}Phe}$ in higher marine consumers is less than the 7.6‰ determined for zooplankton and fish (but see Naito *et al.*, 2010, who obtained reasonable trophic level estimates for sea lions (*Zalophus calitorianus japonicas*) and porpoises (Phocoenidae) calculated with $TEF_{Glu\text{-}Phe} = 7.6‰$). Germain *et al.* (2013) performed a controlled feeding study to investigate nitrogen isotope fractionation in amino acids in harbour seals, measuring $TEF_{Glu\text{-}Phe}$ of ~4.3‰. The authors propose using a multi-TEF calculation of marine mammal trophic position to account for differences in nitrogen cycling between consumers excreting ammonia (e.g. zooplankton and teleost fish) vs uric acid or urea (e.g. elasmobranchs, marine birds and mammals) (Germain *et al.*, 2013; see also Dale *et al.*, 2011). Recalculation of ECA/NWA killer whale trophic position estimates using just a single $TEF_{Glu\text{-}Phe}$ of 4.3‰ (i.e. provides higher trophic position estimates than a dual-TEF approach since the lower TEF is applied to all trophic transfers) and equation (1) increases trophic position estimates to only 2.9–4.6. While the upper end of this range is plausible for killer whales with diets comprising approximately equal amounts of fish and marine mammals, the lower end is less than that of baleen whales foraging exclusively on large zooplankton (trophic position range: 3.2–3.6; Pauly *et al.*, 1998).

Although further research is required before AA-specific $\delta^{15}N$ values can be used to calculate absolute trophic position of marine mammals, we assume differences between trophic and source AA are diagnostic in terms of relative diet comparisons. Differences between $\Delta\delta^{15}N_{Glu\text{-}Phe}$ and $\Delta\delta^{15}N_{\Sigma trophic\ AA\text{-}\Sigma source\ AA}$ in their relative placement of individuals may reflect uncertainty in phenylalanine isotopic measurements, which can be influenced by co-eluting compounds (N. Wallsgrove, University of Hawaii, Honolulu, HI, personal communication). We therefore interpret $\Delta\delta^{15}N_{\Sigma trophic\ AA\text{-}\Sigma source\ AA}$ rather than $\Delta\delta^{15}N_{Glu\text{-}Phe}$. Comparable $\Delta\delta^{15}N_{\Sigma trophic\ AA\text{-}\Sigma source\ AA}$ values among most whales (certainly when error estimates are considered) suggest similar trophic-level diet. Although observational data forming the basis of our understanding of killer whale diet can be limited to conspicuous predation occurring at the surface, and are temporally biased due to seasonal variation in killer whale abundance and observer effort in both the ECA (Reeves & Mitchell, 1988; Higdon *et al.*, 2011) and NWA (Lien *et al.*, 1988; Lawson & Stevens, 2013), observations of killer whale predation in both regions suggest isotope patterns reflect a broad range of marine mammal prey. Monodontids (narwhal and beluga) are the most frequently reported prey of killer whales observed in the ECA (51% of predation records), followed by bowhead whales (32%) and seals (12%) (Higdon *et al.*, 2011). Reinhart *et al.* (2013) identified rake marks left by killer whale teeth on flukes of ~10% of photographed bowhead whales from five regions across the ECA. These observations in the ECA

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correspond with historical and recent observations of killer whale predation off Newfoundland and Labrador. Whalers off southern Labrador in the 1950s encountered killer whales attacking blue (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*) (Mitchell & Reeves, 1988), and sealing and whaling literature from the area describes killer whales tearing at carcasses of harvested whales (Mitchell & Reeves, 1988) and preying on harp seals (*Phoca groenlandica*) within ice fields (Sargeant & Fisher, 1957). Killer whales have recently been observed within nearshore ice fields near breeding harp seals off northern Newfoundland (Lawson *et al.*, 2008), and photo-identified killer whale groups have been recorded regularly killing minke whales (Lawson & Stevens, 2013).

An exception to similar $\Delta\delta^{15}N_{\Sigma trophic\ AA\text{-}\Sigma source\ AA}$ among individuals are the larger $\Delta\delta^{15}N_{\Sigma trophic\ AA\text{-}\Sigma source\ AA}$ values (by ~2–3‰) of whales ECA-RB-2009 and NWA-BP-1998, suggesting the diets of these whales comprised a greater proportion of higher trophic level prey. This pattern is difficult to explain given the strong relationship between bulk and source $\delta^{15}N$ values (one would expect bulk $\delta^{15}N$ values of these two whales to be higher than values predicted by the linear fit if they foraged at a higher trophic level relative to the other whales). Differences in apical tooth wear patterns, which have been associated with foraging differences among killer whale ecotypes (Ford *et al.*, 2011) or ecologically divergent groups (Foote *et al.*, 2009), provide some independent support for diet differences between these two and the remaining individuals. General inspection of the lower mandibles of whale ECA-RB-2009 and ECA-CH-2011 indicated whale ECA-RB-2009 had considerably more tooth wear, despite being an estimated 7 yr younger. NWA-BP-1998 had particularly extensive apical tooth wear exposing the pulp cavity, even though this whale, estimated to have been just 5 yr old when it died, was considerably younger than other whales with intact teeth. Comparable tooth wear has been linked with diets of shark in other killer whale populations (Ford *et al.*, 2011), which would be consistent with the greater $\Delta\delta^{15}N_{\Sigma trophic\ AA\text{-}\Sigma source\ AA}$ of whales ECA-RB-2009 and NWA-BP-1998, given sharks are generally tertiary consumers occupying high trophic positions in marine food webs (trophic position ~4; Cortés 1999; Estrada *et al.*, 2003). Further research into the relative rates of trophic ^{15}N enrichment of individual AAs will likely help elucidate patterns, and eventually clarify trophic position estimates of higher consumers such as killer whales based on AA-specific $\delta^{15}N$.

Evidence of significant baseline isotopic variation among ECA and NWA killer whales suggests consistent, long-term isotopic variation recorded in dentine GLGs reflected spatial segregation, rather than individual diet specialization. Consistent isotope profiles across GLGs spanning periods up to 25 yr suggest both distribution and diet of sampled individuals were fairly stable over the long-term. Future research efforts on ECA and NWA killer whales should focus on microspatial chemical analysis of teeth or tissues with fast turnover rates (e.g. metabolically active blubber) that can allow diet and habitat reconstructions over narrow periods of time, given GLGs sampled with annual resolution limit the scope for investigating seasonal distribution and diet patterns. This would provide a clearer idea of seasonal variation in killer whale diet in these regions, and could help determine, for example, whether killer whales show diet plasticity over the short-term. Diet variation could be especially pronounced in the ECA, where seasonal aggregations of marine mammals offer a predictable food resource, and recent studies (e.g. Higdon *et al.*, 2011; Reinhart *et al.*, 2013) have identified possible spatial and temporal patterns in predation too fine to be detected using diet indices integrated over the entire year. Our results add to a growing literature on killer whale predation patterns globally, and provide critical trophic information necessary for ecosystem management and conservation at broad spatial scales.

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