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Introduction

The annual migratory path of the western arctic population of bowhead whales (Balaena mysticetus) carries them from the winter ice edge in the western Bering Sea northward through the Bering Strait and Chukchi Sea, and through leads in the offshore pack ice to the easternmost Beaufort Sea, where they arrive in early summer. In September and October, the animals move westward along the Canadian and Alaskan coast, returning to the Bering Sea by winter (Figure 15.1). Feeding occurs along this route. The principal prey organisms are the abundant copepods, euphausiids, and other invertebrates in the water column (Wursig et al. 1985; Lowry and Frost 1984; Braham et al. 1980). To capture their prey, the whales have a feeding apparatus that consists of a row of about 300 keratinous plates which grow from each side of the upper jaw. The plates fray on the inside to produce a hairy mat and also erode from the distal tips so that only young whales would be expected to have most of their total growth of baleen present. During feeding, the animal lowers its jaw while swimming and filters large volumes of water, retaining the zooplankton prey for consumption.

Yankee whalers of the late nineteenth and early twentieth centuries nearly extirpated the western arctic population, and the original circumpolar stocks are now reduced to a few hundred animals in the Atlantic and about 4400 animals in the Bering-Beaufort seas (International Whaling Commission 1986). Although

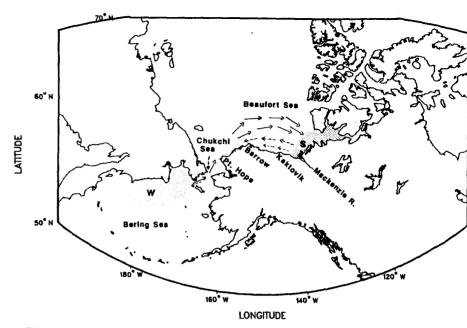
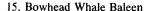


Figure 15.1. Migration route of bowhead whales between wintering areas in the Bering Sea (W) and summering areas in the eastern Beaufort Sea (S). Whales referred to in this paper were harvested at the Eskimo villages shown.

protected from commercial whaling, the bowhead is subject to a small harvest by Alaskan Eskimos. Recently, concerns about the recruitment rate, the harvest, and the potential for environmental impacts by the offshore oil industry have renewed interest in the species. The lack of an accurate method of age determination (Nerini et al. 1984; Davis et al. 1983) has seriously limited the reliability of recruitment rate estimates. Very little information exists on the relative importance of different geographic regions to the animal's annual feeding requirements.

A study of the food webs of the Beaufort Sea coastal zone has shown that the stable carbon isotope ratios in given taxa of zooplankton vary markedly from east to west (Dunton 1985). Although the exact causes for these variations are still uncertain, they are presumed to be a consequence of recycling of ¹³C-depleted carbon during upwelling events near the U.S.—Canada border (Hufford 1974) and possibly from large inputs of terrestrial organic matter in the vicinity of the Mackenzie River delta. Figure 15.2 shows the range of stable isotope variation in copepods and other zooplankton herbivores along the Beaufort Sea coast and from the Chukchi and Bering seas. If the baleen, which is a keratinous protein and metabolically inactive after formation, grows continuously, measurable variation in carbon isotope profiles could be expected along the length of the baleen, reflecting changes in the isotopic composition of the prey as the



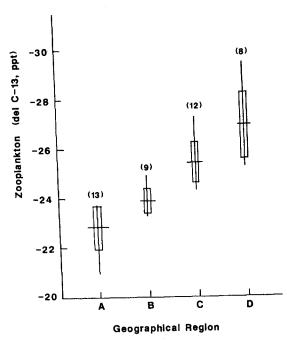


Figure 15.2. δ^{13} C in herbivorous zooplankton (primarily copepods) collected from (A) Bering-Chukchi seas; (B) Beaufort Sea, Point Barrow to Flaxman Island (154–146° W); (C) Flaxman Island to U.S. border (146–141° W); (D) U.S. Border to Mackenzie River delta (141–136° W). Vertical line denotes range; horizontal bar, mean; and box, standard deviation.

animal moved from one feeding area to another. Isotopic compositions of consumers have been shown to reflect their diets with a small enrichment of about 1‰ per trophic level (DeNiro and Epstein 1978; Fry and Sherr 1984). Isotopic distributions within mammals also show an additional enrichment in hair and keratin of another 1 to 2‰ (Tieszen et al. 1983).

Methods

Samples of baleen plates and muscle tissue were obtained from the National Marine Mammal Laboratory and from the North Slope Borough Department of Wildlife Management. Samples from whales collected during the 1960s and early 1970s were obtained from the Los Angeles County Museum and from a private collection. Baleen samples are listed in Table 15.1.

Baleen plates were lightly scrubbed with steel wool and sampled along their length at 2.5- to 5-cm intervals and analyzed for stable carbon isotope abundances. Samples of baleen were mixed with copper oxide and ground to a fine

Table 15.1. Bowhead Whale Baleen Samples, Season Taken, and Source Locations

Whale	Location	Length and Sex
66B (spring)	Point Barrow (71°25′ N, 156°30′ W)	9.7 m, male
71B (spring)	Point Barrow (71°25′ N, 156°30′ W)	16 m, male
78B2 (spring)	Point Barrow (71°25′ N, 156°30′ W)	8.4 m, male
79KK5 (fall)	Kaktovik (70°10′ N, 143°35′ W)	10.6 m, male
79H3 (spring)	Point Hope (68°20' N, 166°55' W)	9.1 m, male

powder and combusted at 570°C for 3 h in sealed, evacuated glass tubes. Samples for both nitrogen and carbon analysis were combusted at 900°C in quartz tubes. The liberated carbon dioxide and nitrogen were cryogenically purified and analyzed for stable isotope abundances with a VG Isogas SIRA-9 mass spectrometer. Machine replicability was $\pm 0.05\%$, and results are reported in standard δ notation relative to PDB for carbon or air for nitrogen.

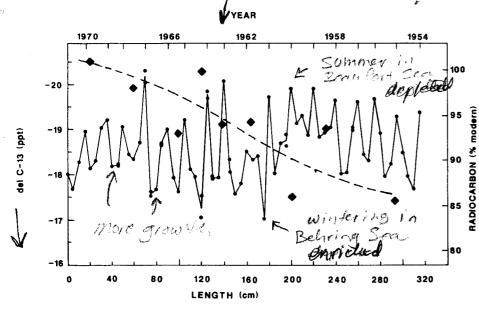
Radiocarbon analyses were performed by Beta Analytic Inc., Coral Gables, Florida, on 10-g samples. Results are reported as percent modern, where 1950 activity = 100%. Samples are 13 C normalized to $\delta = -25\%$.

Results and Discussion

Figure 15.3 shows the isotopic record of whale 71B and the ¹⁴C content at nine points along its length. If the stable isotope peaks represent annual markers, the years span the period of maximum atmospheric inputs of ¹⁴C from nuclear weapons testing, which peaked in 1963 prior to the Partial Test Ban Treaty. The results, although scattered, are consistent with the ¹⁴C increase curve predicted by models (dashed line) describing the bomb ¹⁴C equilibration in Atlantic surface seawater (Roether et al. 1980). Since this major addition of ¹⁴C was a unique event in recorded history, the observed increase strongly supports the time scale in Figure 15.3.

The most rapid rise in radiocarbon content of the surface ocean waters occurred after 1963, during which year over half of the atmospheric nuclear weapons testing took place. Since the majority of the radiocarbon began infiltrating the surface waters of the polar ocean late in the summer and fall of 1963, the marine biota were not severely impacted since most of the primary production for the year had already occurred. By the spring of 1964, however, a sizable fraction of the [14C] carbon dioxide released had had opportunity to equilibrate with the ocean surface and was available for plant uptake in the spring bloom. By 1965, surface water radiocarbon activity had risen over half way to maximum concentration (Broecker et al. 1980).

The radiocarbon concentrations along the plate from whale 71B are widely scattered, but show the rapid rise in concentration over the time spanned by the growth of the plate. Each sample included material from about 2.5 to 3 cm of the length of the plate, and thus represents a minimal time span. This method



D.M. Schell, S.M. Saupe, and N. Haubenstock

Figure 15.3. ¹³C isotope data (solid line) and radiocarbon activities along a baleen plate from a 16-m bowhead (71B) killed in 1971. Jaw end (newest baleen) is at left. Scale at top represents year when corresponding portion of baleen was formed, assuming annual peaks. Also shown are the measured radiocarbon activities in baleen (diamonds) and predicted radiocarbon content in the marine biota in response to atmospheric nuclear weapons testing in the early 1960s (dashed line). After Roether et al. (1980).

of sampling tends to accentuate the normally high variability in the radiocarbon content in marine organisms. This variability is due to the large intra- and interannual variations in nutrient supply through upwelling to the euphotic zone. Upwelling also brings chronologically old water to the surface with an accompanying depression in ¹⁴C. If the upwelling occurs in spring and a thermocline is established soon thereafter, phytoplankton will incorporate the ¹⁴C depression before radiocarbon can equilibrate from the atmospheric pool. As an illustration of the resulting variability in the radiocarbon content of consumers, the 1986 ¹⁴C activity is shown for muscle tissue in seven whales killed during April and May, 1986 at Point Barrow and Wainwright (Figure 15.4). Nevertheless, it would have been impossible for the whale to acquire a radiocarbon content in excess of the 1950 modern value without major inputs of bomb ¹⁴C. The record indicates that this occurred in the early 1960s and provides strong evidence that the peaks correspond to annual increments.

The scatter in the 71B record led us to sample the baleen in a different fashion from whale 66B (this baleen was acquired from the Los Angeles County Museum). The 10-g samples for radiocarbon analysis were cut lengthwise from the baleen plate and spanned 10 to 15 cm of the plate or an assumed interval of 6

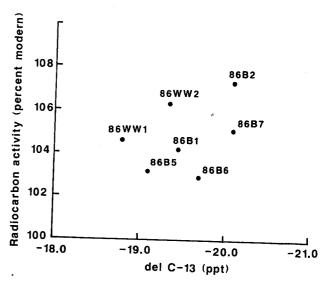


Figure 15.4. Radiocarbon activities and ¹³C isotope abundances in muscle tissue from bowhead whales killed in spring 1986 at the Eskimo villages of Wainwright (WW) and Barrow (B).

to 8 months if each δ ^{13}C cycle represents a year. This technique was chosen to smooth out short-term variability and produce an "average" radiocarbon activity for the period in question. The results are presented in Figure 15.5 along with the stable isotope abundances. Over the seven-peak record in the baleen, the radiocarbon content was approximately 92% modern for four, but after the fifth peak it rose rapidly and by the end of the plate had reached 106%modern, indicating an influx of bomb radiocarbon. The radiocarbon content was above the historical value for the last 28% of the period when the baleen was being formed. Since the whale was killed in the spring of 1966, and the major rise in radiocarbon began late in 1963 in the marine environment, this fraction of the record equals about 2.5 years. Thus the total baleen record is estimated to be about 9 years. This estimate is close to the observed seven cycles in the baleen isotope record. The discrepancy is readily explained in that the baleen appears to have grown faster near the tip, i.e., early in the life of the whale (Figure 15.5). The more rapid growth at the tip took place when the whale was young and is typical of the growth curves seen in other small whales. The combination of the observed geographical gradients in the zooplankton isotope ratios in regions used by the whales each year and the radiocarbon record in baleen grown during the 1960s provides very strong evidence that the observed oscillations are annual.

The stable isotope record thus indicates a 17.5-year feeding record for whale 71B. Since wear has occurred from the tip of the plate, the animal may have been many years older. The peaks in Figure 15.3 result from summer feeding

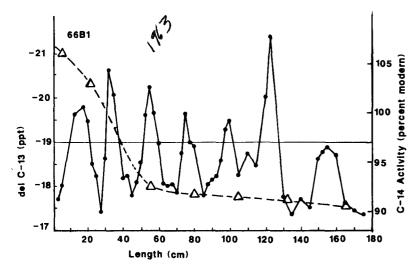


Figure 15.5. Radiocarbon activities (triangles) and stable carbon isotope abundances (solid line) in a baleen plate from a bowhead whale killed in spring 1966.

in the eastern Beaufort Sea on ¹³C-depleted zooplankton, and the variations in peak height may represent year-to-year changes in summer feeding locations. Recently acquired zooplankton samples from the Canadian arctic islands (not shown) are slightly more enriched in ¹³C than samples from off the Mackenzie River delta. However, until a more complete record is available from other parts of the eastern Beaufort Sea, we cannot state which specific areas are responsible for the observed ¹³C depletions in the baleen. No peak is apparent in 1962, and the whale may not have summered in the eastern Beaufort Sea that year; it may have remained in the northern Chukchi or western Beaufort Sea.

Evident in Figure 15.3 is a baseline fluctuation which varies from about -17.5 to -19.0% and presumably reflects year-to-year shifts in the stable isotope content of zooplankton consumed in the Bering and Chukchi seas. The causes of these multiyear fluctuations are not known but may be due to differences in the geographic area of autumn feeding or overwintering. Alternatively, the variations may be a consequence of changing oceanographic productivity governed by upwelling and on-shelf movement of deep Bering Sea water in the wintering area southwest of St. Lawrence Island.

The ratio of valley widths to peak widths indicates that most of the baleen growth occurs in regions having zooplankton enriched in ¹³C. When compared to the isotopic distributions of Figure 15.2, this matches very closely the observed migrational patterns and timetables of these animals and further supports the hypothesis that baleen growth is continuous.

Three additional baleen plates were obtained from the archived samples of the National Marine Fisheries Service, National Marine Mammal Laboratory. These samples (Table 15.1) are from whales killed at geographic locations representing the fall migration (79KK5) and the spring northward migration (78B2 and 79H3). Carbon isotope variations along the plates are shown in Figure 15.6. In addition, ¹⁵N/¹⁴N ratios are shown for 78B2. The plates from 79KK5 and 78B2 were excised from the jaws to include the most recently formed baleen. The distance from the last summer's peak on whale 78B2 to the end point where the whale was killed is the same as the distance between corresponding points along the previous year's cycle, within the limits of analytical precision. This provides further evidence that baleen formation is continuous over the winter months. The isotopic variations shown in Figure 15.6 likely span most of the lives of the animals but since an unknown amount of wear has occurred from the tips of the baleen plates, the ages must be considered lower limits. The ages, 7.5 and 4.5 years, respectively, for 79KK5 and 78B2, are much greater, however, than the estimates of 2 years and 1 made previously for bowhead whales of this length (Nerini et al. 1984).

The baleen from 79H3 grew at nearly 50 cm yr⁻¹, in contrast to the much slower rates observed in the other three animals. If wear at the tip were correspondingly fast, the two years evident may be a large underestimate of the true age. Whether this variability in the rate of baleen growth is common or particular to only a few animals is unknown. Partial analysis of several plates from other adult whales indicates that the normal rate of growth of baleen is 17 to 25 cm yr⁻¹. Whether bowheads can be aged at least roughly by the length of the baleen or their total body length remains to be seen. The three animals shown in Figure 15.6 do not show clear relationships between "baleen age," baleen length, and body length.

In four of the five whales, several summer peaks are depleted to -20% or less and may represent feeding near the Mackenzie River delta, where zooplankton are most depleted in ¹³C. The most recently deposited baleen (0 to 10 cm, Figure 15.6) in the plate of whale 79KK5 shows the accumulation of depleted carbon from summering in the eastern Beaufort and the inflection toward a more ¹³C-enriched diet as it moved westward toward Alaska. Expanded information on stable isotope abundances in zooplankton from the Canadian Beaufort Sea should allow more confidence in describing where the whales fed. Also significant in all whales is the preponderance of values in the enriched range, indicating that much of the feeding occurs in the Chukchi, and Bering, and western Beaufort seas. This is contrary to conventional wisdom, which has presumed that the whales feed primarily in the eastern Beaufort during summer and overwinter on stored fat reserves in the Bering (Lowry and Frost 1984).

8¹⁵N values for whale 78B2 (Figure 15.6) closely mirror the depletions observed in the carbon isotope abundances. This indicates that the ¹⁵N variations arise within the marine environment from seasonal uptake of nitrate versus recycled ammonia nitrogen by phytoplankton (Minagawa and Wada 1984). Although freshwater carbon and nitrogen inputs occur from the Mackenzie River, the ¹³C depletions observed in zooplankton from that area may instead result from upwelling of deep Arctic Ocean water, which also occurs near there (Hufford 1974).

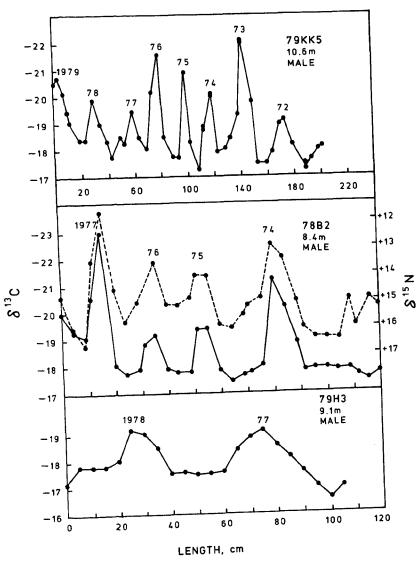


Figure 15.6. δ^{13} C (solid line) and δ^{15} N (dashed line) values in young whales taken during the fall (79KK5) and spring migrations (78B2, 79H3). Multiple points along line represent replicate samples.

Stable isotope abundances in keratinous materials provide useful indicators of variations in regional habitat usage and seasonal changes in diet and assist in aging animals such as baleen whales, for which formidable obstacles hinder field observation. This technique could also be useful in ecological studies of animals that grow horns, claws, or hooves over sufficient time to cover seasonal or annual periods of interest.

Acknowledgments

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