Seasonal foraging behaviour of Eastern Canada-West Greenland bowhead whales: an assessment of isotopic cycles along baleen

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ABSTRACT: Eastern Canada-West Greenland (EC-WG) bowhead whales Balaena mysticetus migrate seasonally between northwestern Hudson Bay/Foxe Basin and Gulf of Boothia in summer and Hudson and Davis Straits in winter. Despite recent advances in knowledge of summer diet composition, determining seasonal variation in foraging behaviour of EC-WG bowhead whales remains a priority for understanding how annual metabolic requirements are met, as well as identifying factors driving seasonal habitat selection. We measured stable nitrogen, carbon, and sulfur isotope composition (δ¹⁵N, δ¹³C, and δ³⁴S) along continuously growing baleen plates (n = 14) to assess alternative seasonal foraging hypotheses, namely winter fasting vs. year-round foraging. Synchronous δ¹⁵N and δ¹³C cycles, with periods of δ¹⁵N enrichment corresponding to foraging on the summer grounds, were inconsistent with standard fasting predictions, although δ¹⁵N cycles could reflect changes in diet-tissue δ¹⁵N discrimination between periods of intense foraging throughout the open-water season and supplemental protein intake during winter/spring. Correlations between δ¹⁵N and δ³⁴S values, potentially mediated through amino acid metabolism, support this interpretation. Reasonable agreement between baleen isotope oscillations and regional baseline δ¹⁵N and δ¹³C variation also indicated foraging occurs within isotopically distinct food webs across the summer and winter ranges. We conclude that EC-WG bowhead whales forage throughout their distribution, and conservatively interpret δ¹⁵N and δ³⁴S cycles to reflect reduced food consumption during winter. Foraging outside of periods of peak productivity likely contributes to annual metabolic requirements and winter habitat selection.

KEY WORDS: Arctic · Balaena mysticetus · Diet · Fasting · Isoscape · Marine mammal · Stable isotopes · Sulfur · Time series

INTRODUCTION

Predictable changes in food abundance have shaped the morphological, behavioural, and physiological adaptations of animals that routinely experience periodic food limitation (Young 1976, Lindstedt & Boyce 1985, Fryxell & Sinclair 1988, Millar & Hickling 1990). Large body size and an extensive blubber layer allow migratory baleen whales to withstand prolonged seasonal fasting after amassing lipid stores on productive summer foraging grounds (Lockyer 1981), with only opportunistic foraging on food resource-poor wintering grounds (e.g. Baraff et al. 1991). Prey abundance during the relatively brief foraging season has been correlated with annual variation in blubber thickness and reproductive success of several baleen whale species (Lockyer 1986, Viknssson 1990, Miller et al. 2011), highlighting the energetic constraints imposed on fasting animals that must partition endogenous reserves among compet-
ing interests such as growth, maintenance, and reproduction. How an animal meets annual metabolic requirements in seasonally variable environments therefore links individual energetics and population dynamics (e.g. Regehr et al. 2007, Rode et al. 2010).

Bowhead whales *Balaena mysticetus* Linnaeus, 1758 are resident within Arctic and sub-Arctic waters year-round (Reeves et al. 1983, Moore & Reeves 1993), where distinct seasonal pulses of primary productivity during the ice algae and phytoplankton blooms support large biomasses of grazing zooplankton (Longhurst et al. 1984, Runge & Ingram 1988). Bowhead whales, which are zooplankton specialists, enjoy optimal foraging conditions on pelagic copepods (primarily *Calanus* spp.) and euphausiids, as well as epibenthic invertebrates (Lowry 1993, Finley 2001, Lowry et al. 2004, Moore et al. 2010, Pomerleau et al. 2011a,b), over several months into late summer and fall, when zooplankton descend to overwintering depths that can exceed 1000 m (Longhurst et al. 1984, Hirche 1991). While there has been general consensus that winter feeding contributes little to overall bowhead nutrition (Lowry 1993, Finley 2001), studies have provided mixed results on the relative importance of foraging across different seasons (Schell & Saupe 1993, Hoekstra et al. 2002, Lee et al. 2005, Noongwook et al. 2007, Citta et al. 2014).

In the eastern Canadian Arctic, Eastern Canada-West Greenland (EC-WG) bowhead whales move into summer foraging grounds in northwestern Hudson Bay/Foxe Basin and Gulf of Boothia as sea ice breaks up (Reeves & Mitchell 1990, NWMB 2000; see Fig. 1). Spring migrations coincide with early season ice algal production (ca. April–June), when calanoid copepods and other zooplankton rise from overwintering depths to feed on ice-associated diatoms and their detritus (Conover & Huntley 1991). Finley (2001) thought spring and early summer zooplankton densities to be too low to be energetically profitable to EC-WG bowhead whales, but Pomerleau et al. (2012) provided evidence of limited foraging on ice-associated zooplankton. Intense feeding occurs during the open-water season (Finley 2001, Pomerleau et al. 2011a,b, 2012), and high levels of fatty acids unique to calanoid copepods in EC-WG bowhead blubber indicates they are a major prey item (Pomerleau et al. 2014). Finley et al. (1993) suggested the bulk of EC-WG bowhead whale annual energy requirements are met during fall foraging on high densities of mature stage *Calanus* copepods, followed by fasting while overwintering within the unconsolidated pack ice in Hudson and Davis Straits. A portion of the population comprising primarily mature females at Disko Bay off western Greenland, however, engage in late winter and early spring (February–May) feeding on high densities of pre-ascension stage calanoid copepods at depths ranging from 100 to 400 m (Laidre et al. 2007, Heide-Jørgensen et al. 2010, 2013). Estimates of high zooplankton consumption during their 4 mo residency at Disko Bay (Laidre et al. 2007) suggest resting zooplankton could be accessible at sufficient densities to be an energetically feasible food resource during periods of minimal productivity.

The incremental measurement of stable nitrogen (δ15N) and carbon (δ13C) isotope composition of baleen to resolve seasonal foraging patterns of baleen whales was developed by Schell et al. (1989a), who matched δ13C oscillations along the length of baleen plates with geographic variation in zooplankton δ13C values to infer when and where Bering-Chukchi-Beaufort (BCB) bowhead whales foraged across their range. Regional baseline isotope values, which vary due to underlying biogeochemical processes, are assimilated by primary producers and propagated more or less predictably into consumer tissues via trophic transfer (Minagawa & Wada 1984, McCutchan et al. 2003). Continuously growing keratinous baleen forms from amino acids in the bloodstream, and its stable isotope composition is presumed to rapidly reflect that of diet (Schell et al. 1989a). Because baleen is metabolically inert after formation, isotopic profiling along its length can provide past foraging information with well-constrained temporal resolution if baleen growth rate is known. When coupled with knowledge of regional baseline isotopic variation across a species’ range, this approach has proven useful for linking temporal and spatial foraging patterns of migratory baleen whales (e.g. Schell et al. 1989a, Best & Schell 1996, Caraveo-Patiño & Soto 2005).

While baleen δ13C variation has invariably been attributed to movements among (and foraging within) isotopically distinct food webs (e.g. Schell et al. 1989a, Caraveo-Patiño & Soto 2005), δ15N cycles along baleen have also been provisionally attributed to seasonal foraging/fasting cycles characteristic of baleen whales (e.g. Best & Schell 1996, Hobson et al. 2004, Summers et al. 2006). Isotopic fractionation during amino acid metabolism causes preferential retention of the heavier nitrogen isotope (15N) in body tissues, which elevates consumer δ15N values relative to diet (DeNiro & Epstein 1981). Tissues formed during periods of negative nitrogen balance, when amino acids are sourced from catabolised body protein pools, undergo further 15N enrichment (Hob-
son et al. 1993, Cherel et al. 2005, Lee et al. 2012). This effect has allowed researchers to consider seasonal fasting as a potential driver of baleen δ¹⁵N cycles, assuming peak values correspond to periods of fasting or negative nitrogen balance (e.g. Best & Schell 1996). However, recent studies have linked δ¹⁵N enrichment in baleen of several whale species with summer foraging, rather than winter fasting (Hobson & Schell 1998, Mitani et al. 2006, Aguilar et al. 2014). Aguilar et al. (2014) suggest fasting mysticetes reduce or prevent catabolism of body protein during the seasonal fast through metabolic adaptations and limited foraging, and that baleen δ¹⁵N cycles reflect shifts in trophic δ¹⁵N discrimination in response to seasonal shifts in food consumption.

Hobson & Schell (1998) measured long-term isotopic records along baleen of 3 EC-WG bowhead whales, and suggested δ¹⁵N cycles in the absence of δ¹³C cycles indicates they (1) migrated annually between regions differing in food web δ¹³N, but not δ¹⁵N values, (2) shifted diet annually by about one third of a trophic level (seasonal δ¹⁵N oscillations were ~1‰, or approximately one third the increase in δ¹⁵N values due to trophic ¹⁵N enrichment [McCutchan et al. 2003]), or (3) underwent seasonal fasting, assuming catabolism of endogenous protein to supply continuous baleen growth would have led to ¹⁵N enrichment of baleen (Hobson et al. 1993). Here we interpret isotopic variation along baleen from an additional 14 EC-WG bowhead whales acquired since Hobson & Schell’s (1998) study to assess alternative seasonal foraging hypotheses, namely seasonal (winter) fasting and year-round foraging. Regional variation in zooplankton stable isotope composition encompassing the EC-WG bowhead range (e.g. Pazerniuk 2007, Pomerleau et al. 2011c) provides spatial context for assessment of baleen δ¹⁵N and δ¹³C profiles. Stable sulfur isotope composition (δ³⁴S) was also measured along a subset of plates. Although rarely applied in studies of cetacean foraging behaviour (e.g. Hoekstra et al. 2002, Niño-Torres et al. 2006), negligible δ³⁴S discrimination with trophic level (McCutchan et al. 2003) and considerable spatial variation in δ³⁴S values along benthic-pelagic (Peterson et al. 1985) and nearshore-offshore (Barros et al. 2010) gradients make δ³⁴S values potentially useful for discerning between trophic and spatial influences that can lead to ambiguous interpretation of δ¹⁵N and δ¹³C values (e.g. Connolly et al. 2004). Recent studies linking trophic ¹⁵N and ³⁴S discrimination with dietary protein content (e.g. McCutchan et al. 2003, Florin et al. 2011) also suggest correlated δ¹⁵N and δ³⁴S values may reflect periods of restricted food consumption.

Clarifying seasonal foraging behaviour of EC-WG bowhead whales remains a priority for understanding individual energy budgets and seasonal habitat selection (Lockyer 1981, Moore et al. 2000, Ferguson et al. 2010), which are relevant for predicting how potential sea ice-driven changes in zooplankton phenology and community composition may impact bowhead whale populations under future climate scenarios (Tynan & DeMaster 1997, Laidre et al. 2008). We predicted fasting or food-restricted whales would show distinct δ¹⁵N cycles (perhaps correlated with δ³⁴S values), but do not necessarily assume that δ¹⁵N enrichment would occur during the winter fast (see Aguilar et al. 2014). On the other hand, we predicted foraging within isotopically distinct food webs across the summer and winter ranges would lead to synchronous δ¹⁵N and δ¹³C oscillations reflecting regional differences in zooplankton isotope composition. Further, we predicted seasonal shifts in foraging depth (Heide-Jorgensen et al. 2013) may lead to inversely correlated δ¹³C and δ³⁴S cycles, as benthic systems are ¹³C enriched and ³⁴S depleted relative to pelagic systems (Peterson et al. 1985, Hobson & Welch 1992).

MATERIALS AND METHODS

Baleen samples

Baleen plates were collected from bowhead whales (n = 14) harvested in Inuit subsistence hunts throughout the eastern Canadian Arctic from 1998 to 2011. Whales were taken during the open-water season (July–September) from Hudson Strait, Hudson Bay, Foxe Basin, Gulf of Boothia, and along northern and eastern Baffin Island (Fig. 1). Several of the longest baleen plates were excised from within the gum (i.e. included the most recent growth) from 10 whales, while those from the remaining 4 whales were cut at the gum and included only erupted baleen (Table 1). All baleen and biological and morphological data (Table 1) were obtained within 24–48 h of death, and baleen was frozen at −25°C.

Sample preparation and stable isotope analysis

The longest complete baleen plate from each whale was cleaned of algae and other adhered material using water and scrubbing pads, then scraped
with a scalpel blade to remove surface baleen. Starting at the base, the entire length of each plate was sampled at 2 cm increments along the outside edge using a hand-held rotary tool fitted with a 1/16 inch drill bit. With an annual baleen growth rate of 16–25 cm yr⁻¹ (Schell et al. 1989a), sample increments represent sub-seasonal to monthly temporal resolution. We assume each baleen plate provided an accurate isotopic history for each whale, based on nearly identical isotope profiles in adjacent baleen plates from a gray whale (Eschrichtius robustus; Caraveo-Patiño & Soto 2005), and those from opposite sides of the mouth of a bowhead whale (Schell et al. 1989a).

Baleen samples were weighed (~1 mg) directly into tin cups for analysis on a Vario EL III elemental analyser (Elementar, Germany) interfaced with a DELTA plus XP isotope ratio mass spectrometer (Thermo Fisher Scientific) at the G.G. Hatch Stable Isotope Laboratory, University of Ottawa, Ontario, Canada. Stable isotope ratios are reported in delta notation (δ) as parts per thousand (‰) deviation from the isotope ratios of international standards atmospheric N₂ and Vienna.

Table 1. Location and biological data for Eastern Canadian Arctic-West Greenland (EC-WG) bowhead whales Balaena mysticetus from which baleen was collected. M: male, F: female. Ratios measured: stable isotope ratios measured

<table>
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<tr>
<th>Whale no.</th>
<th>Whale sample ID</th>
<th>Location</th>
<th>Date (mo/yr)</th>
<th>Sex</th>
<th>Total length (m)</th>
<th>Baleen length (cm)</th>
<th>Ratios measured</th>
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<td>NSA-BM-98-01</td>
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<td>270</td>
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</tr>
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<td>08/2008</td>
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<td>319</td>
<td>δ¹⁵N, δ¹³C, δ³⁴S</td>
</tr>
<tr>
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<td>Gulf of Boothia, Kugaaruk, NU</td>
<td>09/2008</td>
<td>M</td>
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<td>181</td>
<td>δ¹⁵N, δ¹³C, δ³⁴S</td>
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<td>Foxe Basin, Repulse Bay, NU</td>
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<td>F</td>
<td>9.04</td>
<td>176</td>
<td>δ¹⁵N, δ¹³C</td>
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</tbody>
</table>

aTotal length (embedded + erupted)
bErupted length

Fig. 1. Baleen was collected from Eastern Canada-West Greenland (EC-WG) bowhead whales Balaena mysticetus throughout the Eastern Canadian Arctic during July to September, 1998 to 2011. Numbers on map correspond to whales listed in Table 1. Winter distribution (shown in blue) and areas of summer aggregations (pink) were reproduced from COSEWIC (2005), with modifications after Laidre et al. (2007) and Ferguson et al. (2010).
Pee-Dee Belemnite limestone (for \(\delta^{15}N\) and \(\delta^{13}C\), respectively), defined as \(\delta^{15}N = (R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}} \times 1000\), where \(R\) is \(^{15}N/^{14}N\) or \(^{13}C/^{12}C\). Values were normalised 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 measurements of a laboratory reference material not used in calibrations (glutamic acid) was 0.11‰ for \(\delta^{15}N\) and 0.05‰ for \(\delta^{13}C\), and that based on duplicate measures of ~5% of samples was 0.09 and 0.06‰ for \(\delta^{15}N\) and \(\delta^{13}C\), respectively.

Stable sulfur isotopic composition was measured along a subset (n = 3) of the 14 plates (Table 1). Baleen sulfur content is relatively high owing to large amounts of the amino acid cysteine (Block 1937, Gillespie & Inglis 1965), making it amenable to \(\delta^{34}S\) analysis. Samples were weighed (~0.6 mg) into tin cups and analysed on an Isochrom continuous flow stable isotope ratio mass spectrometer (GV Instruments/Micromass-UK) coupled to a Costech elemental analyser (CNSO 4010UK) at the Environmental Isotope Laboratory, University of Waterloo, Ontario, Canada. \(\delta^{34}S\) values are reported in delta notation \((R = \delta^{34}S/\delta^{32}S)\) relative to Canyon Diablo Meteorite calibrated through repeated measures of organic sulfur materials (NIST bovine liver and muscle). Analytical precision based on repeated measures of a homogenous baleen reference material, as well as duplicate measures of ~10% of samples, was 0.24‰.

Data analysis

Methods for exploring seasonality in stationary time series, primarily autoregressive (AR) models, spectral analysis, and sample cross correlation functions (CCF), were used to characterize variation in \(\delta^{15}N\), \(\delta^{13}C\), and \(\delta^{34}S\) profiles. These methods are appropriate for analysis of spatially collected data given an assumed linear growth rate (Shao et al. 2004). Baleen grows at a uniform rate in bowhead whales >12 m body length (Schell et al. 1989a, Schell & Saupe 1993). Given our sample largely comprised whales near or >12 m (Table 1), we assume baleen growth rates were linear over the lengths sampled for most whales, with the exception of whales BM-NSA-2011-03 (9.04 m) and BM-NSA-2008-001 (10.51 m).

Each isotopic series was first detrended using a Gaussian low pass filter to remove long-term trends (e.g. Park & Gambéroni 1995, Klvana et al. 2004). Attempts to characterize cycle parameters such as period, amplitude, and phase shift by fitting a nonlinear model with a cosine term to the seasonal component of each detrended series (e.g. Shao et al. 2004) generally provided poor fits to data (results not shown). Parametric spectral estimation (Parzen 1983, Cowpertwait & Metcalf 2009, Shumway & Stoffer 2011) was therefore used to estimate series periodicity. High-order autoregressive (AR(p)) models, with model order p selected based on minimum AIC, were fit to each detrended series. The spectral peak frequency for each modelled time series was converted to samples per period (1/peak frequency), then multiplied by sample increment (2 cm) to estimate period length.

The magnitude of each cycle (i.e. peak-to-peak amplitude) was calculated as the difference between maximum and minimum values within each oscillation of detrended series with significant periodicity (indicated by AR models). To assess whether \(\delta^{15}N\) and \(\delta^{13}C\) magnitudes were similar among whales whose baleen growth overlapped temporally, calendar year of growth was assigned to each oscillation by assuming the most recent complete oscillation represented the previous year’s growth, and that each oscillation thereafter was annual in nature (Schell et al. 1989b).

Correlations between isotopic series within a given plate were assessed using CCF calculated for each combination of elements (\(\delta^{15}N\) vs. \(\delta^{13}C\), \(\delta^{15}N\) vs. \(\delta^{34}S\), and \(\delta^{13}C\) vs. \(\delta^{34}S\)). All analyses were performed using the TSA package (Chan & Ripley 2012) available for R software (R Core Team 2012).

RESULTS

Considerable variation in \(\delta^{15}N\), \(\delta^{13}C\), and \(\delta^{34}S\) values occurred along all baleen plates for which they were measured, although the degree to which such variation constituted cycles differed for each element, within individuals, and among individuals (Fig. 2). Atomic C:N of baleen samples (3.3 ± 0.1; mean ± SD) was within the range of measured atomic C:N of baleen (Lysiak 2009, Bentaleb et al. 2011) and hair and nail keratin (O’Connell & Hedges 2001).

High order AR models were successfully fit to 13 of the 14 detrended \(\delta^{15}N\) profiles, and estimated periods from peak spectral frequencies of modelled \(\delta^{15}N\) oscillations ranged from 14.4 to 26.3 cm (Table 2).
Fig. 2. Stable nitrogen and carbon isotope ratio ($\delta^{15}$N and $\delta^{13}$C) profiles (not detrended) along baleen plates of 14 Eastern Canada-West Greenland (EC-WG) bowhead whales Balaena mysticetus. Stable sulfur isotope ratios ($\delta^{34}$S) were measured for a subset of the whales ($n = 3$). Sample 0 cm was taken at the base (proximal end), and, in whales from which total baleen was collected (*), represents the most recent growth. Note different scales of y-axes.
Fig. 2 (continued)
Average magnitudes of $\delta^{15}N$ cycles were similar among whales, ranging from 0.63 to 1.10‰ (Table 3). Individual $\delta^{15}N$ oscillations ranged from 0.16 to 2.70‰ (Table 3), and were not synchronous among whales within any given calendar year (data not shown). In baleen for which the total length was collected, which allowed isotope patterns to be temporally anchored to the month of death, $\delta^{15}N$ values decreased gradually through winter and early spring, reaching minimum values in late spring before increasing in summer-grown baleen (samples 0–2 cm of embedded baleen; Fig. 2).

AR models were successfully fit to 10 of the 14 detrended $\delta^{15}C$ series, and periods estimated from peak spectral frequencies were similar to those for $\delta^{15}N$ oscillations, ranging from 14.2 to 28.2 cm (Table 2). Average magnitudes of $\delta^{15}C$ cycles within plates ranged from 0.63 to 1.25‰, while individual oscillations ranged from 0.07 to 2.12‰ (Table 3). Like $\delta^{15}N$ oscillations, $\delta^{13}C$ oscillations differed in magnitude among whales within a given calendar year (data not shown). $\delta^{13}C$ values in most recently grown baleen followed a similar pattern as $\delta^{15}N$ values, with minimal $\delta^{13}C$ values occurring in winter and spring.

Table 2. Periods of $\delta^{15}N$, $\delta^{13}C$, and $\delta^{34}S$ cycles along baleen plates of Eastern Canadian Arctic-West Greenland (EC-WG) bowhead whales *Balaena mysticetus* estimated from spectra of autoregressive models (AR(p), where p is model order) fit to detrended data. $\delta^{34}S$ was measured along a subset of 3 out of 14 plates. nd: not detected

<table>
<thead>
<tr>
<th>Whale sample ID</th>
<th>$\delta^{15}N$ period (cm)</th>
<th>Model</th>
<th>$\delta^{13}C$ period (cm)</th>
<th>Model</th>
<th>$\delta^{34}S$ period (cm)</th>
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<td>AR (6)</td>
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<td>AR (10)</td>
</tr>
<tr>
<td>BM-NSA-2011-03</td>
<td>nd</td>
<td>nd</td>
<td>28.2</td>
<td>AR (4)</td>
<td>17.1</td>
<td>AR (10)</td>
</tr>
</tbody>
</table>

Table 3. Peak-to-peak amplitudes (means, ranges in parentheses) and mean (±SD) peak and trough $\delta^{15}N$ and $\delta^{13}C$ values in baleen plates of Eastern Canadian Arctic-West Greenland (EC-WG) bowhead whales *Balaena mysticetus* with $\delta^{15}N$ and $\delta^{13}C$ cycles. nd: not detected

<table>
<thead>
<tr>
<th>Whale sample ID</th>
<th>$\delta^{15}N$ Peak (%)</th>
<th>$\delta^{15}N$ Trough (%)</th>
<th>$\delta^{13}C$ Peak (%)</th>
<th>$\delta^{13}C$ Trough (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>NSA-BM-98-01</td>
<td>0.86 (0.4−1.56)</td>
<td>14.02 ± 0.29</td>
<td>13.13 ± 0.33</td>
<td>nd</td>
</tr>
<tr>
<td>BM-CH-2000-001</td>
<td>0.78 (0.34−1.62)</td>
<td>13.51 ± 0.18</td>
<td>12.72 ± 0.29</td>
<td>nd</td>
</tr>
<tr>
<td>BM-IG-HB-2002-001</td>
<td>0.64 (0.32−1.06)</td>
<td>13.58 ± 0.33</td>
<td>12.94 ± 0.20</td>
<td>0.72 (0.32−1.34)</td>
</tr>
<tr>
<td>BM-RB-2005-001</td>
<td>0.90 (0.34−1.60)</td>
<td>13.38 ± 0.13</td>
<td>12.49 ± 0.35</td>
<td>0.59 (0.07−1.61)</td>
</tr>
<tr>
<td>BM-01-2008</td>
<td>0.73 (0.33−1.41)</td>
<td>13.09 ± 0.35</td>
<td>12.34 ± 0.34</td>
<td>nd</td>
</tr>
<tr>
<td>BM-NSA-2008-001</td>
<td>0.77 (0.22−1.24)</td>
<td>13.57 ± 0.29</td>
<td>12.78 ± 0.44</td>
<td>1.05 (0.36−1.90)</td>
</tr>
<tr>
<td>BM-NSA-2008-002</td>
<td>0.86 (0.35−1.27)</td>
<td>13.46 ± 0.19</td>
<td>12.59 ± 0.31</td>
<td>0.70 (0.36−1.06)</td>
</tr>
<tr>
<td>BM-01-2009</td>
<td>1.10 (0.20−2.47)</td>
<td>13.18 ± 0.31</td>
<td>12.06 ± 0.58</td>
<td>nd</td>
</tr>
<tr>
<td>BM-NSA-2009-02</td>
<td>0.80 (0.35−1.75)</td>
<td>13.89 ± 0.30</td>
<td>13.08 ± 0.36</td>
<td>0.76 (0.24−1.47)</td>
</tr>
<tr>
<td>BM-NSA-2009-03</td>
<td>0.99 (0.42−2.70)</td>
<td>13.67 ± 0.37</td>
<td>12.67 ± 0.41</td>
<td>0.65 (0.44−0.89)</td>
</tr>
<tr>
<td>BM-NSA-2010-01</td>
<td>0.93 (0.55−1.39)</td>
<td>13.72 ± 0.32</td>
<td>12.80 ± 0.37</td>
<td>0.85 (0.26−1.62)</td>
</tr>
<tr>
<td>BM-NSA-2010-02</td>
<td>0.63 (0.16−1.05)</td>
<td>13.88 ± 0.32</td>
<td>13.24 ± 0.24</td>
<td>1.25 (0.36−2.12)</td>
</tr>
<tr>
<td>BM-NSA-2011-01</td>
<td>0.71 (0.47−1.44)</td>
<td>13.69 ± 0.19</td>
<td>12.96 ± 0.33</td>
<td>0.63 (0.23−1.30)</td>
</tr>
<tr>
<td>BM-NSA-2011-03</td>
<td>nd</td>
<td>nd</td>
<td>nd</td>
<td>0.91 (0.46−1.33)</td>
</tr>
</tbody>
</table>
followed by $\delta^{13}C$ increases in summer (Fig. 2). CCF indicated $\delta^{15}N$ and $\delta^{13}C$ patterns were largely synchronous within plates, with significant positive lag 0 correlations between the 2 measures in all but 3 of the 14 plates, and cycled thereafter over repeated lags similar to periods estimated using parametric spectral estimation (Fig. 3).

Of the 3 plates analysed for sulfur isotope ratios, $\delta^{34}S$ cycles were identified in just one plate (BM-IG-HB-2002-001). Period length estimated from the peak spectral frequency of an AR model fitted to the detrended series (17.3 cm) was similar to those of $\delta^{15}N$ and $\delta^{13}C$ cycles along that plate (Table 2). Significant positive lag 0 correlations between $\delta^{34}S$ and $\delta^{15}N$ values occurred in 2 of the plates (BM-01-2008, BM-IG-HB-2002-001), but not between $\delta^{34}S$ and $\delta^{13}C$ values (Fig. 4).

**DISCUSSION**

Estimated periods of isotopic cycles are consistent with annual bowhead whale baleen growth rates (Schell et al. 1989a), and are assumed to reflect seasonal variation in foraging. The most obvious pattern in our data are synchronous $\delta^{15}N$ and $\delta^{13}C$ cycles, with peaks in both values occurring on the summer foraging grounds. This pattern contradicts standard assumptions that fasting induces $^{15}N$ enrichment in newly grown tissues, although $\delta^{15}N$ declines during the purported winter fasting period may reflect metabolic pathways and limited food consumption that prevent catabolism of body protein reserves (Aguilar et al. 2014). Baleen $\delta^{13}C$ cycles, however, have invariably been linked with migrations between isotopically distinct food webs (e.g. Schell et al. 1989a), rather than fasting physiology. Reasonable agreement between baleen $\delta^{15}N$ and $\delta^{13}C$ values and geographic variation in zooplankton isotopic composition across the EC-WG bowhead range indicates foraging on both the summer and wintering grounds is a plausible explanation of baleen isotope cycles. While baleen $\delta^{34}S$ values could also reflect regional baseline variation (see Strauss 2004), we also consider whether correlated $\delta^{15}N$ and $\delta^{34}S$ values, mediated through changes in amino acid metabolism during periods of restricted protein intake (Florin et al. 2011), could reflect reduced foraging during winter, when zooplankton accessibility is reduced.

Previous interpretations of baleen $\delta^{15}N$ cycles have assumed that catabolism of endogenous protein reserves, which are $^{15}N$ enriched relative to diet (DeNiro & Epstein 1981), under fasting conditions leads to additional $^{15}N$ enrichment of newly formed tissues (see Cherel et al. 2005, Lee et al. 2012). The timing of $\delta^{15}N$ oscillations observed here does not fit this assumption, as $^{15}N$ enrichment occurred on the summer foraging grounds rather than during the purported winter fast (Finley 2001), a point also noted by Hobson & Schell (1998) regarding $^{15}N$ enrichment peaks along baleen of 2 other EC-WG bowhead whales. We assume growth of the basal portion of embedded baleen occurred on the summer foraging grounds when baleen was collected, and that baleen isotope values reflect diet with little delay. Both assumptions are supported by results of several studies linking isotopic composition of newly grown baleen with recent foraging movements among regions of well-characterized isotopic composition (Schell et al. 1989a, Best & Schell 1996, Caraveo-Patiño & Soto 2005). Aguilar et al. (2014) attributed similar patterns of $^{15}N$ enrichment in summer-grown fin whale *Balaenoptera physalus* baleen to migrations between different marine isoscapes (with higher baseline $\delta^{15}N$ values occurring on the summer foraging grounds), as well as maintenance of positive nitrogen balance during winter through protein-sparing and limited foraging, thereby meeting protein demands while avoiding catabolism of endogenous protein reserves that normally elicits $^{15}N$ enrichment associated with fasting. Resumption of intense seasonal foraging, with a concomitant increase in diet-tissue $\delta^{15}N$ discrimination as protein catabolism and urea excretion are ramped up (Martínez del Rio & Wolf 2005), would contribute to relative baleen $^{15}N$ enrichment on the summer foraging grounds (additive to any baseline isotopic variation between the summer foraging and wintering grounds; Aguilar et al. 2014).

It is unclear if baleen whales require limited foraging to avoid substantial endogenous protein catabolism while fasting, as some fasting-adapted mammals endure prolonged fasting with minimal loss of protein reserves (Castellini & Rea 1992, McCue 2010), and if they do not, could relative $^{15}N$ depletion in baleen grown over the winter fast occur entirely as a result of efficient protein sparing (i.e. recycling of $\delta^{15}N$ depleted urea into body proteins)? Polischuk et al. (2001) reported concurrent $\delta^{15}N$ and $\delta^{13}C$ decreases of 1‰ and 0.5‰, respectively, in plasma of female polar bears *Ursus maritimus* that had been fasting for 3–4 mo, which was attributed to preferential catabolism of body fat. This was supported by the fact that $^{15}N$ and $^{13}C$ depletion occurred in bears that had a relatively high percentage of body fat, and continuing to fast for 7–8 mo caused plasma $^{15}N$ and
Fig. 3. Sample cross correlation functions (CCF) show evidence of significant, in-phase correlations between $\delta^{15}$N and $\delta^{13}$C values along eastern Canada-West Greenland (EC-WG) bowhead whale *Balaena mysticetus* baleen. Values falling outside the dotted lines (drawn at $1/n \pm 2/\sqrt{n}$, where $n =$ series length) provide evidence of statistical significance at the 5% level. Lag unit is the sample interval, 2 cm. Note different scales of y-axes.
Matthews & Ferguson: Seasonal foraging behaviour of bowhead whales

13C enrichment, presumably as the animals turned to catabolism of endogenous proteins (Polischuk et al. 2001). Baleen whales similarly rely on catabolism of extensive lipid reserves in blubber to fuel energetic needs while fasting, when food consumption is below maintenance levels (Lockyer 1981). Incorporation of lipid-derived carbon from mobilized blubber stores into amino acids during the fasting period, as observed in black bears Ursus americanus (Ahlquist et al. 1984), could conceivably lead to 13C depletion of baleen, since lipids are 13C depleted relative to dietary protein (DeNiro & Epstein 1978). To our knowledge, however, a fasting effect on δ13C values has not been reported in mysticetes, when periods of fasting inferred from baleen δ15N cycles and, more importantly, declines in lipid reserves (Aguilar & Borrell 1990), have been accompanied by relatively constant baleen δ13C values (A. Aguilar, University of Barcelona, Barcelona, Spain, pers. comm.).

Baleen δ13C cycles, rather, have invariably been attributed to source δ13C variation as migratory whales forage within isotopically distinct food webs across their distribution (e.g. Schell et al. 1989a, Best & Schell 1996, Caraveo-Patiño & Soto 2005, Lee et al. 2005). Compiled records of isotopic compositions of particulate organic matter (POM) and zooplankton communities spanning the summer and winter distributions of EC-WG bowhead whales (Table 4) show reasonable agreement between baleen isotope patterns and regional isotopic variation across the eastern Canadian Arctic, although the latter is based on few studies. Both δ15N and δ13C values were higher, on average, in POM and zooplankton in Gulf of Boothia and Baffin Bay, where EC-WG whales forage during the ice-free season, than in Hudson and Davis Straits, where EC-WG bowheads overwinter, which is consistent with δ15N and δ13C increases in basal baleen grown on the summer foraging grounds. Individual baleen δ15N and δ13C oscillations ranging up to 2.7 and 2.1‰, respectively (Table 3), encompass regional differences in POM and zooplankton δ15N and δ13C values (1.3–1.9 and 0.8–2.1‰, respectively; Table 4), although smaller oscillations, or the altogether absence of regular δ13C cycles in 4 of the plates, are not consistent with regional baseline variation. Inconsistencies may be due to incomplete understanding of spatial and temporal isotopic variation of regional food webs across the eastern Canadian Arctic and western Greenland, given only a small percentage of the EC-WB bowhead range has been surveyed.
for zooplankton isotopic composition over several discontinuous years. For example, recent efforts to characterize isotopic composition of zooplankton across the region (e.g. Pomerleau et al. 2011c) have excluded Hudson Strait, where a large portion of the EC-WG bowhead whale population overwinter (Reeves & Mitchell 1990), and the few existing measurements from summer (Pazerniuk 2007, Kuzyk et al. 2010) may differ from winter values we are assuming they represent.

Seasonal migrations within the open ocean would not be expected to produce δ34S variation in baleen, given the relative uniformity of ocean water sulfate δ34S values (Rees et al. 1978). However, sulfate δ34S values in marginal seas similar to Hudson Bay are, on average, about 0.5–1‰ less than sulfate values in the open ocean due to the greater influence of relatively δ34S depleted riverine inputs in restricted basins (Strauss 2004). Hudson Bay receives considerable terrestrial freshwater inputs from river run-off (Jones & Anderson 1994), potentially lowering food web δ34S values on the EC-WG bowhead whale wintering grounds in Hudson Strait. Baseline data required to assess this hypothesis are unavailable, but a comparison of δ34S values in muscle of EC-WG bowhead whales (18.35–18.66‰; S. H. Ferguson unpubl. data) and beluga whales from Hudson Bay and Hudson Strait (17.25–17.50‰; Kelley 2014) suggests Hudson Bay/Hudson Strait food webs may be relatively depleted in δ34S (assuming beluga muscle integrates a δ34S value that primarily reflects Hudson Bay/Hudson Strait, and bowhead muscle integrates a greater open ocean signal). This admittedly crude comparison does not take into account potential diet- or habitat-related differences (e.g. the summer estuarine habitat of belugas), although similar δ34S values in muscle of bowheads (17–17.6‰) and belugas (17.7‰) off northern Alaska (Hoekstra et al. 2002) suggest little influence of these potentially confounding factors. Lower baleen δ34S values in winter vs. summer would be consistent with a regional δ34S gradient between Hudson Strait and the rest of the east-
ern Canadian Arctic, and $\delta^{34}S$ oscillations on the order of 0.5–1‰ are similar to sulfate $\delta^{34}S$ differences between other marginal seas and the open ocean (Strauss 2004).

Wide differences between seawater sulfate and sedimentary sulfide $\delta^{34}S$ values can also lead to considerable isotopic separation of marine consumers foraging in near vs. offshore regions (Barros et al. 2010). Seasonal shifts in foraging depth of EC-WG bowhead whales in response to vertical zooplankton distribution have been observed at Disko Bay, where whales dove close to the seabed to feed on copepods throughout March, and switched to shallower depths when copepods ascended to surface waters in April and May (Heide-Jørgensen et al. 2013). Descent to winter depths alone would not alter the sulfur isotopic composition of pelagic zooplankton, but seasonal shifts in foraging depth accompanied by consumption, either intentional or incidental, of benthic and epibenthic species (e.g. Pomerleau et al. 2011a) could lead to lower $\delta^{34}S$ values in winter-grown baleen because benthic food webs with sedimentary sulfur inputs are $^{34}S$ depleted relative to pelagic systems (Peterson et al. 1985). However, higher $\delta^{13}C$ values would be expected with consumption of more benthic prey, since benthic components of Arctic marine food webs are $^{13}C$ enriched (Hobson & Welch 1992, Hobson et al. 2002). The lack of inverse correlation between $\delta^{34}S$ and $\delta^{13}C$ values, with $^{13}C$ enrichment during summer rather than winter, therefore does not fit this scenario.

While $\delta^{34}S$ variation in animal tissues has conventionally been attributed to baseline variation, a handful of recent studies suggest synchronous $\delta^{15}N$ and $\delta^{34}S$ cycles may reflect a common trophic influence, potentially mediated through changes in amino acid metabolism during periods of limited food consumption. $^{34}S$ enrichment in keratinous tissues over organic dietary sulfur by 2–5‰ (Tanz & Schmidt 2010) indicates metabolism of sulfur amino acids (methionine and cysteine) has an associated isotopic fractionation. Methionine is the metabolic precursor of cysteine (Stipanuk 1986, 2004, Griffith 1987), which is the most common sulfur amino acid in keratins like baleen (Block 1937, Gillespie & Inglis 1965). Conversion of methionine to cysteine via several intermediates during the transsulfuration pathway involves transfer of the thiol group (Aitken et al. 2011), which introduces potential for kinetic $^{34}S$ fractionation. Cysteine, in turn, is the direct or indirect precursor of other sulfur-containing organic molecules, and the relative $^{34}S$ depletion of its oxidation product (taurine) indicates $^{34}S$ fractionation occurs with cysteine catabolism (Tanz & Schmidt 2010). Methionine and cysteine catabolism is restricted at low intakes in rats and humans, when both sulfur amino acids are channelled to protein synthesis rather than transsulfuration and oxidation (Storch et al. 1988, 1990, Stipanuk et al. 1992). Direct incorporation of sulfur amino acids into proteins during periods of limited protein intake would presumably reduce diet-keratin $\delta^{34}S$ discrimination and lead to lower baleen $\delta^{34}S$ values than when methionine and cysteine are in adequate supply and readily catabolised.

A limited number of studies have linked diet-tissue $\delta^{15}N$ and $\delta^{34}S$ discrimination ($\Delta^{15}N$ and $\Delta^{34}S$) with dietary protein quantity and quality, although none have focused on fasting-adapted animals under natural fasting conditions. McCutchan et al. (2003) found $\Delta^{34}S$ was significantly greater among consumers of high protein (+1.9 ± 0.51‰) than low protein (−0.5 ± 0.65‰) diets, although the authors could not isolate the role of protein quantity from among several potentially confounding variables. However, positive correlation between $\Delta^{15}N$ and $\Delta^{34}S$, which were high when dietary nitrogen exceeded growth requirements, indicates $\Delta^{34}S$ is affected by diet protein content. Similarly, Florin et al. (2011) found $\Delta^{34}S$ was positively correlated with various measures of total dietary sulfur amino acid content fed to rats. Results from these studies are consistent with a trophic, rather than spatial, explanation of concurrent baleen $\delta^{15}N$ and $\delta^{34}S$ cycles. Further, mediation of baleen $\delta^{15}N$ and $\delta^{34}S$ values through changes in amino acid metabolism during restricted protein consumption could explain why observed correlations between $\delta^{15}N$ and $\delta^{34}S$ values were not stronger, since $\delta^{34}S$ values would reflect metabolism of only sulfur amino acids, while $\delta^{15}N$ values would reflect the bulk of amino acid metabolism (see Florin et al. 2011). We also acknowledge that the composition and activity of gut microbial communities can vary with nutrition state in foregut fermenters like bowhead whales (Herwig et al. 1984), with likely influences on amino acid catabolism and synthesis not considered here.

By necessity, we have focused on generalized isotopic trends to assess potential foraging scenarios, but it is worth addressing potential causes of variation in isotopic cycling observed within and among whales. Periodic $\delta^{15}N$ variation in the absence of strong $\delta^{13}C$ cycles, which, despite overall correlations between $\delta^{15}N$ and $\delta^{13}C$ values, occurred at some point in most plates, could mark years when winter foraging was more limited, such that baleen retained $\delta^{13}C$ values acquired on the summer foraging
grounds. Three of the 4 whales lacking $\delta^{13}C$ cycles were mature males, which may be more likely to forego winter foraging when preoccupied with mating. Variable residency and migration patterns could also lead to isotopic variation within and among individuals. Although a majority of EC-WG bowhead whales summer and winter in Prince Regent Inlet/Gulf of Boothia and Hudson Strait, respectively, seasonal aggregations also occur along the east coast of Baffin Island in areas such as Cumberland Sound and Isabella Bay, as well as western Greenland (Reeves et al. 1983, Finley 1990, Dueck & Ferguson 2008, Ferguson et al. 2010). Migration routes also vary, with whales traveling across Davis Strait, along eastern Baffin Island, or between Fobse Basin and Gulf of Boothia (Reeves et al. 1983, Dueck & Ferguson 2008). Females may alter feeding behaviour spatially and temporally with reproductive cycles, possibly feeding earlier in the year at Disko Bay when mating or pregnant, then switching to feeding in Foxe Basin later in summer when with a calf or juvenile (see Cosens & Blouw 2003, Laidre et al. 2007). Different residency and migration patterns could also account for the lack of synchronous isotopic oscillations among whales in any given calendar year, since underlying regional isotopic variation would be synchronously recorded only in baleen of whales foraging within the same region. Interestingly, all whales lacking clear $\delta^{13}C$ cycles were harvested in northern Hudson Bay, Hudson Strait, or Cumberland Sound. If seasonal migrations of these animals were shorter than animals harvested in Foxe Basin/Gulf of Boothia (i.e. between Hudson Strait and Hudson Bay, or within Cumberland Sound), then the absence of $\delta^{13}C$ cycles could reflect their smaller range.

Assuming baleen $\delta^{13}C$ variation reflects regional baseline influences, a conservative interpretation of baleen isotope cycles is EC-WG bowhead whales forage throughout their distribution, although at a reduced rate during winter, given $\delta^{15}N$ and $\delta^{34}S$ cycles may reflect trophic influences to some extent. Late winter/spring foraging on resting calanoid copepods at overwintering depths is well-documented in bowhead whales at Disko Bay, off west Greenland (Laidre et al. 2007, Heide-Jørgensen et al. 2010, 2013). Bowheads overwintering in Hudson Strait in March have also been observed deep diving, which is consistent with foraging well below the surface (W. Koski, LGL Limited, King City, ON, pers. comm.). This interpretation is supported by recent dive data from satellite tagged bowheads in Hudson Strait that regularly dove (>60% of dives) deeper than 250 m during January and February (B. LeBlanc, Fisheries and Oceans Canada, Winnipeg, MB, pers. comm.), likely to reach mature zooplankton near the seafloor. There is also limited evidence that EC-WG bowhead whales take advantage of early season production during the ice algae bloom, when large aggregations of adult calanoid copepods graze near the ice-water interface throughout the eastern and central Canadian Arctic from March to June (Bradstreet & Cross 1982, Conover et al. 1986, Runge & Ingram 1988). Finley (2001) suggested zooplankton are too dispersed over this period to be energetically valuable to bowhead whales, but acknowledged some feeding along ice edges and within pack ice likely occurs. Pomerleau et al. (2012) found the isotopic composition of EC-WG bowhead whale skin reflected limited foraging on ice-associated zooplankton, while fatty acid profiles indicated reliance on diatom-derived food webs (although sympagic and planktonic species could not be differentiated; Pomerleau et al. 2014).

Year-round foraging by EC-WG bowhead whales inferred from baleen isotope cycles is also consistent with foraging behavior of conspecifics from the BCB population. BCB bowheads feed occasionally during spring migrations along the north Alaska coast ca. April–June (Carroll et al. 1987, Lowry et al. 2004, Asselin et al. 2012). While there has been general consensus that winter feeding contributes little to overall nutrition of BCB bowhead whales (Lowry 1993), Schell et al. (1989a) and Lee et al. (2005) concluded the carbon isotopic composition of bowhead muscle was largely derived from fall and winter foraging in the Bering and Chukchi Seas. As with EC-WG bowheads, direct observations of winter foraging by BCB bowheads are limited, although Noongwook et al. (2007) report consistent winter foraging in at least one area of the Bering Sea. Citta et al. (2014) provide supporting evidence from dive profiles that BCB bowhead whales forage throughout the year at core-use areas where oceanographic processes produce high zooplankton densities. Whales overwintered (November–April) in 2 core-use areas in the Bering Sea, spending almost half their time diving near the seafloor, presumably feeding along a subsurface front between a cold water current and warmer shelf waters (Citta et al. 2014). Lydersen et al. (2012) and Falk-Petersen et al. (2014) provide evidence that bowhead whales from the Spitsbergen population off eastern Greenland overwinter at high-latitude locations, where upwelling of Atlantic water along the shelf break may allow foraging on Calanus glacialis as early as mid-January. Similar localized oceanographic features and upwelling events that
aggregate zooplankton within bowhead diving range (Finley 1990, Okkonen et al. 2011, Walkusz et al. 2012) may also determine winter habitat selection by EC-WG bowhead whales, since the bulk of pelagic zooplankton important in their diet have descended to overwintering depths by late summer (Longhurst et al. 1984, Head & Harris 1985). Such oceanographic features may also explain the relatively restricted winter distribution of EC-WG bowhead whales compared with the more expansive summer range, when high densities of grazing zooplankton are widely accessible.

Bowhead whale numbers in the eastern Canadian Arctic are currently recovering from commercial whaling prior to the 20th century (Heide-Jørgensen et al. 2007, Higdon 2010), and understanding seasonal foraging ecology improves our ability to identify and protect critical habitat. Our conclusion that EC-WG bowhead whales engage in limited foraging over winter and spring is conservative, and hinges on whether δ15N (and δ34S) variation is caused primarily by spatial influences, or changes in amino acid metabolism in response to protein intake. Given links between individual energy budgets and population dynamics, and between seasonal food availability and habitat selection, further research into the degree of winter foraging by EC-WG bowhead whales is warranted. Better characterization of spatial and temporal zooplankton isotope values across the eastern Canadian Arctic/western Greenland could be used to retrospectively assess existing baleen isotope data, while advances in stable isotope applications to marine mammal diet studies such as amino acid specific isotope analysis (e.g. Matthews & Ferguson 2014) could help clarify trophic and source influences on isotopic variation in baleen with greater specificity.

Acknowledgements. Baleen was collected by Hunters and Trappers Organizations (HTOs) and wildlife officers in their respective communities across Nunavut and Nunavik, along with Fisheries and Oceans Canada (DFO) offices in Iqaluit, NU, Mont-Joli, QC (P. Carter), and Winnepig, MB (L. Dueck, B. Dunn, P. Hall, T. Kelley, and O. Nielsen), and Makivik Corporation in Kuujjuaq, QC (M. Simard). D. Yurkowski, B. Young, and R. Ibara assisted with baleen sampling, and stable isotope analysis was conducted by P. Middlestead, W. Abdí, and P. Wickham at the University of Ottawa (nitrogen and carbon), and R. Heemskerk and W. Mark at the University of Waterloo (sulfur). D. Gillis and M. Marcoux assisted with R code. Thank you to B. LeBlanc, W. Koski, N. Lysiak, and several anonymous reviewers for thorough reviews of earlier versions of this manuscript, and their recommendations for its improvement. C.J.D.M. received scholarship funding from the Duff Robin Fellowship at the University of Manitoba, the E. Scherer Memorial Scholarship, and the Garfield Weston Foundation, and S.H.F. received NSERC Discovery Grant support. Research funding was provided by Canada’s Species at Risk Act (SARA) through DFO, the Nunavut Wildlife Management Board (NWMB), and Arctic-Net Network of Centres of Excellence of Canada.

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Editorial responsibility: Christine Paetzold, Oldendorf/Luhe, Germany

Proofs received from author(s): February 7, 2015

Submitted: March 31, 2014; Accepted: November 28, 2014