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Mercury and stable isotope cycles in baleen plates are consistent with year-round feeding in two bowhead whale (*Balaena mysticetus*) populations

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Abstract

Previous studies have demonstrated that the analysis of biogeochemical tracers along baleen can provide seasonal, annual, and longer term insights into whale movements, habitat use, diet, and ecosystem processes. We measured the mercury (Hg) concentration and stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope compositions along baleen plates of bowhead whales (*Balaena mysticetus*) harvested between 1988 and 1996 from the Bering–Chukchi–Beaufort (BCB) and the Eastern Canada–West Greenland (EC–WG) populations. These measurements were compared among individuals and between populations to assess seasonal cycling and to determine if bowhead whales forage year-round rather than fasting in winter. Individuals from the BCB population had synchronous cycles with higher Hg concentrations and lower $\delta^{13}C$ values in summer and lower Hg concentrations and higher $\delta^{13}C$ values in winter. EC–WG individuals also had synchronized periodic variations with peak values in isotopic ratios during summer. These results reflect an annual cycle of seasonal migration between distinct food webs in both populations. Spring and fall feeding activity was indicated in the intra-annual Hg and $\delta^{13}C$ cycles along the baleen plates of all whales in our study. These shorter periods, spanning about half the annual growth, have not been previously described in the baleen of these populations, and are consistent with separate foraging areas along the migration routes. The results of this study provide further support for year-round foraging in a species previously thought to fast during winter. Future monitoring of seasonal foraging patterns in baleen would help to determine whether bowhead whales alter their foraging patterns in response to shifts in zooplankton community availability, composition, and phenology.

Keywords Arctic · Baleen · Bowhead whale · Carbon · Mercury · Nitrogen · Stable isotopes · Time series

Introduction

The bowhead whale (*Balaena mysticetus*) is a large mysticete endemic to the Arctic Ocean and its marginal seas. There are two genetically and spatially distinct populations in Canadian waters: the Bering–Chukchi–Beaufort population (BCB) in the Western Arctic and the Eastern Canada–West Greenland population (EC–WG) (Rugh et al. 2003) in the Eastern Arctic (Fig. 1). Both populations undertake long seasonal migrations across their ranges, in part constrained by the distribution of sea-ice, encountering various water masses and associated prey assemblages (Heide-Jørgensen et al. 2003; Ferguson et al. 2010; Pomerleau et al. 2012).

The BCB population overwinters in the Chukchi and the northern Bering Seas and spends the summer in the Alaskan and Canadian Beaufort Sea (Moore and Reeves 1993; Schell and Saupe 1993; Moore et al. 2010; Harwood et al. 2017). The EC–WG population overwinters in Hudson Strait, northern Hudson Bay, east of Baffin Island, and near the ice edge along West Greenland (Koski et al. 2006; Heide-Jørgensen et al. 2007; Ferguson et al. 2010). The summer range for the eastern bowhead population includes the fjords

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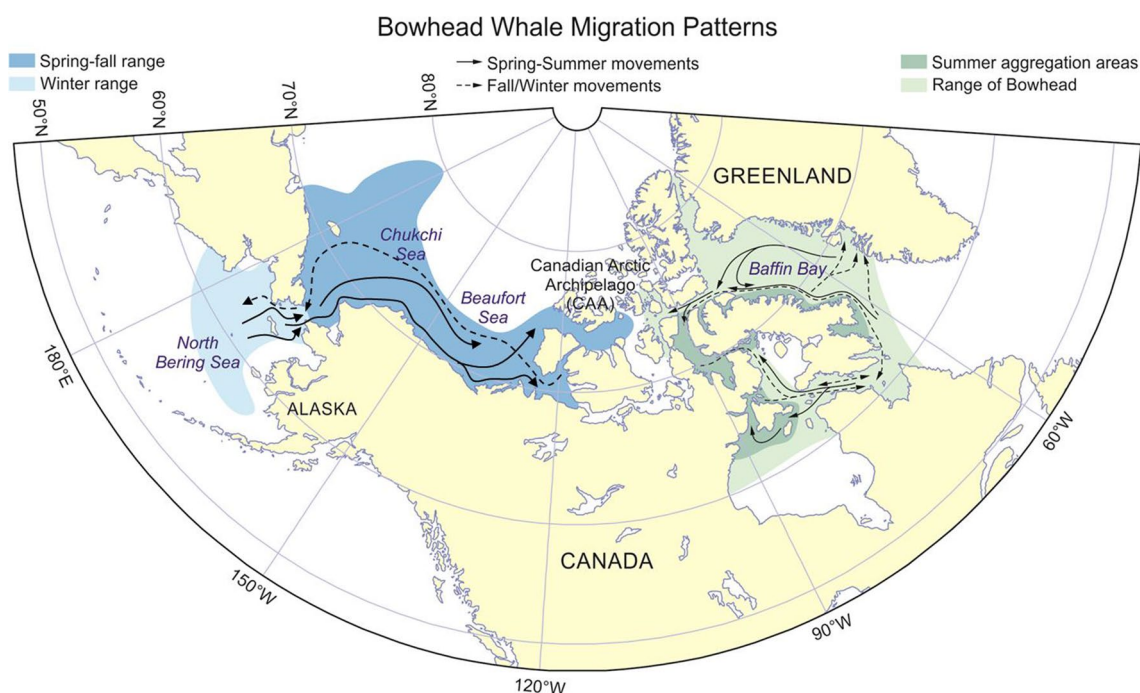
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Bowhead Whale Migration Patterns

Fig. 1 Map showing the seasonal broad distribution ranges of bowhead whales (*Balaena mysticetus*) in the Eastern (green) and Western Arctic (blue). Plain black arrows indicate broad northward migration (spring) and dashed black arrows broad southward migration (fall). Map after COSEWIC (2009), Dueck and Ferguson (2009), Quakenbush et al. (2013), and Harwood et al. (2017). (Color figure online)

and bays around Baffin Island, Hudson Bay, and Foxe Basin (Higdon and Ferguson 2010). Feeding on copepods (e.g., *Calanus* spp.), euphausiids and epibenthic invertebrates (Lowry 1993; Finley 2001; Lowry et al. 2004; Moore et al. 2010; Pomerleau et al. 2011a, 2012, 2014a) mainly occurs in the summer season (highest productivity) in both populations. Segments of the EC–WG population are also known to forage in early spring along the west coast of Greenland (Laidre et al. 2007) and early fall in Isabella Bay, Nunavut (Finley 1990, 2001).

Mysticete whales migrate from low-latitude regions where they mate, but little feeding is assumed to occur, to high latitudes where most feeding happens (Corkeron and Connor 1999). BCB whales have been observed feeding around Alaska during their westbound fall migration (Lowry et al. 2004) and to some extent in the Bering Sea during winter (Lee et al. 2005). Although it has generally been assumed for both populations that foraging is limited in winter (Lowry and Frost 1984; Finley 2001), Schell and Saupe (1993) proposed that significant foraging occurs year-round. Recent studies have shown that winter foraging occurs and may be important in the annual energy budget of bowhead whales (Citta et al. 2014; Matthews and Ferguson 2015).

The baleen plates of mature bowhead whales can measure up to four meters long, which, at an annual growth rate of approximately 17–18 cm per year, contain approximately 20–25 years of growth (Lubetkin et al. 2008). Keratinous

baleen is metabolically inert and includes within it biogeochemical markers such as stable isotopes (Schell et al. 1989a, b). Carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope ratios have been widely used to investigate trophic linkages, foraging ecology and the relative importance of feeding locations of migratory species (e.g., Hobson 1999; Newsome et al. 2010; Matthews and Ferguson 2015). The stable isotope approach is based on the principle that the isotopic composition of a consumer closely reflects the composition of its assimilated diet due to the predictable enrichment of the heavier isotope in consumer tissues during metabolic processes (DeNiro and Epstein 1981; Minagawa and Wada 1984). Nitrogen isotopes are commonly used to assess food web structure including the trophic position of species and patterns of accumulation of contaminants such as mercury (Hg) in marine food webs (Atwell et al. 1998). δ^{13}C is typically applied to distinguish isotopically distinct food webs, which allow tracing of energy flow and foraging habitat. For example, in the Beaufort-Chukchi Sea region, Dunton et al. (1985) discovered a longitudinal δ^{13}C gradient in zooplankton, which are more ^{13}C-depleted in the west, possibly due to large inputs of terrestrial carbon from the Mackenzie River (Saupe et al. 1989; Schell et al. 1998). This δ^{13}C gradient appears to be a robust and persistent feature spanning the migratory route of the western bowhead whales (e.g., Pomerleau et al. 2014b, 2016). A west to east decline in δ^{13}C has not been found in the Canadian Arctic Archipelago,

and regional $\delta^{13}C$ variation in zooplankton in the Eastern Canadian Arctic is less pronounced (Pomerleau et al. 2011b, 2016).

Previous studies have shown that stable isotope ratios along baleen plates provide insight into seasonal movements between feeding grounds (Schell et al. 1989a, b; Hobson and Schell 1998; Caraveo-Patiño et al. 2007; Bentaleb et al. 2011; Ryan et al. 2013; Eisenmann et al. 2016). For instance, the seasonal shift in stable isotope values evident in Southern right whale (*Eubalaena australis*) baleen indicates an annual migration over the south Atlantic convergence (Best and Schell 1996). Hobson and Schell (1998) found no evidence of $\delta^{13}C$ oscillations in bowhead whale baleen from three whales of the EC–WG population but found $\delta^{15}N$ oscillations which they thought could possibly be related to annual migrations. Recently, Matthews and Ferguson (2015) analyzed 14 plates and found synchronous cycles in both $\delta^{15}N$ and $\delta^{13}C$ along the baleen plates of bowhead whales from the EC–WG population, which they linked to movements between isotopically distinct summer and winter habitats.

Mercury (Hg) is a persistent and global pollutant (Dietz et al. 2011; Pacyna et al. 2016) that also deposits in whale baleen (Hobson et al. 2004). Mercury enters the Arctic via several pathways (i.e., atmospheric deposition, riverine transport, ocean currents), which are influenced by various environmental factors including climate variability and sea-ice processes (Stern et al. 2012). To date, few studies have measured Hg and stable isotopes concurrently in baleen plates to investigate whether foraging occurs year-round. A recent study by Pomerleau et al. (2016) found large pan-Arctic regional variations in Hg concentrations at the base of the food chain that were related to regional ecosystem features, such as varying water masses and freshwater inputs, and highlighted an increased exposure to Hg in the marine food chain of the southern Beaufort Sea. Analysis of individual bowhead whale baleen plates has the potential to provide a biogeochemical record of the whale dietary exposure to Hg throughout their geographical range.

In this study, we present total Hg concentrations and $\delta^{13}C$ and $\delta^{15}N$ isotopic compositions along baleen plates taken from eight individual bowhead whales from the BCB and the EC–WG populations. We examine the biogeochemical profiles along the plates to assess relationships between properties within plates; regional differences between bowhead populations; and evidence for seasonal cycling reflecting foraging patterns. The main objective is to assess whether bowhead whales forage year-round, as proposed in recent studies (e.g., Schell and Saupe 1993; Matthews and Ferguson 2015).

Materials and methods

Baleen collection and preparation

Bowhead whale baleen plates ($n = 8$) were collected from four individuals from the BCB population (1988–1996) and from four individuals from the EC–WG population (1996–1998) (Fig. 1). BCB bowhead samples were composed of three males and one female harvested by the Alaskan Inupiat (Table 1). The samples from the EC–WG population, comprising two males, one female, and one individual of unknown sex, were harvested by Inuit hunters or recovered from carcasses found on land (Table 1). A detailed description of each embedded baleen plate extraction and preparation can be found in Schell et al. (1989a) and in Hobson and Schell (1998). Briefly, algae films and other debris were removed from 0.8- to 3-m-long baleen plates using steel wool and a 2:1 chloroform–methanol solvent. Using a measuring tape, each baleen plate was sampled at intervals of 2.5 cm from the base (newest) to the tip (oldest) of each

Table 1 Bowhead whale (*Balaena mysticetus*) baleen sample list

Whale ID	Location	Month/year	Cause of death	Sex	Body length (m)	Baleen length (m)
BCB						
90B5	Barrow (AK)	05/1990	Hunt	Female	15.9	2.79
88WW3	Wainwright (AK)	06/1988	Hunt	Male	13.4	2.07
88B10	Barrow (AK)	09/1988	Hunt	Male	15.1	3.02
9601	Shingle Point (CA)	07/1996	Hunt	Male	11.2	1.68
EC–WG						
9602	Repulse Bay (CA)	08/1996	Hunt	Male	14.9	2.84
9603	Cape Dorset (CA)	08/1996	Unknown	Female	8.9	0.78
9801	Pangnirtung (CA)	07/1998	Hunt	Male	12.8	2.50
IB01	Isabella Bay (CA)	Unknown	Unknown	NA	NA	0.85

BCB Bering–Chukchi–Beaufort population, *EC–WG* Eastern Canada–West Greenland population

plate (see Fig. 2) using a high-speed flexible-shaft engraving device along the outside edge of the plate. This sampling interval provided sub-seasonal temporal resolution (Schell et al. 1989b).

Stable isotope analysis

Approximately 1.5–2.0 mg of powdered baleen material was loaded into tin cups and combusted in an elemental analyzer at 1800 °C. Bulk stable isotopes of $\delta^{13}C$ and $\delta^{15}N$ (the latter was measured in the EC–WG plates and one BCB plate) were measured using a continuous-flow isotope ratio mass spectrometer (CFIRMS) at the University of Alaska Fairbanks Stable Isotope Facility. Stable isotope ratios are expressed in delta (δ) notation, the normalized ratio of an unknown sample to an internationally accepted standard ($\delta^{15}N$ or $\delta^{13}C = ((R_{sample} - R_{standard})/R_{standard}) \times 1000$, where R is $^{15}N/^{14}N$ or $^{13}C/^{12}C$. The standard was atmospheric N_2 for $\delta^{15}N$ and VPDB for $\delta^{13}C$. Analytical error based on replicate analyses of samples and laboratory reference materials was within 0.2‰ for $\delta^{13}C$ and $\delta^{15}N$.

Determination of total mercury (Hg)

Dry samples of about 70 ± 30 mg were weighted precisely in Teflon containers, placed in an ultrasound bath for 15 min with 5 mL of diluted HNO_3 (0.2 N), rinsed with demineralized water, and sonicated again for 30 min in the same

acidic solution. After rinsing, the samples were maintained in dilute HNO_3 (0.2 N) for 12 h and rinsed once more with water. The samples, which remained visually intact throughout the treatment, were then mineralized with 2 mL of concentrated ultra clean HNO_3 on a block heater at 90 °C for 1 h. Once cooled, the digestates were diluted by adding 25 mL of demineralized water. Note that the samples were not reweighed prior to the digestion step with concentrated HNO_3 to avoid risk of contamination due to further manipulations.

The Hg concentrations were determined through external calibration by cold vapor atomic fluorescence spectrophotometry (CVAFS; Bloom and Fitzgerald 1988) using the equipment supplied by Tekran Instruments Corporation (Hg detector, Model 2500). The analysis proceeded in three steps: (i) the reduction of Hg(II) to volatile Hg(0) with $SnCl_2$, (ii) the pre-concentration of the produced Hg(0) by amalgamation on gold-coated sand, and (iii) the subsequent detection of the Hg thermally desorbed from the gold trap. Saturated Hg vapor was used for the calibration (Dumarey et al. 2010): a drop of Hg in was placed in an isolated bottle from which precise volumes (5–25 μL) of air containing Hg at saturation were removed with a gas-tight syringe as the temperature was noted. The concentration of saturated Hg vapor in air (Hg_V) expressed in amol (10^{-18} mol) per liter (L^{-1}) at a given temperature (T (expressed in °K)) was determined with $Hg_V = A\,e^{BT}$ (Beaudin et al. 2010), where A is 2.5456 amol L^{-1} and B is 0.082 T^{-1}. From this
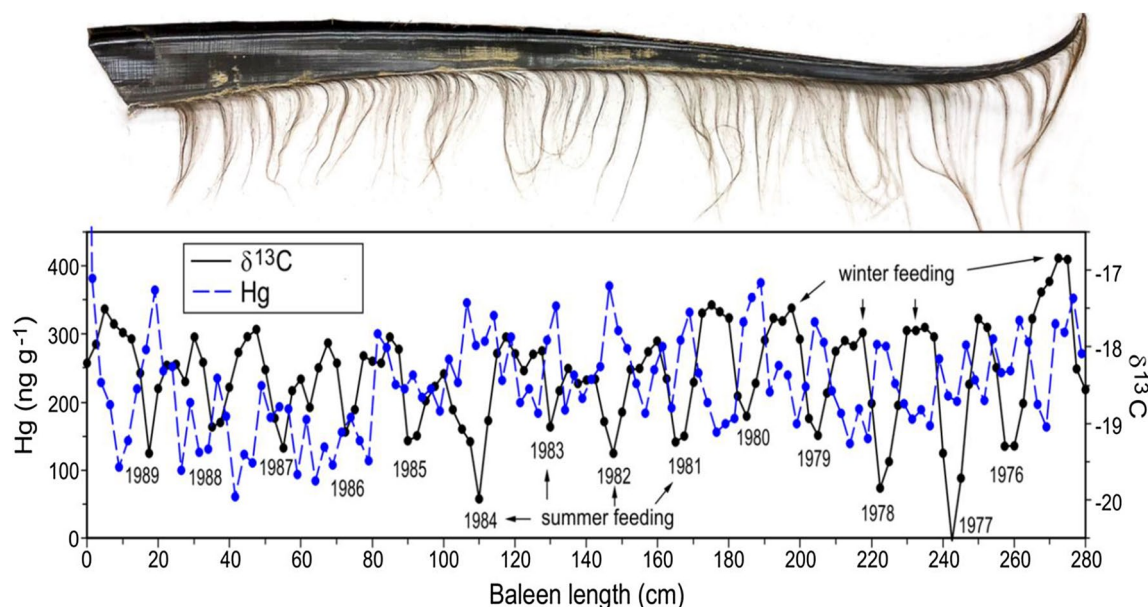

Fig. 2 A schematic diagram showing a representative baleen plate (top) and the record produced for $\delta^{13}C$ and mercury (Hg) by removing samples at intervals along the length of the baleen (bottom). The left (jaw) end of the baleen represents growth during the period just before the whale was caught. This record, which was obtained from a bowhead whale (*Balaena mysticetus*) from the BCB population, shows low $\delta^{13}C$ values reflecting summer feeding in the Beaufort Sea and higher $\delta^{13}C$ values reflecting winter feeding in the Bering Sea. The plate contains a record extending ~15 years preceding capture. Photo credit: DFO

empirical equation, it can be calculated, for example, that Hg_V is 0.6921×10^{11} amol L^{-1} (or 13.8 ng mL^{-1}) at 293 °K. The Hg concentration thus estimated is 4.2% lower than that calculated (14.4 ng mL^{-1}) for the same temperature using a slightly different equation recently proposed by Quetel et al. (2016). It is also close to the value (13.0 ng mL^{-1}) that can be obtained from the previous relationship proposed by Dumarey et al. (2010).

The precision and accuracy of our analyses were assessed by replicate analyses of human hair certified reference material GBW 09101 from the Shanghai Institute of Nuclear Research Academia Sinica. Subsamples of this material were digested in the same manner as the baleen samples using concentrated HNO_3. For $n = 20$ analyses over a 1-month period, we report an average Hg concentration of 2.13 ± 0.16 µg g^{-1} ($\pm$ SD) compared to the certified value of 2.16 µg g^{-1}. Our analytical precision and accuracy are thus estimated to be 7.5 and 1.4%, respectively.

Data analysis

Bowhead baleen grows at an approximately constant rate for individuals with a body length ≥ 12 m (Lubetkin et al. 2008). For the baleen taken from whales near or larger than 12 m (Table 1), the stable isotope and Hg profiles were analyzed as time series assuming that baleen growth rates were constant.

The series of measurements along the plates were first detrended using a Gaussian low pass filter (Park and Gambéroni 1995; Klvana et al. 2004) to extract short-term trends (e.g., seasonal cycling). Cycles in each variable within individual plates were examined using autocorrelation functions, and period lengths were estimated from peak spectral frequencies of high-order autoregressive (AR) models fitted to detrended profiles (Shumway and Stoffer 2011). Cross-correlation functions (CCF) were used to assess relationships between each combination of variables (Hg, $\delta^{13}C$, $\delta^{15}N$) across each individual plate. Analyses were conducted using the base functions and TSA package (Chan and Ripley 2012) in the statistical software R (R Core Team 2015).

Results

In general, baleen from whales in the BCB population had higher mean [Hg] (250.9 ± 120.1 ng g^{-1} (sd)) in comparison to the EC–WG population (141.4 ± 77.3 ng g^{-1}) (Fig. 3). Among all 378 baleen subsamples from the BCB population, [Hg] ranged from 32.5 to 593.7 ng g^{-1}, $\delta^{13}C$ from -23.5 to $-16.9‰$ and $\delta^{15}N$ from 12.7 to 16.0‰ (Fig. 3). The 277 baleen subsamples from the EC–WG population [Hg] ranged from 2.3 to 334.7 ng g^{-1}, the $\delta^{13}C$ from -19.6 to $-16.2‰$ and $\delta^{15}N$ from 11.5 to 15.2‰ (Fig. 3).

All BCB whale baleen plates had Hg and $\delta^{13}C$ cycles, and $\delta^{15}N$ also cycled in the one plate for which it was measured (Fig. 4). Two main periods in the $\delta^{13}C$ records were detected in the four BCB whales: one shorter period of 5.9–9.3 cm in length and a longer period of 16.9–21.0 cm. $\delta^{15}N$ also cycled in baleen from whale 9601, the only BCB plate for which it was measured, with an estimated period (17.6 cm) that was comparable to both the $\delta^{13}C$ and Hg cycles along that same plate (18.8 and 18.2 cm, respectively) (Table 2).

Similar to $\delta^{13}C$, spectral frequencies of modeled Hg oscillations also exhibited two main periods in all four whales: a shorter one ranging from 6.0 to 7.4 cm, and a longer period ranging from 15.5 to 18.5 cm (Table 2). The cross-correlation functions indicated that $\delta^{13}C$ and Hg patterns along the baleen plates were largely synchronous and exhibited an inverse relationship between the two variables in all four baleen plates (Fig. 4).

All EC–WG whale baleen plates had Hg, $\delta^{13}C$, and $\delta^{15}N$ cycles along their lengths (Fig. 5). High-order autoregressive models, fit to three of four detrended $\delta^{13}C$ profiles, revealed a longer period in the plate from whale 9801 (21.0 cm) and shorter periods for plates from whales 9602 and IB01 (13.4–14.1 cm) (Table 2). High-order autoregressive models fit to all four detrended $\delta^{15}N$ profiles revealed one main period (14.0–16.0 cm) (Table 2).
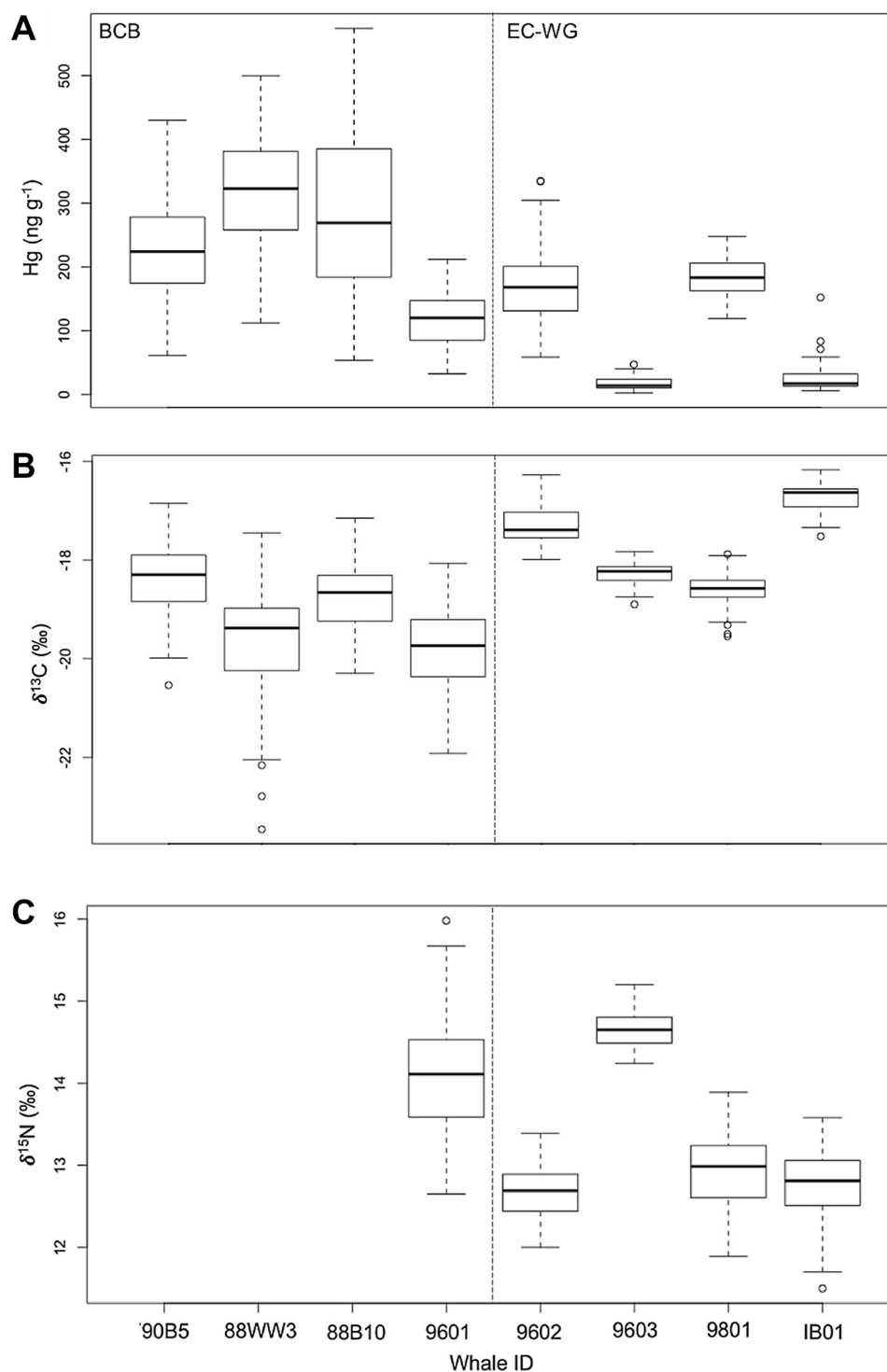
High-order autoregressive models were fit to all four detrended Hg profiles, exhibiting two main periods: one ranging from 5.4 to 8.2 cm and a second one ranging from 10.0 to 14.1 cm (Table 2). A longer period was also found for plates from whales 9603 and 9801 (20.7 and 21.7 cm, respectively). Strong positive cross-correlation functions were found between $\delta^{15}N$ and $\delta^{13}C$ in two plates (9602 and 9801), together with an inverse relationship between Hg and both $\delta^{13}C$ and $\delta^{15}N$ in one plate (9801) (Fig. 5).

Discussion

Seasonal cycling: BCB and EC–WG individual whales

The longer synchronous Hg and $\delta^{13}C$ cycles identified in all BCB whales are approximately the same as annual baleen growth rates (Lubetkin et al. 2008), and are consistent with foraging and seasonal migration between isotopically distinct food webs, with low Hg levels and higher $\delta^{13}C$ peaks in winter (Bering and Chukchi Seas) and higher Hg levels and $\delta^{13}C$ troughs in summer (Eastern Beaufort Sea). Mercury uptake appears to be more important on summer feeding grounds where more elevated values have been detected, especially in individual whales from the BCB population. Only a handful of studies have been conducted on the seasonality of Hg in the polar environment. Recently, Nerentorp-Mastromonaco et al. (2016) found that average

Fig. 3 Inter-individual variations in **a** mercury (Hg), **b** δ^{13}C and **c** δ^{15}N for 8 individual bowhead whales (*Balaena mysticetus*) from both populations (BCB left panel, EC–WG right panel). Each black line, white box, and whiskers outside the box represent the median, the lower/upper quartiles, and the minimum/maximum values, respectively. White dots represent outliers

elemental Hg levels were lower in the environment (e.g., sea ice, snow, seawater) in winter while levels increased over spring and summer (e.g., after polar sunrise and the onset of mercury depletion events, see Stern and Macdonald 2005). They attributed this trend to multiple factors such as atmospheric deposition, temperature, and solar radiation. In the Canadian Beaufort Sea, calanoid copepods have

been found to exhibit lower Hg concentrations during winter (~ 0.02 to 0.06 µg g^{-1}) than during open-water season (0.04–0.127 µg g^{-1}) (Stern and Macdonald 2005; Loseto et al. 2008). However, it is important to note that the year-long study conducted by Stern and Macdonald (2005) was part of the SHEBA drift program, which commenced in the Canada Basin/Beaufort Sea in October, 1997 and drifted
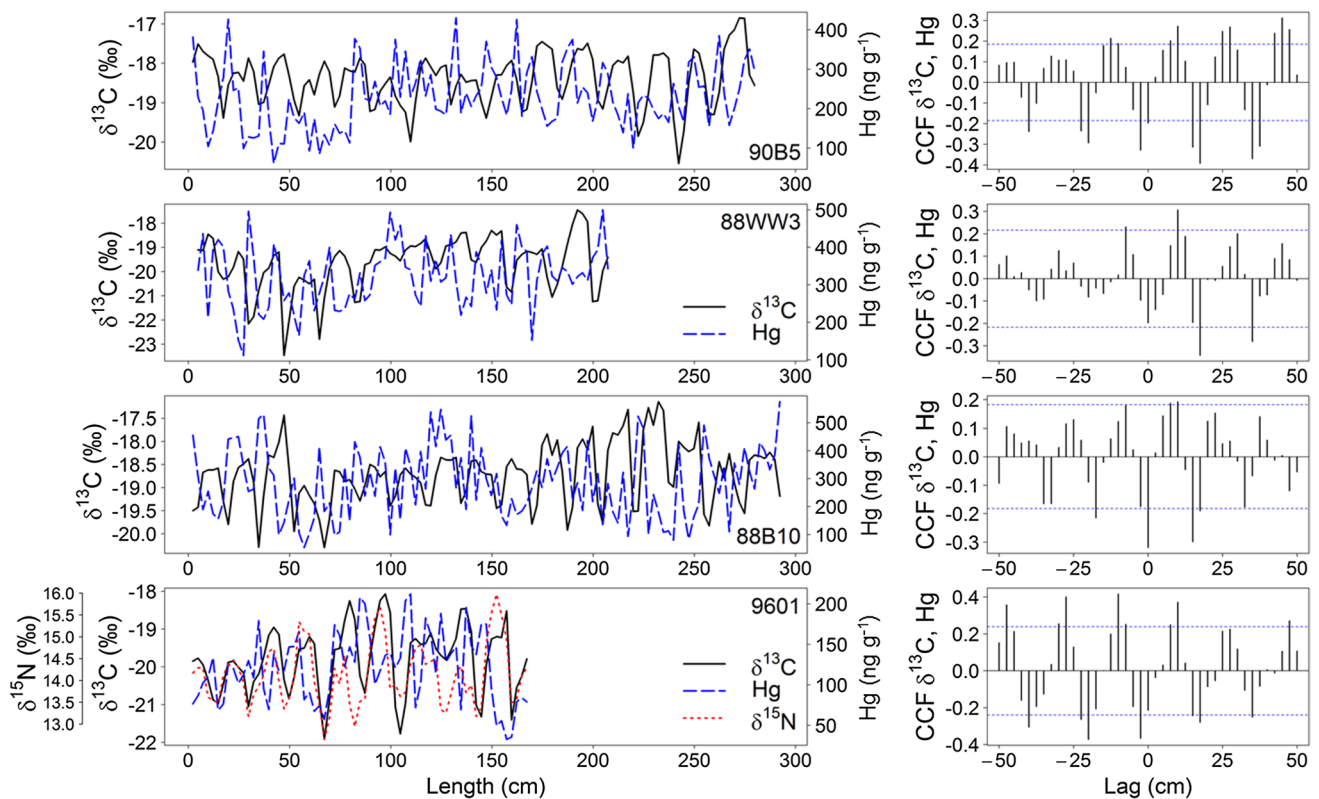
Fig. 4 Mercury (Hg) and δ^{13}C profiles (not detrended) along baleen plates, with sample cross-correlation functions (CCF) between detrended δ^{13}C values and Hg in four Bering–Chukchi–Beaufort (BCB) bowhead whales (*Balaena mysticetus*). The CCF is the set of sample correlations between $\delta^{13}C_{t+h}$ and Hg$_t$, where t = the same sample (lag 0) and $h = \pm 2.5$ cm, ± 5 cm, ± 7.5 cm, etc. 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. Negative correlations at 0 or lag -2.5 cm, with cycling apparent every 6–7 samples (15–17.5 cm), indicate an inverse relationship between δ^{13}C and Hg cycles

Table 2 Periods of δ^{15}N, δ^{13}C, and mercury (Hg) cycles along baleen plates of Bering Chukchi Beaufort (BCB) and Eastern Canada–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

Population	Whale sample ID	δ^{15}N period (cm)	Model order (p)	δ^{13}C period (cm)	Model order (p)	Hg period (cm)	Model order (p)
BCB	90B5	Not measured		9.3, 18.8	AR (16)	6.0, 17.0	AR (13)
	88WW3	Not measured		5.9, 8.8, 19.4	AR (8)	6.3, 9.2, 13.8, 18.5	AR (17)
	88B10	Not measured		8.4, 16.9	AR (12)	6.3, 15.5	AR (14)
	9601	17.6	AR (9)	18.8	AR (14)	7.4, 11.2, 18.2	AR (13)
EC–WG	9602	5.6, 14.0, 29.1	AR (14)	14.1	AR (11)	5.4, 14.1	AR (15)
	9603	16.0	AR (3)	Not detected		6.3, 10.0, 20.7	AR (6)
	9801	21.7	AR (7)	21.0	AR (7)	8.2, 12.9, 21.7	AR (9)
	IB01	8.2, 14.1	AR (5)	6.3, 13.4	AR (4)	5.5, 10.5	AR (8)

westward to eventually reach the Chukchi Abyssal Plain and Mendeleev Basin in October, 1998. On examining their THg and MMHg data in the context of the oceanographic features along the drift track, Stern and Macdonald concluded that variation in zooplankton Hg concentration along the track primarily reflected ocean structure; Beaufort Sea/Canada Basin samples were approximately twofold higher in Hg than Chukchi Sea samples.

In a more recent paper, Loseto et al. (2015) examined data for western beluga (*Delphinapterus leucas*) populations, which, like bowhead whales, migrate annually between the Bering and Beaufort Seas. After removing the effects of
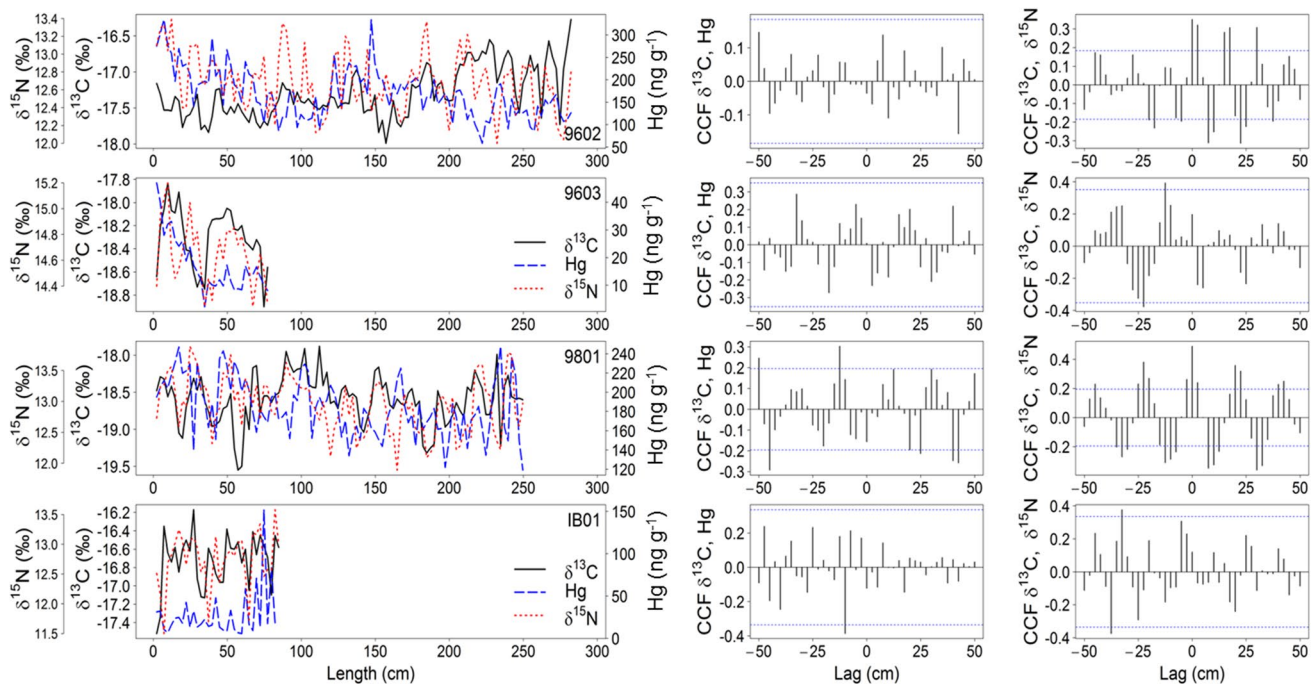
Fig. 5 Mercury (Hg), δ^{13}C, and δ^{15}N profiles (not detrended) along baleen plates and sample cross-correlation functions (CCF) between detrended δ^{13}C values and Hg and detrended δ^{13}C and δ^{15}N values in four Eastern Canada–West Greenland (EC–WG) bowhead whales (*Balaena mysticetus*). See Fig. 4 legend for explanation of CCFs, which show a less obvious relationship between δ^{13}C and Hg in EC–WG whales than BCB whales, but positive correlations between δ^{13}C and δ^{15}N at or near lag 0 (indicating largely synchronized cycling)

age and dietary factors, Loseto et al. (2015) found residual trends in Hg with time that could not be explained by recent declines in anthropogenic Hg emissions. They concluded that the observed biogeographical differences in zooplankton Hg concentration coupled with decadal variation (e.g., Pacific Decadal Oscillation) offered a more plausible explanation. With respect to our bowhead baleen data, the pattern of higher [Hg]/lower δ^{13}C when animals were foraging in the Beaufort Sea conforms to the dominant biogeographic distribution found by Stern and Macdonald (2005). Unlike the δ^{13}C data base, we do not yet have sufficient temporal data for the Beaufort and Bering populations to say whether or not the large-scale Hg differences between these seas are perennial, but a long-standing puzzle has been the observation that western Arctic (Beaufort Sea) populations are more exposed to Hg than populations in the eastern Archipelago and Baffin Bay (Brown et al. 2018). This higher Hg exposure could be due to a number of factors including atmospheric deposition, or the intensity of Hg methylation within Beaufort Sea subsurface waters (e.g., see Wang et al. 2012).

The food web utilized by bowhead whales from the BCB population in summer is characterized by well-documented depletion in δ^{13}C values (e.g., Dunton et al. 1985; Schell et al. 1989a, 1998; Stern and Macdonald 2005; Pomerleau et al. 2014b) that may possibly derive from the large amount of terrestrial/riverine dissolved organic carbon supplied by

the Mackenzie River and other smaller Arctic rivers (Gordeev et al. 1996; Lobbes et al. 2000). On the other hand, zooplankton isotopic signatures from the Bering Sea and Bering Strait areas are more ^{13}C-enriched than those from the Eastern Beaufort Sea, as values increase along an east-to-west gradient (Dunton et al. 1985; Pomerleau et al. 2014b). Bowhead stomach content analysis (Sheffield and George 2009) found that winter feeding in the Bering Sea, especially near St. Lawrence Island, was significant given that over a third of the samples analyzed contained food (mainly copepods).

Similar to BCB bowhead whale baleen plates, the EC–WG plates exhibited Hg, δ^{13}C, and δ^{15}N cycles consistent with annual baleen growth and reflecting seasonal foraging patterns. The synchronized cycles in all three variables were noted in the two whales with the longest plates, with peak values in isotopic ratios during summer feeding. Fasting physiology, at least as we understand it from studies of other animals in negative protein balance, cannot explain these nitrogen isotope trends. Animals deprived of enough protein to meet daily metabolic requirements display higher δ^{15}N values in their tissues, which is thought to reflect ^{15}N enrichment as they catabolize endogenous protein stores. However, higher δ^{15}N values in the baleen of EC–WG whales occurred in the most recently grown baleen in summer, when they are known to feed heavily on zooplankton blooms. Recent studies such as Aguilar et al. (2014) and

Matthews and Ferguson ([2015]) observed a similar pattern of ^{15}N enrichment in summer in baleen plates of a larger sample of EC–WG bowhead whales and in fin whales (*Balaenoptera physalus*), respectively, that are also contrary to the proposal that fasting leads to higher δ^{15}N values (e.g., Best and Schell [1996]; Cherel et al. [2005]; Lee et al. [2012]). It is more likely that summer feeding in regions with different baseline values or different types of prey led to depletion in ^{15}N (e.g., Aguilar et al. [2014]). The stable isotope ratios of bowhead whales' main zooplankton prey (*e.g.*, *Calanus* spp.) are known to vary spatially and/or temporally within their Eastern Arctic range (Hobson et al. [2002]; Pomerleau et al. [2011b]). The seasonal cycling observed in the isotopic ratios of the baleen plates is probably related, in part, to the geographic variability in the isotopic signatures of zooplankton across the bowhead foraging domain. The well-described, perennial pattern of δ^{13}C depletion from west to east in the western arctic has been observed in sediments, several taxa of zooplankton and has been clearly linked to bowheads migrating (and feeding) longitudinally across this region (e.g., Schell et al. [1989a]; Stern and Macdonald [2005]). Analyzing different whales from the ones used in our study, Matthews and Ferguson ([2015]) found the amplitudes of both δ^{13}C and δ^{15}N along baleen of EC–WG whales were consistent with spatial differences in zooplankton across the region reported by Pomerleau et al. ([2011b]).

The records in the EC–WG whales were noisier making cycles less clear and likely reflecting more variable movement/migration patterns coupled with shorter distances and less isotopically distinct food webs. In the eastern Canadian Arctic, the paths of seasonal migrations and the locations of winter and summer grounds (Fig. [1]) of EC–WG bowhead whales are more variable than for the BCB population. For instance, a portion of the EC–WG population, mainly large adult females, travel across Baffin Bay in late winter to forage along the coast of West Greenland in spring (Heide-Jørgensen et al. [2003]; Laidre et al. [2007]) while another segment of the population overwinter in Hudson Strait, northern Hudson Bay and/or Cumberland Sound (Finley [1990]; Reeves and Mitchell [1990]). Similarly, summer feeding locations are variable and comprise various fjords and bays in the Eastern Canadian Arctic (e.g., Cumberland Sound, Foxe Basin, Lancaster Sound, Admiralty Inlet and Hudson Bay) (Koski et al. [2006]; Higdon and Ferguson [2010]). Previous satellite telemetry studies have also shown large inter-individual variability in seasonal movement (Heide-Jørgensen et al. [2003]).

Mercury levels in BCB and EC–WG whales

Our findings suggest that individual whales from the BCB population have a greater uptake of Hg on their summer feeding grounds. Several factors could contribute to the higher Hg concentrations observed in the western Arctic

bowhead baleen plates, which also contained lower δ^{13}C values. For example, the Mackenzie River, which supplies large amounts of terrigenous organic carbon with low δ^{13}C is also known to supply Hg to the Eastern Beaufort Sea in summer (Leitch et al. [2007]; Andersson et al. [2008]; Emmerton et al. [2013]). Although the underlying cause(s) remain unclear, it has long been observed that biota from the Canadian western Arctic exhibit higher Hg concentrations than their eastern Arctic counterparts (e.g., Braune et al. [2014]). A recent study by Pomerleau et al. ([2016]) found increased exposure to Hg in the marine food chain of the southern Beaufort Sea together with more depleted δ^{13}C in zooplankton (bowhead whales' prey) from that region compared to other pan-Arctic locations. High Hg concentrations have been found in the Beaufort Sea beluga whale population, which forages in that region during summer (Loseto et al. [2008], [2015]). Furthermore, polar bears (*Ursus maritimus*) and ringed seals (*Pusa hispida*) also show higher Hg exposure in the Eastern Beaufort Sea compared to other Arctic regions (AMAP [2011]).

Concentrations of Hg were lower for EC–WG individual plates compared to the BCB plates. In the Eastern Arctic, there is no known large primary source of Hg to the marine environment like the Mackenzie River in the Northwest Territories. However, Hg enters the Arctic via a range of processes including long-range atmospheric transport and deposition, coastal erosion and riverine transport and inflowing ocean currents (Macdonald et al. [2005]; Stern et al. [2012]). Kirk et al. ([2012]) suggested that the long-range transport of Hg from Asian countries represent a dominant source of atmospheric Hg to the Arctic. But it is important to note that differences in Hg methylating processes between ocean regions, associated with differences in respective carbon cycles, may be as important, or more important, in determining the concentrations of Hg accumulated by whales, than differences in the supply of Hg from atmospheric deposition or river inflow (Macdonald and Loseto [2010]).

Shorter periods: BCB and EC–WG individual whales

The shorter Hg and δ^{13}C cycles along the baleen plates of all whales in our study, spanning about half the annual growth, have not previously been described in the baleen of these populations (Fig. [1]). These signals may reflect feeding in isotopically different regions while migrating during the spring and fall. Both the BCB and EC–WG populations migrate seasonally across their ranges between winter and summer grounds. As shown in Fig. [1], BCB bowhead whales generally travel north of their main wintering ground in the Bering Sea during the spring migration and usually pass northeast of Point Barrow along the Alaskan coast towards Canada from late April through June (Moore et al. [2010]), although some whales have also been observed to travel up the northern coast of Chukotka in the spring (Citta et al.

2012). In the fall, BCB bowheads migrate back to the Bering Sea by traveling along the Alaskan coast and southwest towards the Chukotka Peninsula (Harwood and Borstad 1985; Quakenbush et al. 2010). About a third of the bowhead whale stomach samples analyzed from spring harvest in Barrow were found to contain food (Lowry et al. 2004). Similarly, bowhead whales travel past Barrow again in the fall, from late September through October. Fall feeding in that region has also been documented through the analysis of stomach contents of freshly harvested whales and has been described as generally more intensive than feeding in the spring (Moore et al. 2010).

EC–WG bowhead whales are also known to use key feeding sites outside the main summer feeding season. Disko Bay, along the coast of West Greenland, is a well-known late winter-early spring feeding ground for bowhead whales foraging primarily on *Calanus* spp. (Laidre et al. 2007; Simon et al. 2009). In the Eastern Canadian Arctic, Finley (1990) suggested that a major part of the energetic requirement of EC–WG bowhead whales during the fall season derives from foraging on large concentrations of mature stage diapausing calanoid copepods in area such as Isabella Bay along the east coast of Baffin Island. Detailed analysis of Hg and SI spatial variation in these foraging areas relative to the summer and winter ranges would help to confirm our interpretation.

Conclusion

Using Hg in addition to $\delta^{13}C$ and $\delta^{15}N$ measured along baleen plates, we found that individual whales from western and eastern populations feed year-round throughout their respective geographic ranges, but the nutritional contribution of winter foraging remains unclear. The previously unreported shorter periods of $\delta^{13}C$, $\delta^{15}N$, and Hg suggest foraging in spring and fall, either along migration routes or in key areas where bowhead whales have been observed feeding in late fall. The seasonal pattern was stronger (clearer) in the BCB whale baleen. The EC–WG whale baleen exhibited more muted seasonal cycles, probably reflecting more variable migration routes and/or less contrast in foodweb properties between foraging locations.

The characterization of the Hg load in individual bowhead whales from ~ 1960 to 1998 in our study can be compared with future studies to determine how or if mercury loadings to these animals are affected by climate change and the resulting increase in industrialization of the Arctic. Given the rate of change now occurring in Arctic seas, and especially in the nearshore habitats important to migratory species like bowhead whales, it seems all the more urgent to develop time series taking advantage of media like baleen, which have the potential to produce records of foraging and reproduction for individuals for periods spanning as much

as 25 years (e.g., Hunt et al. 2014; Solazzo et al. 2017). Although complex, these records have the potential to reveal changes in food webs and consequent changes in whale foraging.

Compliance with ethical standards

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