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A note on geographic and seasonal fluctuations in the isotopic composition of baleen in four North Atlantic right whales (Eubalaena glacialis)

ERIN L. SUMMERS¹, JAMES A. ESTRADA² AND STEPHAN I. ZEEMAN²

Contact e-mail:erin.l.summers@maine.gov

ABSTRACT

Despite management efforts, studies suggest that the North Atlantic right whale (Eubalaena glacialis) population may still be in decline. Due to its endangered status and propensity for human interactions, it is critical that all habitats and migratory routes utilised by the right whale are identified and protected. We conducted incremental stable isotope analysis along the baleen plates of three North Atlantic right whales, an adult female, a juvenile male and a neonate male, showing seasonal oscillation patterns in $\delta^{15}N$ and $\delta^{13}C$ values associated with migrations between summer and winter habitats. The δ^{15} N and δ^{13} C values displayed seasonal variability with enriched values occurring in the winter and depleted during the summer. Comparisons with published values for a fourth adult female (NEAq1014) showed that summer values differed significantly between adults. While the small sample size prevents firm conclusions, these data suggest differential habitat use between adult individuals as well as age classes. Isotopic ratios from plankton in the Labrador Sea indicate that portions of the population may be utilising this habitat as an alternative summer feeding ground.

KEYWORDS: NORTH ATLANTIC RIGHT WHALE; MIGRATION, MOVEMENTS; FEEDING GROUNDS; HABITAT; NORTHERN HEMISPHERE

INTRODUCTION

Prior to the 15th century, right whales were abundant throughout the western North Atlantic, ranging from Florida to as far north as the southern waters of Greenland (Knowlton et al., 1992; Kraus and Brown, 1991; Kraus and Kenney, 1991; Winn et al., 1986). However, extensive whaling over the next four and a half centuries depleted these populations to recent estimates of 300 animals, making the North Atlantic right whale one of the most endangered species of baleen whales (IWC, 2001; Knowlton et al., 1994; Kraus et al., 2001). Despite management efforts, some studies suggest that the population may still be in decline (Caswell et al., 1999; IWC, 2001). Therefore, it is critical that all habitats and migratory routes utilised by the right whale are identified and protected.

Incremental stable isotope sampling along the length of the baleen is an effective way of tracing the migratory and feeding patterns of whales (e.g. Best and Schell, 1996; Hobson and Schell, 1998; Lee et al., 2005; Schell et al., 1989a; Schell et al., 1989b), as isotopic ratios in the baleen directly reflect the diet of the animal during the tissue's formation. Migratory related changes in δ^{13} C and δ^{15} N values have been reported in the Arctic bowhead whale, Balaena mysticetus (Schell et al., 1989a; 1989b) and the Southern right whale, E. australis (Best and Schell, 1996). Northern right whales are known to undergo annual migrations from calving grounds in Florida to feeding and nursery grounds in Cape Cod Bay (Hamilton and Mayo, 1990), the Great South Channel (Kraus and Kenney, 1991; Winn et al., 1986), the Bay of Fundy and Roseway Basin (Gaskin, 1987; Kraus et al., 1988; Murison and Gaskin, 1989) (Fig. 1). However, despite continuous research, substantial portions of the population remain unaccounted for in known winter and summer habitats (Kraus et al., 1986; Mead, 1986), suggesting alternative residency and migratory patterns. Northern right whales feed primarily on late stages (IV and V) of Calanus finmarchicus copepods (Gaskin, 1982) and do not change their feeding preference as they age. Any variability in the stable isotopic signatures of their tissues, therefore, would reflect geographical differences in the isotopic signatures of food webs that individuals encounter during migration. This provides a unique method of tracking seasonal patterns in habitat use.

This study explores the value of stable isotope analysis as a determinate for differential migratory behaviours between age classes and same sex adult individuals in the North Atlantic right whale population.

MATERIALS AND METHODS

Attempts were made to locate North Atlantic right whale baleen plates for sampling from a number of museums and agencies around the US, Canada and Europe, but for only three plates could the proper permitting for destructive sampling be obtained. The three plates were sampled for stable ¹³C and ¹⁵N isotopic analyses (Table 1). An adult plate was obtained from NOAA Fisheries, Beaufort, NC (VMSM2004-1004; female, 1,600cm total length). This individual was estimated to be at least 25 years old when killed by a ship strike and stranded off the coast of Cape Hatteras, NC in 2004. The length of the plate, including the unerupted portion, was 193cm. A plate from a juvenile male was sampled at Harvard Museum of Natural History (MCZ 62052; 1,030cm total length). Age estimations indicated that this animal was 2.5 years of age when it stranded in Rhode Island due to line entanglement. The baleen plate measured 108cm. Lastly, a neonate (UF 28470; male, 417cm total length) that stranded in Florida after complications during parturition was sampled through the Florida Museum of Natural History. The baleen plate measured 12cm.

¹ Marine Department of Marine Resources, PO Box 8, West Boothbay Harbor, ME 04575, USA

² University of New England, 11 Hills Beach Road, Biddeford, ME 04005, USA.

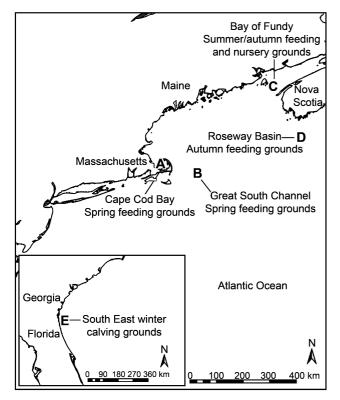


Fig. 1. Right whale critical habitat areas of the western North Atlantic.

The baleen plates, from the unerupted portion to the tip, were sampled along the outside edge in 2cm intervals, which corresponds to about one month of growth in adults (Schell and Saupe, 1993). All samples were obtained by using a flexible shaft hand-held drill fitted with a 1.6mm bit. The resulting powder was collected and dried at 55°C for 24hrs.

Approximately 1mg of ground tissue was used for carbon and nitrogen isotopic analysis. Samples were combusted using a Finnigan *MAT Delta Plus* mass spectrometer plumbed to a Carlo Erba NC2500 elemental analyser through a Conflo II open split interface. Stable isotope abundances were measured by comparing the ratio of the two most abundant isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) in the baleen tissue to the standard reference material. Results are expressed in terms of parts per thousand (‰) deviation from the standard using the equation:

$$\delta \mathbf{X} = \left[\frac{\mathbf{R}_{\text{sample}}}{\mathbf{R}_{\text{standard}}} - 1\right] \times 1,000\%$$

where X is the heavy isotope $({}^{13}C \text{ or } {}^{15}N)$ and R is the isotopic ratio ${}^{13}C/{}^{12}C \text{ or } {}^{15}N/{}^{14}N$. Standards used for carbon and nitrogen analysis were Pee Dee Belemite (PDB) and

atmospheric nitrogen (N_2) respectively. Seasons and years were assigned to the various sampling locations on the baleen plate using the distance between annual oscillations, the date of stranding, and estimated rates of growth as taken into account in the sampling interval (Best and Schell, 1996).

In addition to these three animals, the results from an adult female right whale, NEAq1014, were reconstructed from Wetmore (2001). This animal was estimated to be more than 28 years old when it was found dead in Cape Cod Bay in April 1999; likely due to a ship strike. This baleen plate measured 247cm and was sampled similar to the above methods. Those methods can be found in Wetmore (2001). A single-factor analysis of variance (ANOVA) was used to compare the summer and winter peak isotopic values for VMSM2004-1004 to published values for NEAq1014.

Vertical plankton tows were conducted in the Labrador Sea 26 May-7 June 2005 aboard the CCGS *Hudson* (Fig. 2), using 200µm mesh nets from a depth of 100m. Sampling locations ranged from coastal to deep basin habitats with depths ranging from 135-3,570m. Samples were immediately picked for *C. finmarchicus*, with priority given to stages IV and V. Copepod preparation and analysis for stable isotope ratios were identical to those for baleen.

RESULTS

Temporal oscillation patterns in $\delta^{15}N$ and $\delta^{13}C$ values were apparent along the baleen plate of VMSM2004-1004 with the enriched values for each isotope occurring during winter months and the depleted values during the summer (Fig. 3a). Values fluctuated broadly, ranging from 6.0 to 11.9‰ for ¹⁵N and -21.9 to -17.4‰ for ¹³C.

One notable exception existed in the oscillation pattern of δ^{13} C values. During a period between the 142 and 174cm sampling locations, the δ^{13} C values, with the exception of one smaller peak, fluctuated by less than 0.5‰ while nitrogen continued with the typical oscillation pattern (Fig. 3a). This anomaly occurred during winter months.

The δ^{13} C values for NEAq1014 fell mostly within the range of VMSM2004-1004, fluctuating between –20.9 and –16.6‰ (Fig. 3b). However, values of δ^{15} N were slightly heavier in NEAq1014, ranging 8.2 to 12.5‰. A single factor ANOVA yielded a significant difference between the two adults' summer δ^{15} N values (p<0.01). Summer δ^{13} C values were not significantly different when all values were included. However, when one outlier from VMSM2004-1004 was removed, the ANOVA showed significant differences between individuals (p<0.05). Results showed no significant differences in either δ^{15} N or δ^{13} C during winter months.

The beginning of the temporal oscillation pattern seen in the two adults was evident in the baleen plate of the juvenile MCZ 62052 (Fig. 3c). ¹⁵N and ¹³C values showed less

Table	1
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Summary information taken from the stranding records of VMSM2004-1004, NEAq1014, MCZ 62052 and UF 28470.

	VMSM2004-1004	NEAq1014	MCZ 62052	UF 28470
Sex	Female	Female	Male	Male
Estimated age (yr)	25+	28 +	2 1/2	Neonate
Stranding date	Feb. 2004	Apr. 1999	Jul. 1995	Jan. 1997
Stranding location	Cape Hatteras	Cape Cod Bay	Rhode Island	Florida
Total length (cm)	1,600	?	1,030	417
Baleen length (cm)	193	247.65	108	12
Notes	Ship strike	Ship strike	Entanglement	Died during parturition

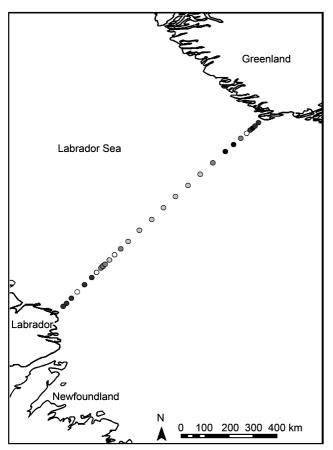


Fig. 2. Stations sampled for *Calanus finmarchicus* during the DFO Canada's *CCS Hudson* cruise May 26-June 7. δ¹⁵N is given in parts per million.

variability, ranging 10.4 to 12.3‰ and -19.8 to -17.0%, respectively. Encompassing two years of growth, the plate records the end of the nursing period and subsequent weaning from the 60-96cm sampling locations (Fig 3c). The annual oscillation pattern was apparent from the 6-60cm sampling locations, with the first residence in summer feeding grounds occurring around 36cm. A similar pattern to the anomaly in the ¹³C values of VMSM2004-1004 was seen between the 46 and 82cm sampling locations, where ¹³C values levelled off and fluctuated by less than 0.5‰. Additionally, samples taken from the most recently laid down baleen (2-12cm) become erratic. This time period corresponds to the entanglement event that led to the stranding of the individual.

Values for the neonate male UF28470 (Fig. 3d) showed very little variation, ranging 10.9 to 11.1‰ in ¹⁵N and –18.9 to –18.5‰ in ¹³C. These values corresponded only to baleen formed during late gestation and fell within the ranges of the two adults during the proposed winter periods.

 δ^{15} N values for *C. finmarchicus* sampled in the Labrador Sea ranged from -1.2 to 13.3%. Values were consistent in deep waters (>2,000m) in the centre of the trackline, ranging from 2.0 to 4.2‰. Nitrogen values became highly variable along either shelf, but were generally higher in the coastal waters, with values between 5.9 and 7.9‰. Anomalies occurred in areas characterised by steep slopes at or around the shelf break resulting in some negative δ^{15} N values.

DISCUSSION

The baleen record of VMSM2004-1004 details eight years of monthly seasonal migratory behaviour (Fig. 3a). This annual oscillation pattern is reflective of dietary changes due to migrations between winter and summer habitats, with values fluctuating between enriched and depleted ratios respectively. In fasting animals, the catabolism of body tissues produces substantial enrichments in $\delta^{15}N$ values (Hobson et al., 1993). Since right whales are thought to fast during the winter, this would appear to be a likely explanation for the enriched ¹⁵N values during these months. Additionally, each peak in ¹⁵N is associated with a cluster of δ^{13} C values that differ by less than 0.5‰ (Fig. 3a), indicating that the diet of the whale is not changing during this time. This pattern of peaks in nitrogen during periods in which the carbon isotope remains constant has been linked to migratory-related fasting in the Arctic bowhead whale (Hobson and Schell, 1998) and the southern right whale (Best and Schell, 1996). However, the broad range in δ^{15} N values between summer and winter months suggests that fasting is not solely responsible for this enrichment. Typically, the breakdown of body tissue would be expected to produce a ¹⁵N enrichment of approximately 3.0 to 4.0‰, roughly the equivalent of one full trophic position (Post, 2002; Tiezen et al., 1983). In several years, VMSM2004-1004 shows an enrichment of nearly 6.0‰, a two-level trophic shift. Lee et al. (2005) found similar broad ranges in the isotopic values of bowhead whales and suggested that this pattern may be due to sporadic feeding during early migratory movements coupled with seasonal fasting. Wetmore (2001) found that copepod prey in Cape Cod Bay and Bay of Fundy were substantially enriched, when compared to those found off the shelf of Nova Scotia. Therefore, it is likely that winter enrichments in δ^{15} N values represent opportunistic feeding during the start of the southward migration, followed by a subsequent period of fasting prior to arrival in winter habitats.

The δ^{15} N values of VMSM2004-1004 are highly depleted in the late summer, sometimes dropping to as low as 6.0%. Assuming a trophic enrichment of 3.0 to 4.0% for ¹⁵N, this would suggest that this whale is utilising a summer feeding ground in which the primary prey has a $\delta^{15}N$ value of 3.0 to 4.0‰. However, copepod data presented by Wetmore (2001) indicate that prey values in the common summer habitat in the Bay of Fundy are substantially more enriched at this time, ranging from 7.1 to 10.6‰ (Table 2). Additionally, the summer $\delta^{13}C$ (outlier removed) and $\delta^{15}N$ values for VMSM2004-1004 were found to be statistically different than those of NEAq1014, which was commonly sighted in the Bay of Fundy during the summer (S. Kraus, pers comm). Therefore, it seems likely that VMSM2004-1004 is utilising a different habitat during this season. Isotopic analysis of copepods taken near the shelf break of Nova Scotia during August of 1998 by Wetmore (2001) (Table 2) and samples taken in the Labrador Sea basin during May and June 2005 (Fig. 2), indicate that VMSM2004-1004 may have been using this region as an alternative summer feeding habitat. For the latter, $\delta^{15}N$ values between 2.0 and 4.1‰, approximately one full trophic level below VMSM2004-1004, occurred through the deepest part of the trackline (Fig. 2), an area that is within the historic range of the North Atlantic right whale (Aguilar, 1986; Knowlton et al., 1992; Lien et al., 1989; Mead, 1986). It is possible that certain segments of the population are still exploiting this region as a feeding ground and as a result are displaying lower summer ¹⁵N values and broader seasonal ¹⁵N fluctuations than other segments of the population.

One exception to the seasonal patterns of VMSM2004-1004 can be seen in samples between 142 and 174cm (Fig. 3a). Here, carbon changes only slightly during a one-year period, indicating little, if any, migration during this period.

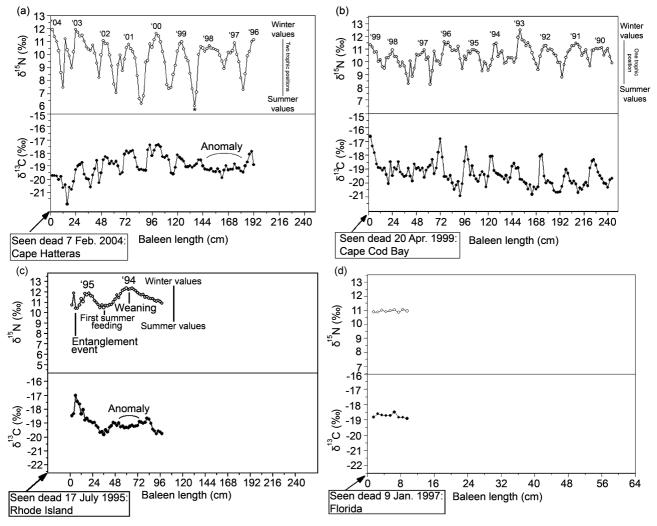


Fig. 3. Time series for adult female VSMS2004-1004 (a), adult female NEAq1014 (b), juvenile male MCZ 62052 (c) and neonate male UF28470 (d); δ^{15} N and 13 C ‰ versus baleen length in centimetres. All peaks represent winter values, while all valleys correspond to summer values. VSMS2004-1004 (a) stretches over two trophic positions with the asterisk identifying an exceptionally depleted δ^{15} N value. NEAq1014 (b) is reconstructed for comparison purposes from Wetmore (2001) published values. Both MCZ 62052 (c) and UF28470 (d) fall within the adults' value ranges, with MCZ 62052 detailing the first feeding cycle of a calf's life.

Table 2

 δ^{15} N and δ^{13} C values (‰) of plankton taken from Wetmore (2001). Samples taken in the Bay of Fundy (BOF), Roseway Basin (RB), and the Nova Scotia Shelf (NSS) were taken during July and August over the three year period 1998-2000. Plankton samples from Cape Cod Bay (CCB) were taken in January and March of 2001.

	CCB	BOF	RB	NSS
Min. $\delta^{13}C$	-21.27	-22.69	-24.59	-23.59
Max. $\delta^{13}C$	-9.97	-20.12	-20.18	-18.30
Mean δ ¹³ C	-17.48	-21.16	-22.64	-21.99
Min. δ ¹⁵ N	6.94	7.12	5.40	3.14
Max. $\delta^{15}N$	9.97	10.60	9.84	9.96
Mean δ ¹⁵ N	8.15	8.16	8.05	7.24

Since this occurred over the course of two winter seasons, we hypothesise that this anomaly is due to a calving event and prolonged residency in Florida waters. This hypothesis is supported by the isotopic values in the baleen of MCZ 62052 and UF 28470. MCZ 62052's baleen recorded residency time in the calving ground during its first year of life. This period corresponds to the section of baleen between the 46 and 82cm sampling locations (Fig. 3c). Here, the lack of fluctuation indicates little to no migratory movement and closely matches the ¹³C values and pattern of the adult, VMSM2004-1004, between 142-174cm. Additionally, UF 28470's ¹⁵N and ¹³C values correspond to

the adult's values immediately prior to the hypothesised parturition (sample location 174cm in VMSM2004-1004; Fig. 3a). Baleen, being formed directly from amino acids in the bloodstream (Schell and Saupe, 1993), has a high turnover rate and shows no fractionation from mother to fetus, suggesting that the values of UF 28470's baleen correspond directly to the calving ground. The smaller fluctuations in the summer isotope values of VMSM2004-1004 during this period also support the proposed calving event. $\delta^{15}N$ and $\delta^{13}C$ at 166cm closely match summer values from NEAq1014, which can be linked to the Bay of Fundy. This suggests that VMSM2004-1004 may have undergone a shorter migration to the Bay of Fundy when she was with her calf, but extended her migration further north in subsequent years. However, the summer isotopic values of MSC 62052 are higher than those of VMSM2004-1004 even in the proposed calving year. It is plausible that since the recorded summer would have been this juvenile's first attempt at feeding, it was utilising a different portion of the water column or habitats closer to shore and therefore had different isotopic values.

Winter values for δ^{15} N and δ^{13} C were not significantly different between adults. This would be expected since calving females are known to winter in Florida waters. However, females only calve approximately once every two to five years (Kraus *et al.*, 1986), leading to speculation regarding their residency patterns in non-calving winters. The sighting record of NEAq1014 during years in which she was not seen with a calf (1998 and 1999) indicates that she was seen feeding in Massachusetts Bay in January and February (Wetmore, 2001). This behaviour has also been identified in several other right whales (Schevill *et al.*, 1986; Watkins and Schevill, 1982; Wetmore, 2001). Plankton sampled by Wetmore (2001) during this time from Cape Cod Bay showed ¹⁵N values ranging from 6.9 to 9.7‰, which is approximately one trophic level below NEAq1014's corresponding values of around 11.0‰ (Table 2). Therefore, it seems plausible to assume that in non-calving years some females may be feeding on locally dense patches of copepods in Cape Cod Bay or other northern habitats.

By using stable isotopes to compare two adult females, as well as different age classes, it is apparent that while there may be substantial overlap in habitat usage in some regions, such as the calving and spring feeding grounds, many of their migratory patterns differ and remain unknown. While NEAq1014 appears to utilise the same specific habitats throughout multiple seasons, VMSM2004-1004 has a more variable record with broader fluctuations. These fluctuations indicate the use of alternative habitats in different years, including the potential for utilisation of an unidentified summer feeding ground and periods of fasting. These results demonstrate that while sampling a single animal is useful in gaining information about that individual, many animals will need to be analysed before conclusions regarding the behaviour of the population can be drawn. Future studies on northern right whale baleen involving isotopes should focus on comparing multiple individuals that differ in sex and matrilineal lines in order to determine how much variability exists within the population and how each segment is using habitats differently. A more complete understanding of the migratory and residency patterns of North Atlantic right whales will have significant impacts on the future conservation and management protocols for this endangered species.

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