

Using Stable Isotopes in Baleen to Examine Migratory Behavior of Bering-Chukchi-Beaufort Sea Bowhead Whales (*Balaena mysticetus*): A pilot study

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ABSTRACT

We analyzed stable-carbon ($\delta^{13}\text{C}$) and -nitrogen ($\delta^{15}\text{N}$) isotopes of baleen from bowhead whales (*Balaena mysticetus*) harvested at St. Lawrence Island (SLI) and Barrow, Alaska, to investigate the possibility of a non-migratory group of whales within the Bering-Chukchi-Beaufort seas (BCBS) stock. The distribution patterns of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ along the lengths of baleen were grossly similar for the two groups. The mean $\delta^{13}\text{C}$ values of baleen from SLI and Barrow were significantly different within and between groups. The oscillating pattern of $\delta^{13}\text{C}$ values in SLI baleen was likely attributed to feeding in both, thus migration between, the Bering/Chukchi and Beaufort Seas. The baleen $\delta^{15}\text{N}$ values provided little evidence for fasting in either SLI or Barrow whales. When the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data were examined in unison, they suggested that feeding and fasting bouts (i.e., by a non-migratory group of bowhead whales) could not produce the patterns of isotope distributions found in the SLI-harvested whales. Therefore, we concluded that stable isotope values of baleen from SLI bowheads examined in this study provided evidence for migratory behavior.

INTRODUCTION

Knoche et al. (2006) reported new data on stable-carbon ($\delta^{13}\text{C}$) isotopes of baleen from recently harvested bowhead whales (*Balaena mysticetus*) at St. Lawrence Island (SLI), Alaska, and found evidence for migratory behavior. Oscillations of $\delta^{13}\text{C}$ in baleen from bowheads landed at St. Lawrence Island (SLI) were remarkably similar to those patterns found in baleen from bowheads killed at Barrow, Alaska (Schell and Saupe, 1993), providing evidence for migration between the Bering/Chukchi and Beaufort Seas (Moore and Reeves, 1993). However, in 2006 the International Whaling Commission's Scientific Committee requested that additional research investigating the relationship between periodic fasting/feeding and migratory behavior in whales be conducted. The committee was concerned that fasting/feeding bouts could produce similar isotopic patterns in a non-migratory population of bowheads that resided in the Bering/Chukchi region (i.e. a sub stock) (Rugh et al., 2003; IWC, 2006).

Stable isotope analyses of protein-based tissues can be used to examine migratory movements (Schell and Saupe, 1993; Best and Schell, 1996; Hobson and Schell, 1998; Hobson 1999; Mitani et al., 2006), feeding behaviors (Hobson et al., 1997; Hobson and Sease, 1998; Born et al., 2003), and nutritional status (Hobson et al., 1996; Polischuk et al., 2002) of marine mammals. Stable-carbon and -nitrogen ($\delta^{15}\text{N}$) isotopes from protein in the diet are assimilated into newly formed protein-based tissues in a predictable manner that indicates protein sources at the time of synthesis (Deniro and Epstein, 1978; 1981). For example, baleen plates from bowhead whales killed at Barrow had a marked oscillation in $\delta^{13}\text{C}$ values along their length that resulted from seasonal migration and feeding in the isotopically distinct regions of the Bering/Chukchi area and the Beaufort Sea (Schell and Saupe, 1993). Best and Schell (1996) hypothesized that sections of baleen from southern right whales (*Eubalaena australis*) with periods of prolonged, unchanged $\delta^{13}\text{C}$ values that occurred simultaneously with highly enriched ^{15}N composition likely indicated

fasting during the austral winter. Enrichment of protein-based tissues in the heavier ^{15}N isotope can indicate fasting and/or nutritional stress because organisms preferentially excrete lighter ^{14}N isotopes that result in a measurable net increase of the heavier ^{15}N isotope in tissues after catabolic and anabolic processes (Hobson et al., 1993; Gannes et al., 1998; Podlesack and McWilliams, 2006). Stable-carbon and -nitrogen isotopes of baleen provided useful information regarding migration, feeding, and fasting by various species of whales in previous studies.

We analyzed stable carbon and nitrogen isotopes of baleen plates from whales killed at SLI with the objective of determining whether SLI whales use the full range of the Bering-Chukchi-Beaufort seas (BCBS) stock of bowheads. We statistically compared $\delta^{13}\text{C}$ values of baleen from SLI and Barrow whales to examine differences in patterns of carbon isotope distribution. The $\delta^{15}\text{N}$ composition of baleen was examined in relation to $\delta^{13}\text{C}$ values for evidence of fasting or nutritional stress that could produce isotopic distributions that may confound interpretations of migratory behavior.

METHODS

Baleen plates from six adult bowheads caught by hunters at SLI, Alaska, between 1998 and 2005 and six adult bowheads killed in the northeast Chukchi Sea and Beaufort Sea in 1986 and 1988 were sampled (Table 1, Fig. 1). Three of the six pieces of baleen from whales 86KK2, 86WW1, and 86WW2, from the Chukchi and Beaufort seas were also used in a previous study (Schell and Saupe, 1993). Bowhead samples from Kaktovik, Wainwright and Barrow, Alaska, are referred to as “Barrow” whales throughout the text. Whaling captains of the Alaska Eskimo Whaling Commission (AEWC), and biologists from the Alaska Department of Fish and Game or the North Slope Borough Department of Wildlife Management provided or collected the baleen.

Table 1: Individual, kill date, body and baleen lengths, and location of harvest from St. Lawrence Island (1998-2005) and Barrow (1986, 1988), Alaska.

Individual	Kill date	Sex	Length (m)		Location
			Body	Baleen	
01G2	12/5/01	M	15.4	3.05	SLI
02G2	12/5/02	F	16.2	2.75	SLI
05S3	4/22/05	M	14.0	2.48	SLI
05S4	4/22/05	M	14.1	2.58	SLI
05S5	11/29/05	F	16.5	2.7	SLI
05S6	11/29/05	F	17.1	3.0	SLI
86KK2	9/17/86	F	17.1	3.8	Kaktovik
86WW1	5/10/86	M	15.9	2.7	Wainwright
86WW2	5/10/86	F	17.7	3.1	Wainwright
88B9	9/15/88	M	14.6	2.6	Barrow
88B10	9/17/88	M	15.1	3.3	Barrow
88B11	9/17/88	F	15.6	3.2	Barrow

Baleen plates were cleaned using metal scrapers and/ or steel wool to remove non-keratinous tissues and rinsed with water. We sampled ~ 0.5g of baleen at 2.5 cm intervals along the outside edge of the plate using a dremel tool (Schell and Saupe, 1993). We obtained $\delta^{13}\text{C}$ and

$\delta^{15}\text{N}$ values of baleen using continuous flow stable isotope-ratio mass spectrometry (CFSI-RMS). Instrumentation and calibration follow procedures described by Knoche et al. (*In press*). Precision was $< \pm 0.16$ ‰ for $\delta^{13}\text{C}$ and $< \pm 0.4$ ‰ for $\delta^{15}\text{N}$.

We normalized the $\delta^{13}\text{C}$ data from baleen because it was collected nearly two decades apart. Schell (2000) recognized a declining trend in $\delta^{13}\text{C}$ values in baleen of 0.063% yr^{-1} over several decades in the Bering Sea. We corrected baleen $\delta^{13}\text{C}$ values with the following equation:

$$X = Y - (2005 - \text{year}) * 0.063\% \text{ yr}^{-1},$$

where X is the corrected average $\delta^{13}\text{C}$ value of peaks, Y is the mean of the $\delta^{13}\text{C}$ at an annual peak, and year represents the year of the oscillation. It follows that values from the first oscillation of baleen plates from whale killed in 2005 would not be changed.

We chose the ten highest (i.e., most enriched in ^{13}C) and ten lowest (i.e., most depleted in ^{13}C) from individual whales to statistically compare values within and between groups (i.e. SLI and Barrow). We assumed that sampling the ten highest and lowest peaks (years) would encompass the magnitude of potential differences and a sufficient number of years given the potential record of 20 years. The highest $\delta^{13}\text{C}$ values were likely acquired during fall or winter feeding in the Bering/Chukchi region and lowest in summer in the Beaufort Sea (Schell and Saupé, 1993). We believed that using only these values yielded a conservative test because it maximized the within group sums of squares. Therefore, if statistical significance were found using these values, it should surpass any reasonable threshold for significance. We performed ANOVA and t-tests for two groups using SYSTAT 10.2 to examine within-group (i.e. SLI or Barrow groups) and between-group variation, respectively. Descriptive analyses of the data revealed that the transformed $\delta^{13}\text{C}$ values were normally distributed. Means were reported ± 1 S.D.

Bouts of fasting or nutritional stress were tested indirectly by comparing the relationship of occurrences of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ peaks (e.g., Fig. 2). Peak $\delta^{15}\text{N}$ values were categorized as occurring (1) after, (2) coincident, (3) before, (4) no peak occurring, (5) occurring at $\delta^{13}\text{C}$ troughs or Beaufort signature, or (6) undetermined in relation to $\delta^{13}\text{C}$ peaks. We performed no statistical tests on the $\delta^{15}\text{N}$ data because stable-nitrogen isotope data is generally used to examine trophic position and often does not vary regionally (Owens 1987). Instead we examined peaks of occurrences relative to $\delta^{13}\text{C}$ values for each group specifically to examine fasting.

Differences between SLI whales (i.e. Gambell and Savoonga) and genders within group (i.e. Barrow and SLI) were not tested because of sample size constraints. We did not include baleen from immature/ young whales (i.e. $< 13\text{m}$ in length) (Koski et al., 1993) in the comparisons because the distribution pattern of stable-carbon and stable-nitrogen isotopes in young bowheads could be influenced by feeding in shallower waters than adults (Schell and Saupé, 1993) as immature whales may have alternate food sources there (Hazard and Lowry, 1984; Lowry, 1993). Similarly, higher baleen growth rates in immature whales and maternal nutritional contributions (i.e. milk) make the stable-isotope distribution patterns (Schell and Saupé, 1993) and signatures very different from adults (Jenkins et al., 2001; Dehn et al., 2007).

RESULTS

Baleen from SLI and Barrow whales demonstrated a marked oscillation of $\delta^{13}\text{C}$ values along their length (Fig. 3). Mean baleen $\delta^{13}\text{C}$ values were significantly different within SLI (ANOVA $F = 4.1$, $d.f. = 5$, $p < 0.002$) and Barrow groups (ANOVA $F = 4.5$, $d.f. = 5$, $p < 0.001$). Mean $\delta^{13}\text{C}$ values between Barrow and SLI baleen were significantly different using pooled variance t-tests ($t = 6.25$, $d.f. = 238$, $p = 0.0001$). Baleen $\delta^{13}\text{C}$ values from SLI whales ($n = 120$, Mean = -17.45 ± 2.01) were isotopically lighter than baleen from Barrow whales ($n = 120$, Mean = -18.82 ± 1.34)

There was also a marked oscillation in the $\delta^{15}\text{N}$ values along the baleen length (e.g., Fig. 2). Peak $\delta^{15}\text{N}$ values occurred after $\delta^{13}\text{C}$ peaks 15 % and 9 % of the time in SLI and Barrow

whales, respectively (Table 2). The majority of peak $\delta^{15}\text{N}$ values occurred before or coincidentally with peak $\delta^{13}\text{C}$ values (Table 2).

Table 2: The percentage of peak $\delta^{15}\text{N}$ values from baleen of St. Lawrence Island (SLI) and Barrow whales scored as to where the isotopic peak occurred in relation to peak $\delta^{13}\text{C}$ values representing dietary intake in the Bering/Chukchi region. Peak $\delta^{15}\text{N}$ values were categorized as occurring as; (1) after, (2) coincident, (3) before, (4) no peak occurring, (5) occurring at $\delta^{13}\text{C}$ troughs or Beaufort signature, or (6) undetermined. BCBS whales are thought to cease feeding after the fall when $\delta^{13}\text{C}$ values reach oscillation peaks. If nutritional stress is occurring during this period, it is not evidenced by consistent peaks in $\delta^{15}\text{N}$ values from baleen occurring *after* $\delta^{13}\text{C}$ peaks in either group (see Best and Schell, Fig. 8).

Category	Location	
	SLI	Barrow
After	15 %	9 %
Coincident	32 %	42 %
Before	37 %	41 %
At $\delta^{13}\text{C}$ troughs	7 %	3 %
No $\delta^{15}\text{N}$ peak occurred	5 %	1 %
Undetermined	5 %	5 %

DISCUSSION

Distribution patterns of $\delta^{13}\text{C}$ values along the length baleen were similar in SLI and Barrow whales. Statistical comparisons of mean $\delta^{13}\text{C}$ values, however, revealed significant differences within and between SLI and Barrow baleen. Within group differences in SLI and Barrow baleen likely reflect individual variation associated with age (Hobson et al., 1993), tissue-specific isotopic routing and fractionation rates (Gannes et al., 1997), environmental factors (e.g., temporal and spatial prey abundance, availability, or type; ice extent and influence among years, etc.; Hobson, 1999; Kelly, 2000), and/or small sample size. The grossly similar patterns in the $\delta^{13}\text{C}$ distribution or oscillation between groups and their consistency with the findings of Schell and Saupe (1993), suggest the difference between means may be an artifact of small sample sizes and may not be biologically meaningful. It is implausible for SLI whales to exhibit the oscillating pattern of $\delta^{13}\text{C}$ if they remained in the Bering Sea throughout the year. The Bering Sea and other areas adjacent to the Bering Sea, other than the Beaufort Sea, do not contain an isotopic gradient sufficient to produce the observed oscillation (Dunton et al., 1989; Saupe et al., 1989; Schell et al., 1998). Furthermore, whales that do not migrate between distinct isotopic regimes, such as the Hudson Bay stock of bowhead whales, do not show marked oscillations in $\delta^{13}\text{C}$ value along the length of their baleen but instead have a characteristically “flat” signature (Hobson and Schell, 1998). Isotopic oscillations in baleen as a result of regional feeding or migratory behavior have been observed in southern right whales (*Eubalaena australis*) (Best and Schell, 1996), gray whales (*Eschrichtius robustus*) (Caraveo-Patino and Soto, 2005), and common Minke whales (*Balaenoptera acutorostrata*) (Mitani et al., 2006). The ubiquitous oscillation $\delta^{13}\text{C}$ pattern of baleen from SLI whales most likely supports their migration between and feeding in the Bering Sea in winter and the Beaufort Sea in summer.

Differences between mean $\delta^{13}\text{C}$ values of baleen from SLI and Barrow provide further support for migratory behavior. The mean $\delta^{13}\text{C}$ values of baleen from SLI whales were more negative or isotopically “lighter” than those from Barrow whales. Prey items such as euphausiids are more commonly found and consumed by whales in the Bering Sea and are more positive or

isotopically “heavier” than copepods which are abundant in the Beaufort Sea (Schell et al., 1998; Dehn et al., 2006). Thus, if SLI whales were non-migratory or residents of the Bering/Chukchi region we would have expected to find the opposite of our results; their mean $\delta^{13}\text{C}$ baleen values would have been isotopically heavier.

Examination of $\delta^{15}\text{N}$ in baleen may provide insights into whether or not whales have fasted (Best and Schell 1996, Hobson and Shell 1998). The $\delta^{15}\text{N}$ values of baleen from SLI and Barrow demonstrated annual oscillations along the baleen lengths occurring at a similar periodicity as the peak in $\delta^{13}\text{C}$. Typically, $\delta^{15}\text{N}$ values reflect an organism’s trophic position within a food web and, therefore, do not change under normal circumstances (Kelly 2000). However, changes in $\delta^{15}\text{N}$ may reflect dietary changes (Deniro and Epstein, 1981; Mitani et al., 2006) and increases may result from nutritional stress associated with fasting (Hobson et al., 1993; Polischuk et al., 2001; Cherel et al., 2005). The $\delta^{15}\text{N}$ values of known bowhead dietary items (e.g., euphausiids, copepods) do not differ between summer and winter areas (Schell et al., 1998) so it is improbable that diet produced the observed oscillation (Lee et al., 2005). Lee et al. (2005) suggested that Beaufort Sea summer-fasting or “near-fasting” produced a shift towards higher $\delta^{15}\text{N}$ values. Our results demonstrated that the majority of peak $\delta^{15}\text{N}$ values occurred at or before the same location on the baleen as peak $\delta^{13}\text{C}$ values for both groups. The simultaneous or near-simultaneous occurrence of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ peaks did not provide support for fasting because ^{13}C composition of tissues do not become enriched as a response to fasting, rather they remain constant or may deplete slightly (Hobson et al., 1993; Cherel et al., 2005). Baleen from southern right whales demonstrated elevated $\delta^{15}\text{N}$ values and prolonged, unchanged $\delta^{13}\text{C}$ values (i.e., flat) with the cessation of feeding (Best and Schell 1996, see Fig. 8). We did not observe this pattern in the baleen from the current study when fasting would presumably have occurred (according to Lee et al. 2005). Instead we observed concurrent enrichment of ^{13}C and ^{15}N in baleen that likely occurred during fall feeding. Though the increase of baleen $\delta^{13}\text{C}$ values in the fall can be attributed to changes in diet, the cause of the increase of baleen $\delta^{15}\text{N}$ values remains unknown. We could speculate that the increase may have resulted from feeding on prey not previously documented as bowhead dietary sources in the Bering/Chukchi region. As an example, Arctic cod had similar $\delta^{13}\text{C}$ but higher $\delta^{15}\text{N}$ composition than euphausiids in the Chukchi Sea (see Schell et al., 1998; Hoekstra et al., 2002) which could potentially produce the observed oscillation. When we considered the distribution patterns of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of baleen from in SLI whales in unison they did not provide support for fasting.

The findings of this study provided evidence that SLI bowhead whales exhibited similar migratory behavior to Barrow whales. The distribution pattern (i.e., the oscillation) and lighter means of $\delta^{13}\text{C}$ values suggested migratory behavior in the SLI whales from this study. When the distribution patterns of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in baleen were considered together, they did not suggest that feeding/fasting bouts could produce similar isotopic distribution patterns in a non-migratory population of bowheads that resided in the Bering/Chukchi region. The cause for the oscillating pattern of $\delta^{15}\text{N}$ values remains unknown and warrants further investigation. We have attempted to explore possible causes other than migratory behavior for the isotopic distributions observed in baleen from SLI and Barrow bowheads. However, given the known dietary sources, feeding and migratory behaviors, observed stable isotope gradients within the range of BCBS bowheads, alternative explanations were not well supported. Future studies will focus on increasing the number of baleen plates sampled from both locations, comparing isotopic values from metabolically active tissues, and improving statistical methodology.

ACKNOWLEDGEMENTS

We would like to thank the North Slope Borough, the National Oceanic and Atmospheric Administration, and the Alaska Eskimo Whaling Commission (AEWC) for funding this project. We are grateful to the hunters of the AEWC for providing us with baleen. Tim Howe and Norma Haubenstock performed the stable isotope analyses and provided technical assistance at the Alaska

Stable Isotope Facility, University of Alaska, Fairbanks. George Noongwook, Chester Noongwook, Merlin Koonooka (from St. Lawrence Island), and Gay Sheffield (Alaska Department of Fish and Game) were particularly helpful in procuring specimens for this study. Brandy Jacobsen and Link Olson provided access to baleen plates at the Museum of the North, University of Alaska, Fairbanks. Laura Phillips and Cheryl Rosa provided useful comments on previous versions of this report.

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Figure 1. Bowhead whale (*Balaena mysticetus*) sampling locations at St. Lawrence Island, Wainwright, Barrow, and Kaktovik, Alaska. Extent of Bering-Chukchi-Beaufort seas bowhead whales geographic range from the Bering Sea to the Eastern Beaufort Sea.

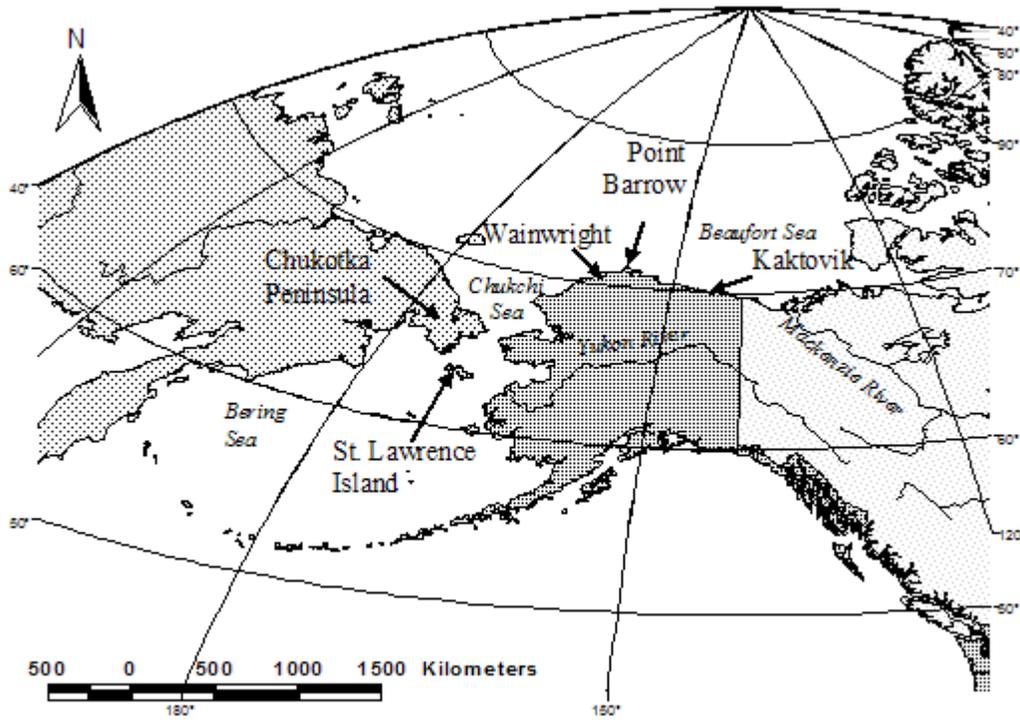


Figure 2. The oscillation patterns of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values along the length of baleen from whales 05S6 (SLI) and 86KK2 (Barrow). Peak occurrences of $\delta^{15}\text{N}$ values were compared to those of $\delta^{13}\text{C}$ values to examine potential fasting in SLI and Barrow bowhead whales. Vertical lines demonstrate the relationship of occurrence between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ peaks. The relationship was analyzed for each individual $\delta^{13}\text{C}$ peak and reported as percentage of occurrence (Table 2). Not all baleen data is shown.

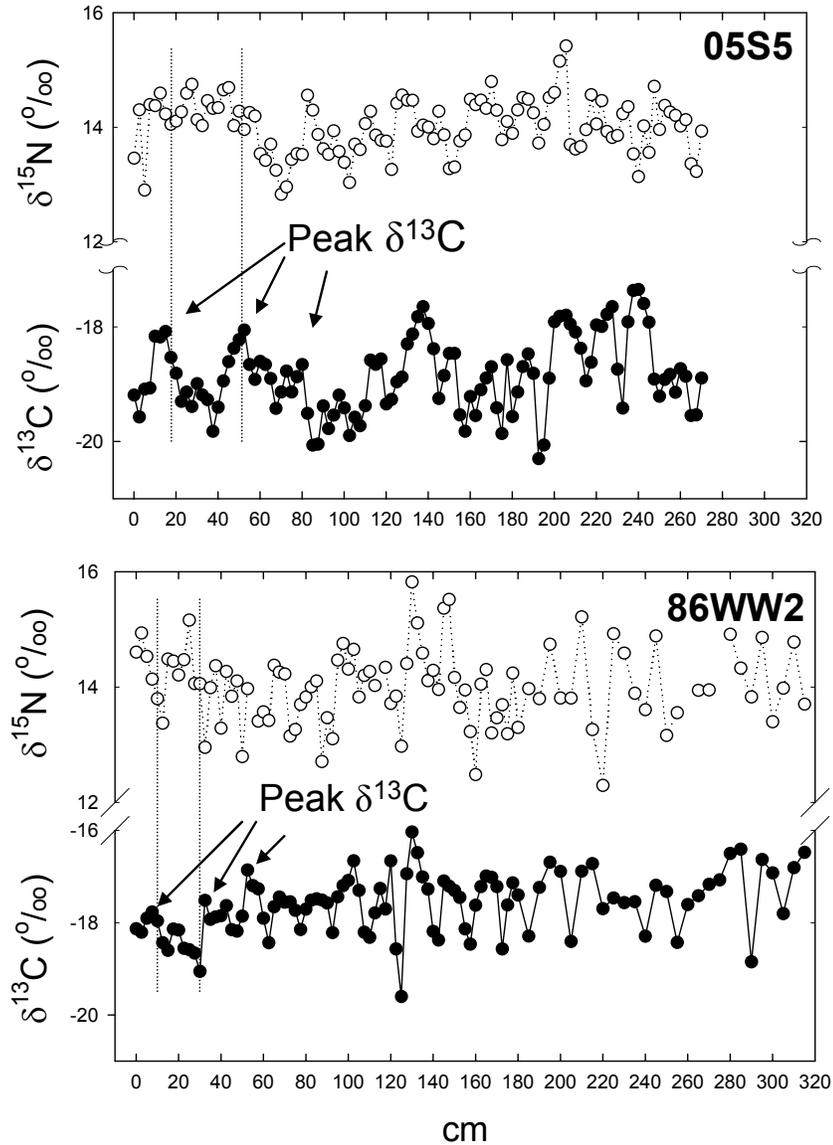


Figure 3. Stable carbon isotope values sampled at 2.5 cm intervals along the length of baleen plates from bowheads harvested at St. Lawrence Island and Barrow, Alaska. The horizontal line placed at -19‰ on the $\delta^{13}\text{C}$ axis is a reference to examine differences within and among individuals.

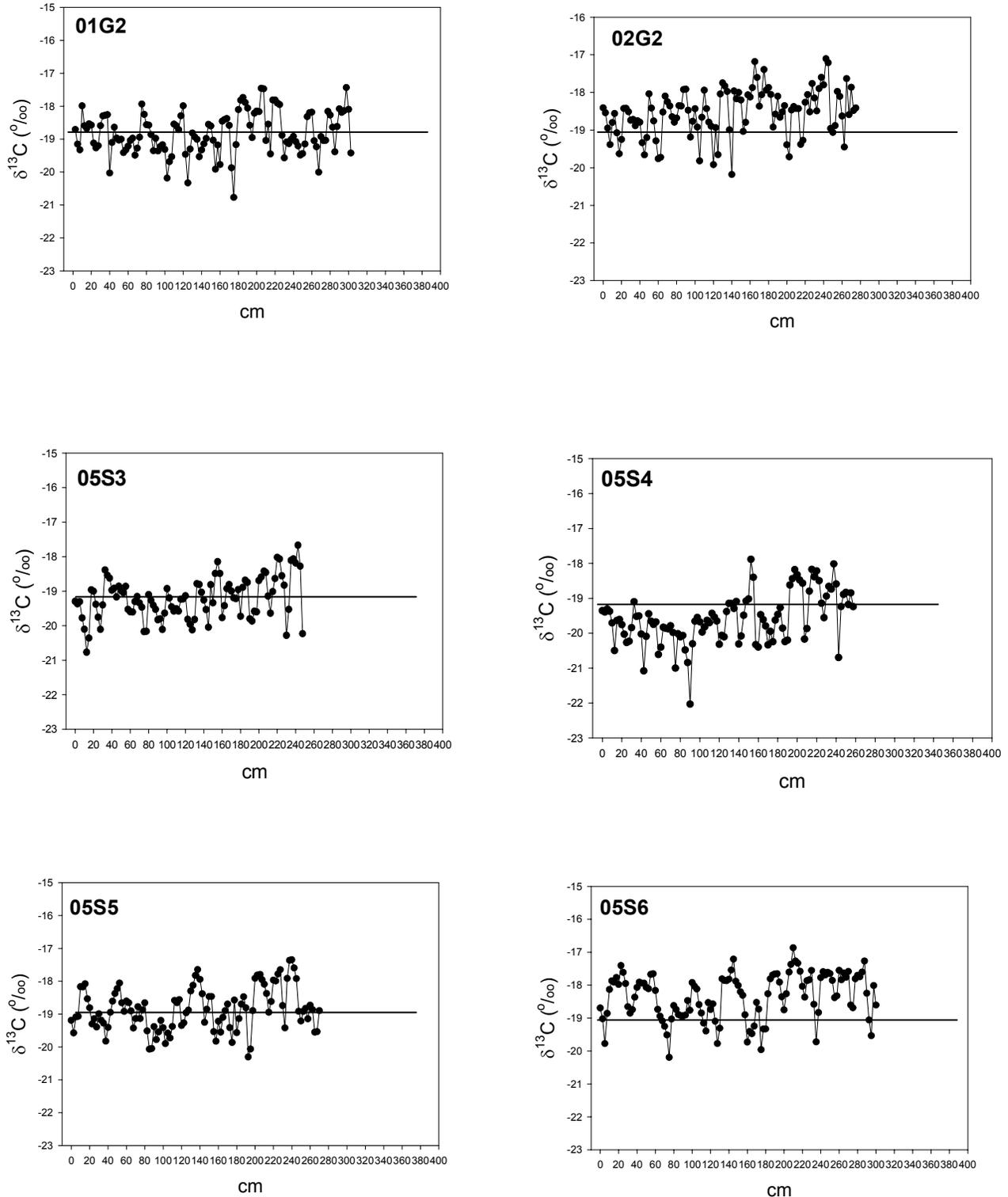


Figure 3. (concluded)

