USE OF BEAUFORT SEA AS FEEDING HABITAT BY BOWHEAD WHALES (*Balaena mysticetus*) AS INDICATED BY STABLE ISOTOPE RATIOS

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A
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Abstract

The feeding habitats of the Western Arctic bowhead whales (*Balaena mysticetus*) during summer are generally known, but the precise amounts of food consumed from the eastern Beaufort Sea (EBS) are not known. $\delta^{13}C$ and $\delta^{15}N$ ratios in whale tissues were used to estimate the amounts of food acquired from EBS. The feeding strategies of adults and subadults were also compared. For all whales, the $\delta^{13}C$ values in muscle sampled in fall were not significantly different from those in the muscle sampled in spring, indicating most food of adults and subadults comes from the Bering/Chukchi seas. The $\delta^{13}C$ data from baleen showed, however, that EBS may be a significant feeding area for subadults. $\delta^{15}N$ values are significantly different between fall and spring muscle in subadults, suggesting a shift to different prey and/or nutritional stress during winter followed by feeding in EBS in summer.

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My project was supported by the U. S. Minerals Management Service through a subcontract from LGL Ltd. I thank the Barrow and Kaktovik whaling captains for providing samples from whales taken in 1997 to 1999, Todd O'Hara of the North Slope Borough Department of Wildlife Management and Gay Sheffield of Alaska Department of Fish and Game for processing and delivering samples. I also thank W. Griffiths of LGL Ltd. for collecting and providing the zooplankton samples. Special thanks go to Shunpu Zhang of the Mathematical Sciences Department for helping me with statistics.

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INTRODUCTION

Rationale for Study

Most of the Western Arctic bowhead whale (*Balaena mysticetus*) population spend the summers in the eastern Beaufort Sea. They were believed to feed intensively and build energy reserves in that area for non-feeding periods during the winter. Over the past three decades, offshore oil exploration and developmental activities have been underway in several parts of this summer range, which borders the migration routes (Richardson et al. 1987). Government agencies needed to determine whether offshore oil exploration and development were likely to harm marine mammals such as the bowhead whale (Richardson 1987). The U.S. Minerals Management Service (MMS) planned a two-year field study of the importance of the eastern Alaskan Beaufort Sea for feeding and the possible effects of offshore industrial activities on feeding bowhead whales (Richardson 1987). A multi-disciplinary study was conducted during 1985-86 to quantify what proportion of the annual energy requirements of the western Arctic bowhead whale stock is contributed by food obtained from the eastern Alaskan Beaufort Sea. It was concluded that the Western Arctic bowhead population acquired very little of its total annual food requirements from the eastern Alaskan Beaufort Sea. However, the North Slope Borough Science Advisory Committee

(1987) reviewed the report and concluded that two years were not enough to determine the importance of the region to feeding bowhead whales because of interannual variations arising from changing oceanographic conditions, plankton distribution, and whale distribution. Although the isotopic data were consistent with observations, they concluded there were too few data on zooplankton from all potential feeding areas as well as from the actual feeding sites. Also, they mentioned the lack of data regarding the cause of the purported isotopic shift of zooplankton between the southwestern and northeastern waters of the migratory range, suggesting further isotope studies of dissolved inorganic carbon and phytoplankton.

The current Project Plan (Thomson and Richardson 1998) was designed to repeat the work conducted in the same area during 1985 and 1986, including changes and refinements to deal with concerns about the earlier study raised by the North Slope Borough Science Advisory Committee (SAC) in 1987. This study is an extension of the LGL study on bowhead whale feeding strategy and uses stable isotope ratios as an indicator of food sources from the environment. This work was performed under subcontract to LGL Ecological Research Associates, King City, Ontario.

Overview of Bering, Chukchi, and Beaufort seas

Bowhead whales of the Bering Sea stock range from the Bering Sea into the Chukchi and Beaufort Seas (Braham 1984; Moore and Reeves 1993). Since these seas have different oceanographic characteristics, the whales meet different environments as they migrate from one region to another during spring and fall.

Bering Sea

The Bering Sea is one of the world's most productive seas, with a tremendous variety of biological resources including many species of marine mammals, seabirds, fish and shellfish. Primary productivity in the Bering Sea has been estimated to fall in the range of 120 to 400 $gCm^{-2}yr^{-1}$ (Sambrotto et al. 1984; Walsh et al. 1989; NRC 1996).

The Dimensions of the Bering Sea are about 1,500 km from the Bering Strait to the Aleutian Island Arc and about 3,000 km from Bristol Bay to Kamchatka (Niebauer and Schell 1993). Four distinct hydrographic domains occur within the Bering Sea, consisting of the coastal, middle shelf, outer shelf, and oceanic domains (Kinder and Coachman 1978). These domains are separated by fronts, consisting of the inner front near the 50 m isobath, the middle front near the 80 to 100 m isobaths, and the shelf break front near the 170 m isobath (NRC 1996). Of the four domains, the middle and outer shelf domains are the important habitat for bowhead whales, primarily in the western Bering Sea. (Niebauer and Schell 1993).

The northeastern half of the Bering Sea overlies the widest continental shelf outside of the Arctic, while the southwestern half overlies an abyssal plain (3,900-4,000 m depth) (Niebauer and Schell 1993). The continental shelf of the northern Bering Sea is generally 50 meters in depth or less (Springer 1988; NRC 1996).

The northward flow of water through the narrow, shallow Bering Strait separating the Bering and Chukchi seas results in characteristic water mass distributions of the shelf regions of the southern Chukchi Sea (Niebauer and Schell 1993). The Anadyr Water, Bering Shelf Water, and Alaskan Coastal Water (Figure 1) comprise the bulk of the primarily barotropic northward flow through the Bering Strait (Springer 1988). The Alaskan Coastal Water (ACW) has a low salinity (less than 32.2) due to fresh water input from rivers emptying into the southeastern Bering Sea. Anadyr Water originates along the Bering shelf break and is a high salinity northern branch of the Bering Slope Current. The Bering Shelf Water, which is colder (0-3 °C) and more saline (32.5-33) than ACW, originates south of St. Lawrence Island (Coachman et al. 1975; Kinder et al. 1975; Weingartner 1994). Of these sources, the Anadyr water supplies the Bering and Chukchi continental shelf with nutrients that promote abundant phytoplankton growth throughout summer and transport oceanic zooplankton onto the shallow

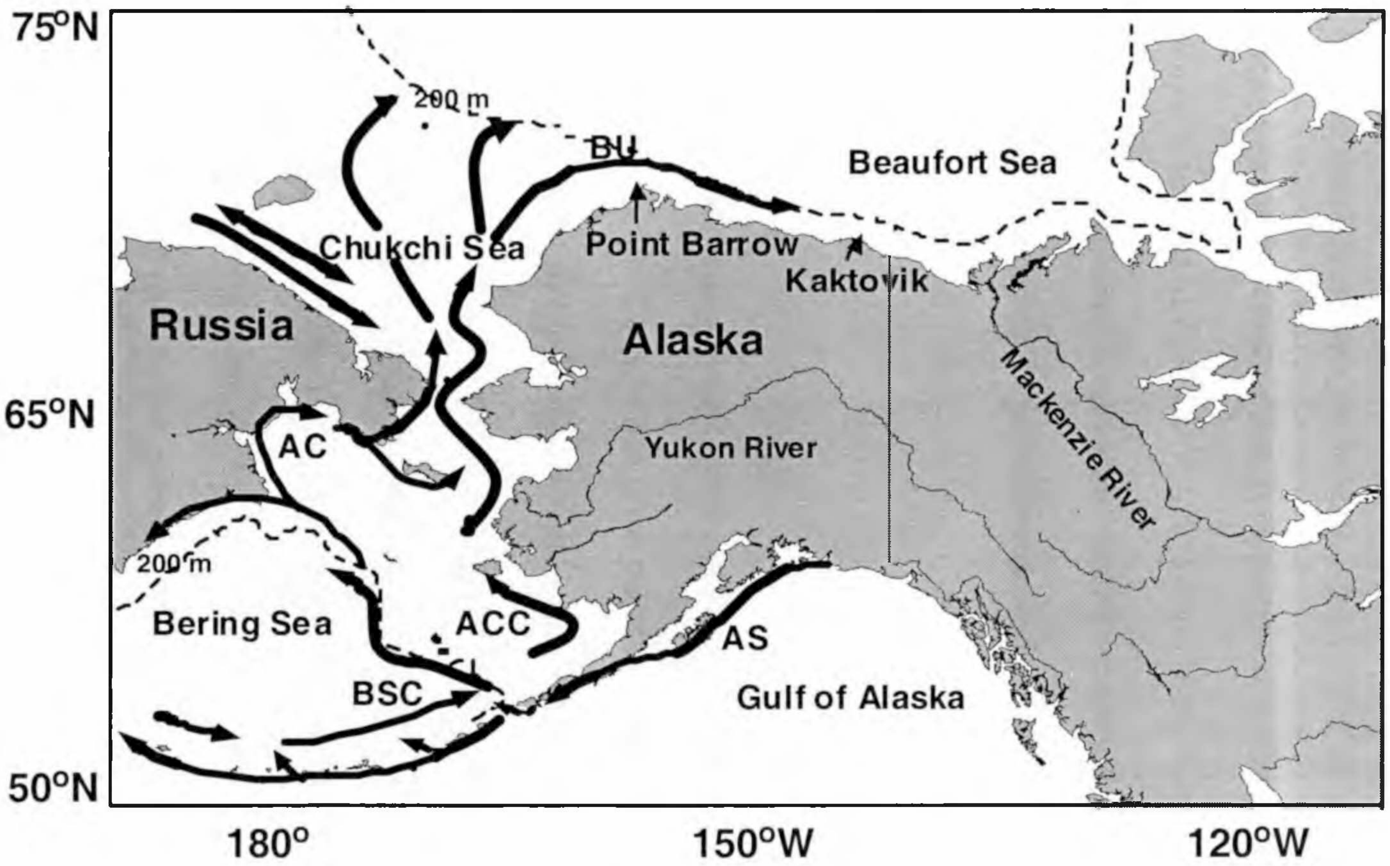


Figure 1. The major circulation patterns along the migration pathway of whales. AS: the Alaska Stream, BSC: the Bering Slope Current, ACC: the Alaska Coastal Current, AC: the Anadyr Current, and BU: the Beaufort Undercurrent (Schell et al. 1998).

northern shelf and into the Chukchi Sea through western Bering Strait (Springer 1988; Springer et al. 1989).

Zooplankton biomass on the order of 1.8×10^{12} gC per yr is carried from the Bering Sea to the Chukchi Sea. It represents an amount equal to 15-70 % of estimates of total standing stock of zooplankton in the Arctic basin (Springer et al. 1989). These transported zooplankton, mostly euphausiids and oceanic copepods, support immense numbers of planktivorous seabirds on the northern Bering shelf (Springer et al. 1989).

Chukchi Sea

The Chukchi Sea extends northward over 1,200 km from the Bering Strait to Point Barrow. The Chukchi Sea is the eastern end of the great arctic continental shelf system of the Arctic Ocean (Weingartner 1994; Aagaard 1987). The shelf is remarkably wide (600-800 km) and relatively shallow (20-60 m) with Herald Shoal (20-30 m) located about 200 km due north of the strait (Aagaard 1987; Niebauer and Schell 1993). These characteristics greatly affect marine conditions (Aagaard 1987). North of the Bering Strait, the Anadyr and Bering water combine and flow northward and slightly eastward (15-20 cm/sec). The flow bifurcates in the region between the Point Hope-Cape Lisburne headlands and Herald Shoal (Niebauer and Schell 1993; Weingartner 1994). Alaska Coastal Water also flows at 25-30 cm/sec along the Alaska coast in the eastern Chukchi Sea (Niebauer and

Schell 1993). Because the northward flow is anomalously warm and of low salinity in summer, the Chukchi Sea becomes ice-free much earlier in the year than it otherwise would (Aagaard 1987) and refreezes between October and early December. The retreat of sea ice begins in early June, with maximum retreat occurring in September (Stringer and Groves 1987).

Beaufort Sea

Sea ice dominates the entire Beaufort Sea. Ice cover is almost 100 % for 9-10 months per year (Norton and Weller 1984). The presence or absence of ice profoundly affects fish, bird, and marine mammal movement and behavior in this region. Many species congregate near the edge of the pack ice and move with the ice (Norton and Weller 1984).

Wind and currents are the two major influences on the environment in the Beaufort Sea. The wind along the coast is a major influence on the shelf oceanography of the Beaufort Sea (Kozo 1984). Surface wind conditions influence the times of sea ice breakup or freeze-up, create nearshore currents, and move ice floes (Kozo 1984). The southern Beaufort Sea is generally a region of mean westward water and ice motion corresponding to the anticyclonic gyre of the Canadian Basin. In contrast, over the continental slope and outer shelf seaward of about the 50 m isobath, there is a strong mean eastward current at depth called the

Beaufort Undercurrent (Aagaard 1984). The Beaufort Undercurrent is characterized by a temperature maximum associated with eastward flow originating in the Bering Sea (Niebauer and Schell 1993).

Estimated annual primary production in the Beaufort Sea is 16-36 $gCm^{-2}yr^{-1}$, including both ice algae and phytoplankton (Schell et al. 1984). The stable Arctic Surface Layer and its ice cover for 9-10 months per year effectively prevent wind mixing and advection of nutrients into the euphotic zone over most of the Beaufort Sea. Due to the scarcity of available nutrients and the persistent ice cover, the primary and secondary productivity throughout the region are low (Niebauer and Schell 1993). Overall, in Beaufort Sea trophic systems, biological productivity is very low, species are few and food webs are simple (Norton and Weller 1984).

Life History of the Bowhead Whale (*Balaena mysticetus*)

There are five bowhead stocks presently recognized: Okhotsk, Western Arctic, Hudson Bay, Davis Strait, and Spitsbergen stocks. Of these, the Western Arctic stock (also called the "Bering-Chukchi-Beaufort"or "Bering Sea" stock), which inhabits the Bering, Chukchi, and Beaufort seas, is now the largest (Nerini et al. 1984). The most recent estimate of the size of this stock is around 8,000 (95 % CI 6,900-9,200) (Zeh et al. 1995).

The calving interval of bowhead whales is believed to be every three to six years (Nerini et al. 1984). This is a major reason for the slow recovery rate of the western arctic bowhead population following the cessation of commercial exploitation in 1914. Most calves are born during April and May in the northward migration (Koski et al. 1993). The approximate length at birth is 4-4.5 m (Nerini et al. 1984) and growth is very rapid during the first year of life. Little or no growth occurs for several years following the first year (Schell and Saupe 1993), until approximately age 6.

Natural mortality is generally low after their first year. The principal predator is the killer whale (*Orcinus orca*) and bowhead whales can be easily attacked because of their slow swimming speeds (Philo et al. 1993). Killer whales are known to frequent bowhead whale habitat throughout the Bering and Chukchi seas in relatively low numbers (Nerini et al. 1984). They have been observed in all waters surrounding western Alaska and the eastern Canadian Arctic (Philo et al. 1993). Attacks on bowhead whales by killer whales have been documented (Philo et al. 1993). In addition to predation by killer whales, ship collisions, line entanglement, and ice entrapment have been reported (George et al. 1994; Philo et al. 1993).

All females greater than 14 m were considered as sexually mature by Nerini et al. (1984). Some become mature by the time they are 13 m long and possibly by

12.3 m (Koski et al. 1993). Based on photogrammetric studies, most females probably become sexually mature at about 13-13.5 m long (Koski et al. 1993). Although virtually no information is available concerning the length of sexually mature males, it is believed that most male bowheads reach maturity at 12-13 m (Koski et al. 1993). In this study, the 13.5 m length was used to differentiate adults and subadults for both males and females.

Western arctic bowhead whales overwinter from December to March in polynyas and in the pack ice edge in the western and central Bering Sea (Braham et al. 1984; Braham 1980) (Figure 2). Distribution in this time period is influenced by ice cover (Moore and Reeves 1993). The spring northward migration usually begins in March-early April and progresses through leads developed in the Bering, Chukchi, and Beaufort seas (Braham et al. 1984). The patterns of lead formation differ each year in response to wind direction and ocean currents (Braham et al. 1984). From June to September, most whales are in the Canadian Beaufort Sea and Amundsen Gulf, although small numbers of bowheads occur in the eastern Chukchi and the western Beaufort seas in June (Moore and Reeves 1993).

Although most bowheads are believed to feed while in the eastern Beaufort Sea during the summer and autumn, aerial photogrammetry (Richardson et al 1987) and initial isotopic (Schell and Saupe 1993; Schell et al. 1989) results suggested differences in feeding patterns and feeding areas between adults and

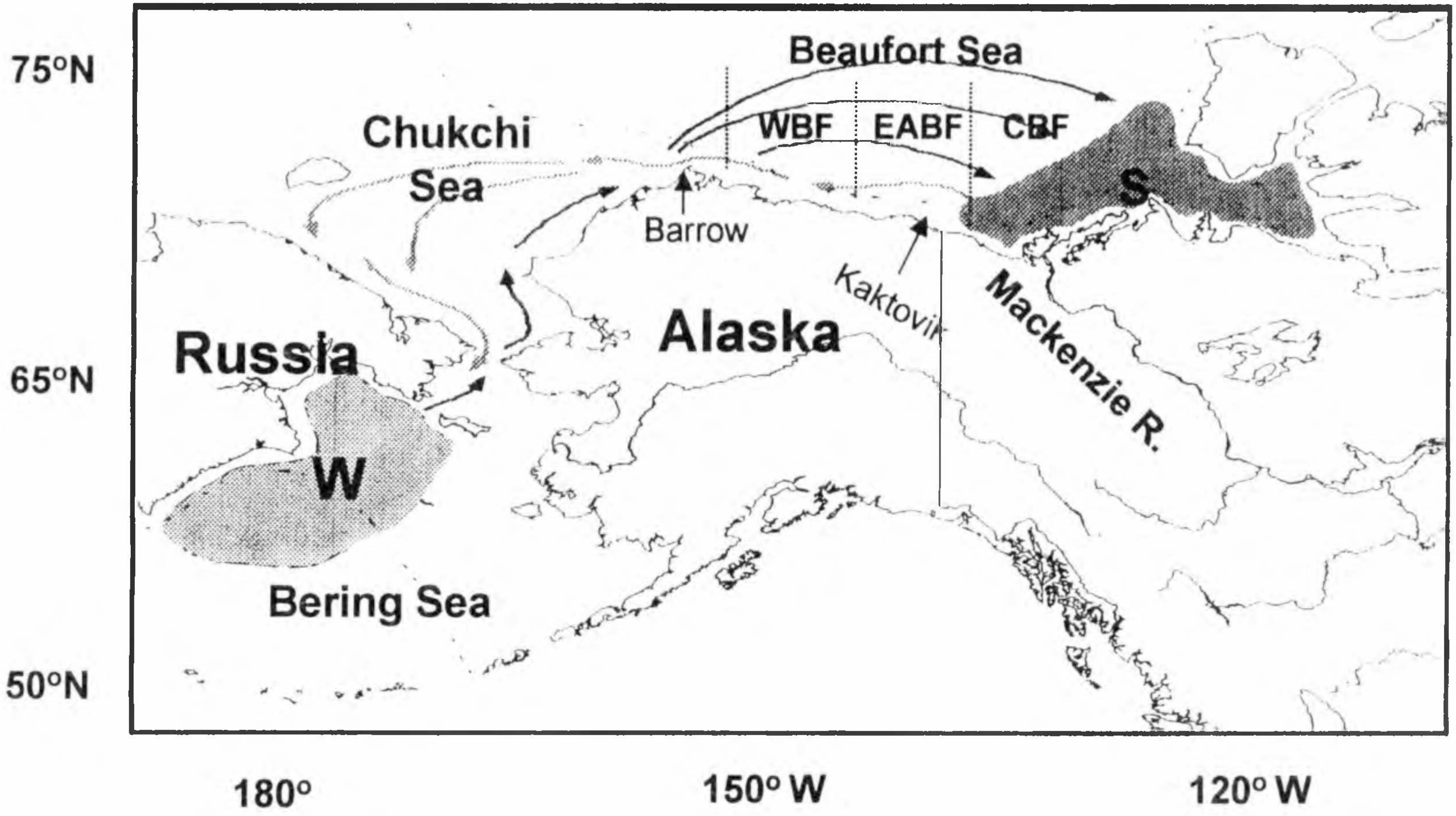


Figure 2. Bowhead whale migration pathway (from Schell et al. 1989). S: summering ground, W: wintering ground, WBF: western Beaufort Sea, EABF: eastern Alaskan Beaufort Sea, and CBF: Canadian Beaufort Sea.

subadults. For adult whales, the muscle and fat $\delta^{13}C$ values of fall-killed whales were not different than those of spring-killed whales. In comparison, the fall-killed subadult whales were more ^{13}C-depleted, indicating that they had consumed substantial amounts of feed from the Beaufort Sea (Schell et al. 1989). They also suggested a possible alternative scenario that the feeding areas or/and the types of prey consumed in summer may differ between adult and subadult whales. Aerial photogrammetry (Richardson et al. 1987) has shown differences in the distribution between adult and subadult whales in the eastern Beaufort Sea. Most subadults were found in the coastal waters of the eastern Beaufort Sea, whereas relatively higher numbers of adults spend much of the summer in offshore waters.

The fall westward bowhead migration route occurs close to the Alaskan coast across the Beaufort Sea and into the northern Bering Sea from September through November (Moore and Reeves 1993). The bowhead migration route across the Chukchi Sea has not been as well-documented as that across the Beaufort Sea (Moore and Reeves 1993). During this time, feeding probably occurs in the Chukchi and northern Bering seas. An abundant pelagic community of large copepods and euphausiids is transported northward in the Anadyr water mass through the Bering Strait and into the western and central Chukchi Sea (Springer 1988). Schell and Saupe (1993) noted that baleen plates have a major increase in thickness and width from feeding in fall and early winter.

Physical Characteristics of the Baleen Plate

Bowhead whales concentrate and filter small prey from seawater using a filtering mechanism composed of several hundred baleen plates lining each side of the mouth (Lambertsen et al. 1989). By means of filter feeding, the whale obtains chemical energy and essential nutrients from the marine environment for use in growth, maintenance, locomotion, reproduction, and lactation (Lambertsen et al. 1989).

Baleen plates are composed of keratinous proteins similar to hair, feathers and hooves, and are biochemically inert after being laid down from amino acids supplied by the blood stream (Schell et al 1989). They are long, narrow isosceles triangles with many hairs on the inner side and a posteriorly curved outside edge. Baleen growth rate is approximately 65 cm in the first year of life, between 35 and 45 cm in the second and by year 3, 27.5 to 35 cm (Schell and Saupe 1993). In subadult and adult whales, the growth rate is 16 to 25 cm per year (Schell and Saupe 1993; Schell 2000). The plates are arranged along each side of the upper jaw in a transverse series. The upper jaw is strongly arched and has 250-350 baleen plates on each side (Lowry 1993). The filtration efficiency of a baleen rack is 97.2 % in laboratory test (Lowry 1993).

Using Stable Isotope Ratios to Determine Feeding Habitats of Migratory Animals

Generally, there have been two conventional methods for determining feeding habitats and the amounts of food consumed by populations of animals. One is an observational method, which often has limitations. It is difficult to determine how much food the animal consumes in a given feeding place. Furthermore, feeding behavior may be confused with other behavior, especially in marine mammals, which are difficult to observe. Identification of feeding behavior usually requires repeated observations, which are very difficult for whales in extensively ice-covered areas (Moore and Reeves 1993). Another technique is stomach content analysis, which shows what an animal has most recently eaten and what quantity is present in the stomach when collected in specific regions. However, this analysis is valid only for a short time and part of the animal diet (Hobson et al. 1996; Hobson and Clark 1992).

Stable isotope ratio analysis provides an alternative approach that enables the determination of important feeding habitats for migratory animals (Fry 1981; Schell 1987; Schell et al. 1989), because the animals acquire a natural isotopic tag from their diet (Fry 1981). This assumes that the stable isotopic ratios in the food from specific regions are different from each other and are transferred conservatively and predictably to the animals. If sufficient isotopic gradients exist between regions where feeding occurs, it allows estimation of habitat significance (Schell and Saupe 1993; Schell 1999). DeNiro and Epstein (1978) found that the transfer of carbon isotope composition is nearly conservative with regard to the whole bodies of animals and that the whole body is enriched in $\delta^{13}C$ by about 1 ‰ relative to the diet in laboratory. In contrast to $\delta^{13}C$, the $\delta^{15}N$ values typically show an increase of 3-3.5 ‰ between diet and consumer (DeNiro and Epstein 1978; Wada et al. 1987; Fry and Sherr 1984; Minagawa and Wada 1984). A marked change in $\delta^{13}C$ and $\delta^{15}N$ of animals could indicate a change in their feeding ecology, an isotopic change at the primary producer level, or both (Wainright et al. 1993).

Fry (1981) used stable carbon isotope analysis to trace shrimp movements by matching the $\delta^{13}C$ values of migrating shrimp with the $\delta^{13}C$ values of resident shrimp living in specific habitats. Schell et al. (1989) reported annual oscillations of $\delta^{13}C$ and $\delta^{15}N$ along the length of bowhead baleen plates apparently resulting from the annual migrations of the whales, from relatively ^{13}C-depleted food sources in the summering grounds in the eastern Beaufort Sea to the more ^{13}C- enriched food of the wintering grounds in the Bering and Chukchi seas (Schell et al. 1989). These studies, using the natural ratios of isotopes in migratory animals, have provided new insight into their feeding habitats in a remote area.

Composition and Stable Isotope Ratios of Bowhead Whale Diets

Zooplankton distribution in the Beaufort Sea

Total zooplankton biomass has been found to be much higher in areas where whales are observed feeding in the eastern Beaufort Sea (Griffiths et al. 1987; Griffiths 1999). This is reasonable in that bowheads must feed in areas where the biomass of zooplankton is higher than the average biomass in the water column to meet energetic requirements (Griffiths et al. 1987).

Figure 3 presents major bowhead prey-species as fractions of total zooplankton biomass in the water column across the Beaufort Sea. Euphausiids comprised about 90 % of total biomass, copepods contributed less than 7 %, and amphipods and mysids made up 3 % in samples collected near Barrow. These are derived from Bering Sea zooplankton advected northward over the summer season. In contrast, copepods contributed more than 90 % of total biomass and euphausiids comprised only a small fraction of zooplankton biomass in the eastern Beaufort Sea (Saupe et al. 1989). However, zooplankton biomasses and dominant species in water column vary from year to year (Griffiths 1999), probably depending on regional and local meteorological events (Moore and Reeves 1993). In addition, there is often a discrepancy between the species composition of zooplankton found near feeding whales and the stomach contents of whales landed

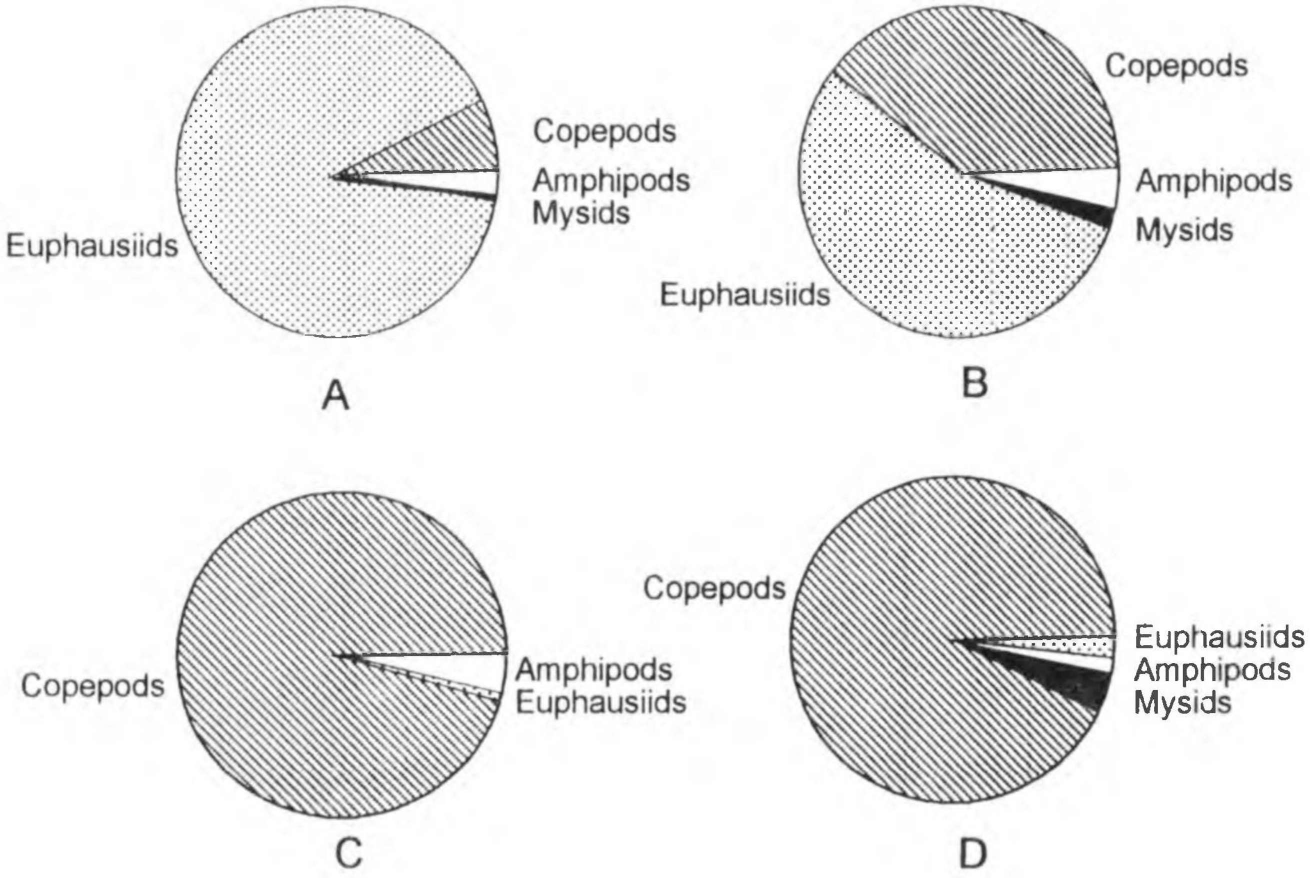


Figure 3. Proportional biomasses of major bowhead prey taxa across the Beaufort Sea: (a) western, (b) central, (c) eastern Alaskan Beaufort Sea, and (d) Canadian Beaufort Sea (Saupe and Schell 1989).

at Kaktovik (Griffiths 1999), because some zooplankton, especially euphausiids, are difficult to sample quantitatively (Saupe et al. 1989). Furthermore not all of the bowhead feeding habitats were sampled in the eastern Alaskan Beaufort Sea, especially offshore regions (Griffiths 1999).

Lowry (1993) approximated the overall composition of the diet for bowheads near Barrow and at Kaktovik by analyzing stomach contents of whales taken over 10 to 12 years (Table 1). The abundance of euphausiids and mysids in the bowhead diet is slightly higher than present in the water column in the eastern Beaufort Sea (Figure 3). In contrast, the abundance of copepods is much lower in stomach contents than in the biomass present in the water column. Interestingly, there are few copepods in whale stomach contents in the western Beaufort Sea. Overall, copepods and euphausiids are the most important foods for bowhead whales in the region. Mysids and amphipods are concentrated in some regions and might be locally important (Lowry and Burns 1980).

$\delta^{13}C$ and $\delta^{15}N$ values of major zooplankton taxa

Saupe et al. (1989) showed the regional differences in $\delta^{13}C$ of zooplankton in the Bering, Chukchi, and Beaufort seas. Schell (1992) expanded and detailed the $\delta^{13}C$ and $\delta^{15}N$ values of major zooplankton taxa in the seas surrounding Alaska, in which bowheads presumably feed. These data were updated with new information collected during the subsequent years up to 1995 by Schell et al. (1998).

All zooplankton taxa in the eastern Beaufort Sea are more depleted in ^{13}C and ^{15}N than the same taxa in the western Beaufort Sea and the Bering and Chukchi Seas. Copepods and euphausiids in the western Beaufort Sea are depleted in ^{13}C relative to those of the Bering and Chukchi Seas in Figure 4 and 5. Conversely, $\delta^{15}N$ values from the western Beaufort Sea are more enriched than those of the Bering and Chukchi Seas (Table 2).

Euphausiids show a minimum of 1 ‰ enrichment in $\delta^{13}C$ relative to copepods in all three regions (Table 2). The relative depletion in ^{13}C in copepods might be due to higher lipid contents (Schell et al. 1998), since lipids are depleted in $\delta^{13}C$ relative to other biochemical fractions (McConnaughey and McRoy 1979; Wada et al. 1987). Saupe et al. (1989) suggested that the relative enrichment in $\delta^{13}C$ of euphausiids over copepods might also be a result of a more omnivorous diet in euphausiids. The geographic differences in $\delta^{13}C$ are 3.4 ‰ for copepods and 2.9 ‰ for euphausiids between the eastern Beaufort Sea and the Bering and Chukchi seas. In contrast, there is little difference in $\delta^{15}N$ between two regions (Table 2). $\delta^{13}C$ values were more useful for determining which region provided the most food for the annual energy budgets of bowhead whales, when estimating from a simple linear mixing model.

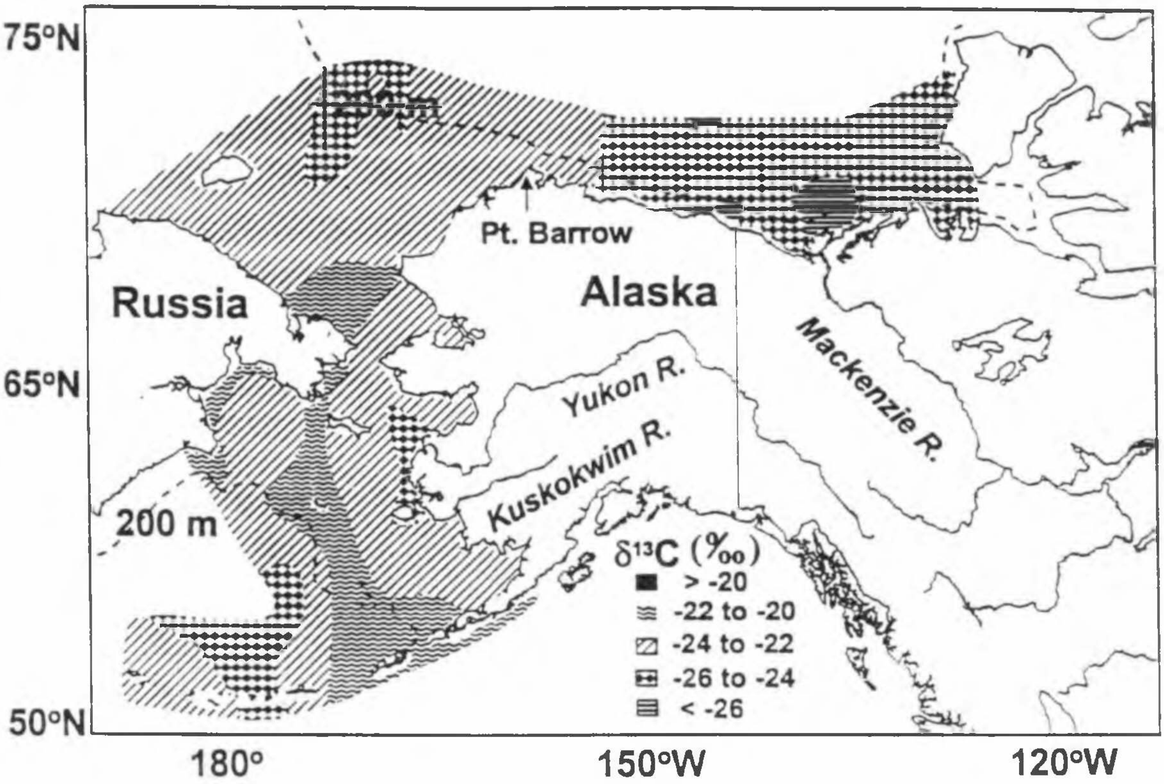


Figure 4. Carbon isotope ratios ($\delta^{13}C$) for calanoid copepods in Alaskan waters (from Schell et al. 1998).

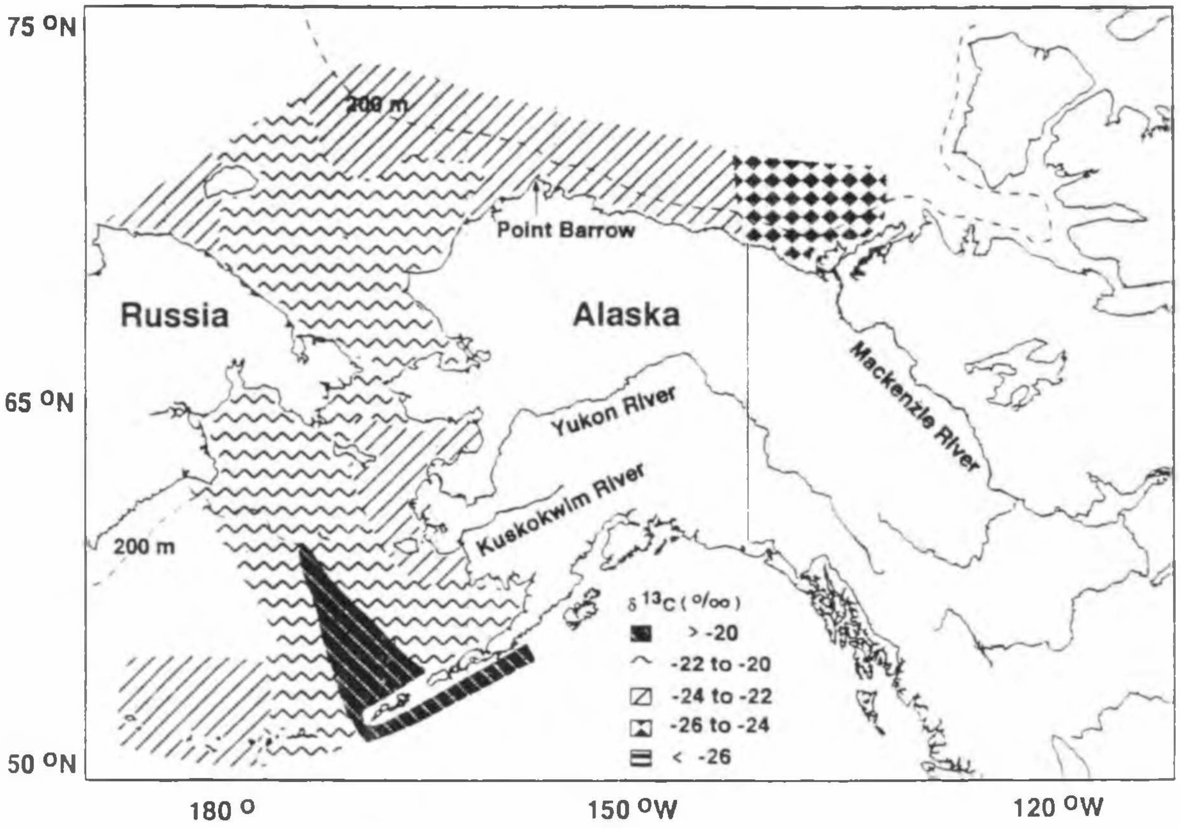


Figure 5. Carbon isotope ratios ($\delta^{13}C$) for euphausiids in Alaskan waters (from Schell et al. 1992).

Table 1. Approximate composition of bowhead whale diets (from Lowry 1993, CBF: the eastern Canadian Beaufort Sea, EABF: the eastern Alaskan Beaufort Sea, WBF: the western Beaufort Sea).

	copepods	euphausiids	mysids	amphipods
CBF +EABF	59.6 %	26.3 %	10.1 %	4.0 %
WBF		96%	1%	3%
Bering +Chukchi	65%	35 %		

Table 2. Approximate average values of $\delta^{13}C$ and $\delta^{15}N$ for main prey taxa using data from Schell et al. (1998) and Schell (1992).

	copepods		euphausiids		mysids		amphipods	
	$\delta^{13}C$(‰)	$\delta^{15}N$(‰)	$\delta^{13}C$(‰)	$\delta^{15}N$(‰)	$\delta^{13}C$(‰)	$\delta^{15}N$(‰)	$\delta^{13}C$(‰)	$\delta^{15}N$(‰)
CBF + EABF	-25.6	10.4	-23.7	9.2	-23.6	8.5	-23.9	8.2
WBF	-23.4	11.6	-22.1	11.2	-19.9	12.1	-21.3	12.2
Bering + Chukchi	-22.2	10.5	-20.8	10.13				

STUDY OBJECTIVES

The feeding habitats of bowhead whales during the summer and fall migration are generally known, but the precise feeding habitats and amounts of food consumed from various regions along the migration route have not been understood, due to harsh environmental conditions in areas in which the whales live.

The 1985-86 multi-disciplinary study concluded that the eastern Alaskan Beaufort Sea is not an important feeding area and provides less than 2 % of the annual food requirements for the total population (Richardson 1987). The authors acknowledge that two years is too short of a study to fully determine feeding habitat usage of bowheads, because the distribution and behaviors of bowheads may vary from year to year (Richardson and Thomson 1999). This study is an extension of the study of the importance of the eastern Beaufort Sea (the eastern Alaskan Beaufort and Canadian Beaufort seas) to the feeding of bowhead whales.

The objectives of my study were to:

1. Determine and quantify the relative importance of the eastern Beaufort Sea (the eastern Alaskan Beaufort and Canadian Beaufort Seas) as a summer feeding habitat for the western arctic bowhead whale.

2. Compare feeding strategies of subadult and adult whales in the Bering, Chukchi, and Beaufort Seas.
3. Investigate how the climatic shifts in the North Pacific and Arctic region have affected bowhead whale feeding strategy in the Bering, Chukchi, and Beaufort Seas.

MATERIALS AND METHODS

Baleen Plates

Baleen plates were obtained from 4 whales killed at Barrow and 10 whales landed at Kaktovik between 1997 and 1999 (Table 3). Baleen and muscle samples from 33 whales taken in 1986-1988 were used in comparisons (Table 4). Plates were cleaned of adhered gum tissue at the proximal end and then scrubbed with steel wool in order to remove surface layers of foreign matter such as diatoms and whale oil. Each plate was labeled along its length with adhesive tape and marked at 1 cm intervals and sampled. From 0 cm to 100 cm, samples were taken at 1 cm intervals, using a flexible shaft engraving tool. After 100 cm, plates were sampled at 2 cm intervals. This defined the isotopic ratios along the entire temporal span of each plate, with particularly high temporal resolution of the recently-grown baleen. As an example, the data obtained from whale 97KK2 are shown in Figure 6.

The fine powdered baleen was weighed into cups (0.8-1.0 mg) and the isotope ratios analyzed using a Europa continuous flow isotope ratio mass spectrometer. All $\delta^{13}C$ and $\delta^{15}N$ isotope values are reported against PDB (carbon) and air (nitrogen) standards as:

Table 3. Bowhead whale samples collected during 1997-1999.

Whale	Date Landed	Village	Whale Length (m)	Baleen Length (m)	Sex	Collected Samples
97B8	15 May 97	Barrow	13.6	2.54	F	baleen
97B11	11 Sept 97	Barrow	13.6	3.00	M	baleen
97B12	12 Sept 97	Barrow	15.3	3.12	M	baleen
97B14	20 Sept 97	Barrow	8.6		F	muscle, blubber
97B16	20 Sept 97	Barrow	8.3		F	muscle
97B18	22 Sept 97	Barrow	10.8		M	muscle
97B20	26 Sept 97	Barrow	8.6		M	muscle
97B21	27 Sept 97	Barrow	9.2		F	muscle
97B22	27 Sept 97	Barrow	9.4		F	muscle, blubber
97B23	27 Sept 97	Barrow	10.3		M	muscle
97B24	28 Sept 97	Barrow	8.6		F	muscle, blubber
97B25	28 Sept 97	Barrow	11.7	2.08	M	muscle, baleen
97B26	29 Sept 97	Barrow	13.5		M	muscle
97B27	2 Oct 97	Barrow	9.5		M	muscle, blubber
97B28	2 Oct 97	Barrow	8.4		M	muscle
97B29	17 Oct 97	Barrow	8.5		M	muscle
97B30	18 Oct 97	Barrow	8.0		F	muscle
97KK1	3 Sept 97	Kaktovik	8.7	1.50	F	muscle, baleen, blubber, skin
97KK2	6 Sept 97	Kaktovik	13.2	2.50	M	muscle, baleen, blubber, skin
97KK3	11 Sept 97	Kaktovik	8.3	1.32	F	muscle, baleen, blubber, skin
97KK4	27 Sept 97	Kaktovik	14.6	3.06	M	muscle, baleen, blubber, skin
98KK1	4 Sept 98	Kaktovik	10.4	1.92	M	muscle, baleen, blubber, skin
98KK2	10 Sept 98	Kaktovik	8.9	1.44	F	muscle, baleen, blubber, skin
98KK3	14 Sept 98	Kaktovik	9.2	1.70	M	muscle, baleen, blubber, skin
99KK1	11 Sept 99	Kaktovik	7.7	0.86	F	muscle, baleen, blubber, skin
99KK2	12 Sept 99	Kaktovik	12.9	2.44	M	muscle, baleen, blubber, skin
99KK3	16 Sept 99	Kaktovik	8.3	1.32	M	muscle, baleen, blubber, skin

Table 4. Bowhead whale samples from 1986 to 1988 (from Schell, 1992).

Whale	Date Landed	Village	Whale Length (m)	Baleen Length (m)	Sex	Collected Samples
86B1	27 Apr 86	Barrow	8.2	1.18	M	muscle
86B2	27 Apr 86	Barrow	8.7	0.52	M	muscle
86B3	3 Apr 86	Barrow	8.9	1.60	F	muscle, baleen
86B4	1 May 86	Barrow	8.9	1.30	M	muscle, baleen
86B5	4 May 86	Barrow	8.1	0.85	M	muscle, baleen
86B6	5 May 86	Barrow	12.3	2.30	F	muscle
86B7	6 May 86	Barrow	10.7	2.01	M	muscle, baleen
86KK1	10 Sept 86	Kaktovik	7.6	1.30	F	muscle
86KK2	17 Sept 86	Kaktovik	17.1	3.80	F	muscle, baleen
86KK3	26 Sept 86	Kaktovik	10.4	1.85	M	muscle, baleen
86WW1	5 May 86	Wainwright	15.9	2.69	M	muscle, baleen
86WW2	10 May 86	Wainwright	17.7	3.10	F	muscle, baleen
87B1	1 May 87	Barrow	9.3	1.68	M	baleen
87B2	2 May 87	Barrow	8.9	1.50	F	baleen
87B3A	4 May 87	Barrow	11.0	1.95	M	baleen
87B4	2 May 87	Barrow	16.8	2.95	F	baleen
87B5	15 June 97	Barrow	15.7	3.00	F	baleen
87B6	22 Oct 87	Barrow	15.7	3.15	F	muscle, baleen
87B7	29 Oct 87	Barrow	8.5	0.85	M	muscle
87G2	24 Apr 87	Gambell	16.8	3.45	F	baleen
87N1	5 Oct 87	Nuiqsut	15.2	3.30	F	muscle, baleen
87WW2	08 May 87	Wainwright	13.5	2.15	M	baleen
88B1	24 Apr 88	Barrow	8.9	0.98	M	muscle, baleen
88B2	25 Apr 88	Barrow	8.8		M	muscle
88B3	25 Apr 88	Barrow	7.8		F	muscle
88B4	25 Apr 88	Barrow	9.0	1.30	F	muscle
88B5	25 Apr 88	Barrow	8.9		M	muscle
88B6	2 May 88	Barrow	8.3		F	muscle
88B7	5 May 88	Barrow	8.2	0.78	F	muscle
88B8	6 May 88	Barrow	7.5	1.30	F	muscle
88B9	15 Sept 88	Barrow	14.6	2.57	M	baleen
88B10	17 Sept 88	Barrow	15.1	3.02	M	baleen
88G2	25 Apr 88	Gambell	15.3	2.75	F	muscle
88KK1	24 Sept 88	Kaktovik	14.9	2.97	F	baleen

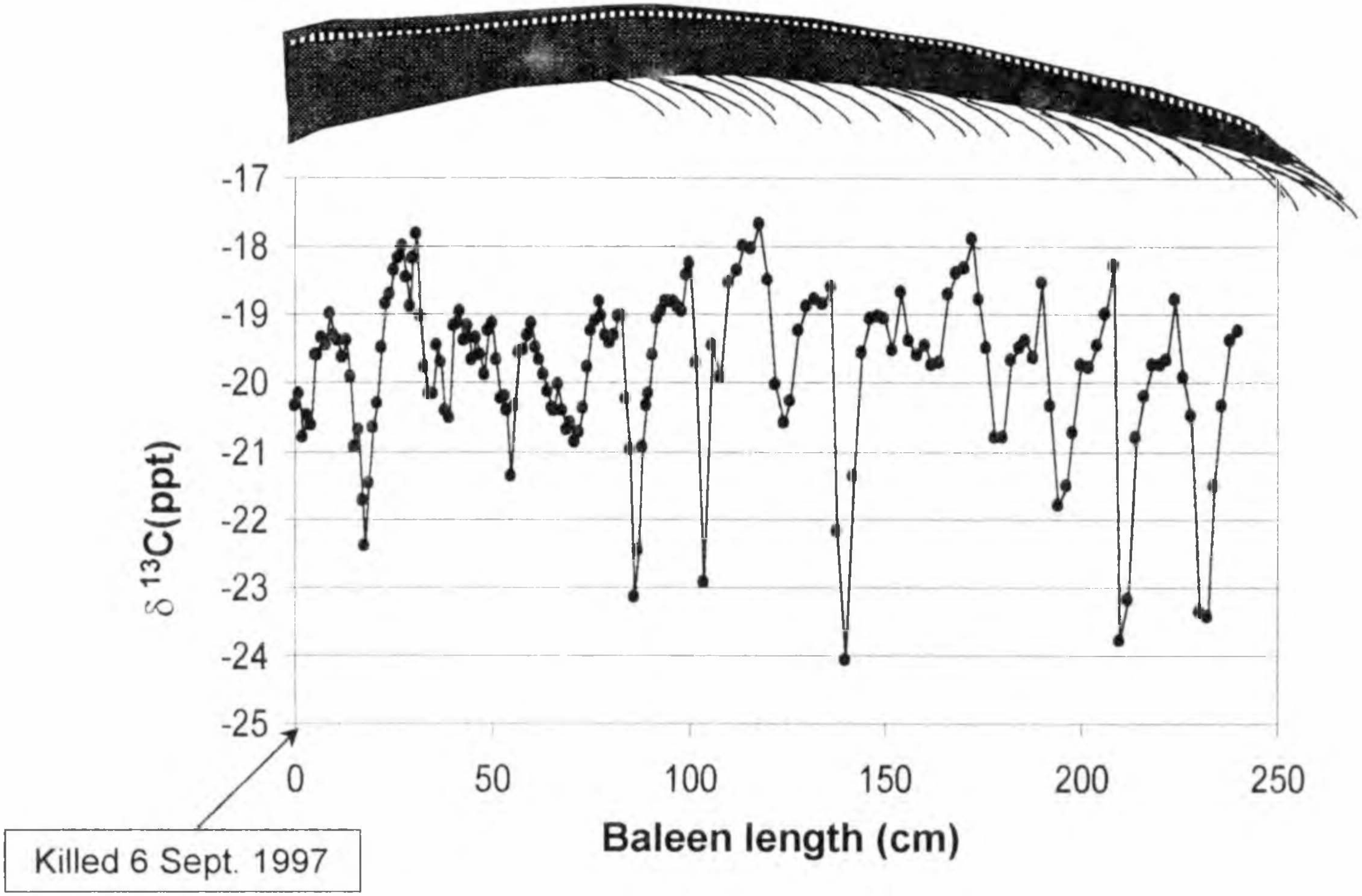


Figure 6. Carbon isotope ratios along the baleen plate from whale 97KK2, a 13.2 m male taken at Kaktovik, Alaska by Herman Aishanna on 6 Sept 1997.

$\delta^{13}C_{PDB}$ (‰) or $\delta^{15}N_{air}$

$$= \frac{R_{sample} - R_{standard}}{R_{standard}} * 1000$$

Where R is the ratio of ^{13}C: ^{12}C or ^{15}N: ^{14}N.

Isotope Ratios in Whale Tissues

Approximately 5 g of muscle, blubber and skin were collected from each whale by personnel from the North Slope Borough Dept. of Wildlife Management. Subsamples of each tissue were dried at 65 °C for 2 days to constant weight. Muscle and skin tissues became hard during drying, but blubber tissue was rendered to yellowish oil. Muscle and skin tissue were powdered in a mortar and pestle and then the fine powder analyzed for carbon and nitrogen isotope ratios. The oil from blubber was subsampled onto a piece of precombusted glass fiber filter and then analyzed. No nitrogen samples were collected from the oil because of the extremely low N content.

Muscle and skin samples were weighed into tin cups (0.8-1.0 mg) and analyzed in a Europa Continuous flow isotope ratio mass spectrometer. All samples were run in replicate and repeated when isotope values differed by over 0.3 ‰.

Zooplankton Sampling and Treatment

Zooplankton samplings were conducted in the eastern Alaskan Beaufort Sea during September 1998 and 1999. Some sampling sites were located near feeding bowheads. Samples of zooplankton were collected with horizontal or oblique net tows at each station. After each tow, the entire sample from one of the bongo nets was preserved in 10 % formalin and sub-samples from the other net were frozen for isotopic analysis (Griffiths, 1999). Samples were sorted at UAF for calanoid copepods, euphausiids, and chaetognaths in the laboratory. Sorted zooplankton samples were acidified with a few drops 10% hydrochloric acid to remove any carbonates and dried to a constant weight at 60-70 °C. No lipids were extracted as the data were also being used to assess food consumption by whales from different habitats. After weighing into cups (0.8-1.0 mg), all dried zooplankton samples were run directly on a Europa continuous flow mass spectrometry system, which determines both $\delta^{13}C$ and $\delta^{15}N$ on the same sample. All samples were run in duplicate and rerun when the two values differed by over 0.3 ‰.

Statistical Treatment of Data

Since most data sets were small, a Student's t-Test program (Microsoft Excel) was used to identify significant differences in each tissue between the adult and subadult from 1986-1988 and 1997-1999. For the baleen data analysis, the histogram tool in the Microsoft Excel program was used to calculate frequencies of $\delta^{13}C$ and $\delta^{15}N$ for each individual whale.

Estimation of Regional Feeding Activity using Baleen Isotope Ratios.

Approximate dietary composition and stable isotope values of the diet were defined for three regions listed in Tables 1 and 2. Because the primary feeding grounds of western arctic bowheads appears to be the eastern Beaufort Sea and Bering/Chukchi seas, only two of those regions were used as end members. Anticipated $\delta^{13}C$ and $\delta^{15}N$ values for the total consumed prey from the Bering/Chukchi and the eastern Beaufort regions were calculated by summing the taxon $\delta^{13}C$ times abundance for the two regions as follows;

In the eastern Beaufort Sea,

$\delta^{13}C = (-25.6)*0.596 + (-23.7)*0.263 + (-23.6)*0.101 + (-23.9)*0.04 = -24.83$ ‰

$\delta^{15}N = 10.4*0.596 + 9.2*0.263 + 8.5*0.101 + 8.2*0.04 = 9.81$ ‰

In the Bering and Chukchi Seas,

$\delta^{13}C = (-22.2)*0.55 + (-20.8)*0.45 = -21.57$ ‰

$\delta^{15}N = 10.5*0.55 + 10.1*0.45 = 10.33$ ‰

These values are anticipated values for total consumed prey for each region. The eastern Beaufort Sea could not be divided into Alaskan and Canadian values due to the lack of significant differences in $\delta^{13}C$ and $\delta^{15}N$ values for zooplankton from the two regions. Hence, the eastern Beaufort Sea end member includes both regions. For simple mixing models, $\delta^{13}C$ is more practical because a marked isotopic gradient is present in progressing from the Bering and Chukchi Seas to the eastern Beaufort region.

In order to correct for metabolic fractionation in the formation of baleen, 2.8 ‰ for $\delta^{13}C$ (Schell et al. 1989; Hobson et al. 1996) was added to each regional value. Therefore, $\delta^{13}C$ values of points on 0 to 50 cm (recent 2 or 3 years) of the baleen plates ≥ -18.8 ‰ suggest that those values come from 100 % Bering and Chukchi Seas food, whereas $\delta^{13}C$ values ≤ -22.0 ‰ were estimated as 100 % from the eastern Beaufort Sea. The $\delta^{13}C$ values between -18.8 and -22.0 ‰ are believed to result from mixing the two end members (Bering/Chukchi and eastern Beaufort). The percentage of intermediate points in the total points from 0 to 50 cm was multiplied by the fraction of feeding time from the eastern Beaufort Sea (f_{EBF}) using a simple mixing equation (Schell 1999) as

$$f_{EBF} = \frac{\delta^{13}C_{average} - \delta^{13}C_{BC}}{\delta^{13}C_{EBF} - \delta^{13}C_{BC}}$$

where

f_{EBF} = fraction of feeding time derived from the eastern Beaufort,

$\delta^{13}C_{average}$ = the average of $\delta^{13}C$ values between -18.80 and -22.00 ‰ from 0 to 50 cm of baleen plates,

$\delta^{13}C_{BC}$ = the average $\delta^{13}C$ of zooplankton from the Bering/Chukchi after the compensation for metabolic fractionation of baleen (2.8 ‰),

$\delta^{13}C_{EBF}$ = the average $\delta^{13}C$ of zooplankton from the eastern Beaufort Sea after the compensation for metabolic fractionation of baleen (2.8 ‰)

As a result, total percent of the feeding time from the eastern Beaufort Sea for recent years is the percent of $\delta^{13}C$ values $\leq$ -22.00 ‰ in the total points from 0 to 50 cm plus the percent derived from the eastern Beaufort Sea using $\delta^{13}C$ values between -18.80 and -22.00 ‰.

An additional correction in also needed in the calculation because baleen carbon isotope ratios have shown an overall 0.81‰ decrease in the Bering and Chukchi seas over the years 1994-1998 compared to1983-1987 (Table 8). As a result, an additional 0.81 ‰ was added to the average $\delta^{13}C$ of Bering/Chukchi zooplankton from this period so that data from the recently collected baleen could be directly compared to regional zooplankton data. For this study, it was assumed that the carbon isotope ratios in the zooplankton of the eastern Beaufort Sea were not changing between 1983-1987 or between 1994-1998.

RESULTS

Zooplankton Isotope Ratios from the Eastern Alaskan Beaufort Sea, 1998-1999

The average $\delta^{13}C$ and $\delta^{15}N$ values and standard deviations for copepods, euphausiids, and chaetognaths collected in 1998 and 1999 are summarized in Table 5. To examine inter-annual variability, the average $\delta^{13}C$ and $\delta^{15}N$ values of zooplankton from 1986-1990 and 1993-1995 studies (Schell et al. 1998) from the same region were included in Table 5. The average $\delta^{13}C$ values for copepods in 1998 are different from those in 1999 and from 1986-1990. Student's t-Test shows a significant difference in $\delta^{13}C$ of copepods between 1998 and 1999 ($p < 0.001$).

Isotope Ratios in Muscle and Baleen

Muscle and baleen tissues from 27 whales were analyzed for $\delta^{13}C$ and $\delta^{15}N$. Table 6 summarizes $\delta^{13}C$ and $\delta^{15}N$ values of newest baleen (0 cm) and soft tissues for each whale. The $\delta^{13}C$ and $\delta^{15}N$ values along the baleen plates have been plotted for each whale (Figure 13). Muscle tissue results reported by Schell (1992) are listed in Table 7.

Table 5. Average zooplankton isotope ratios, standard deviation and number of samples collected during this study from the Eastern Alaskan Beaufort Sea from 1998 to 1999, compared with samples from 1986-1995 reported in Schell et al. (1998).

	1998						**1999**						**Schell et al. 1998**					
	$\delta^{13}C$	**S.D.**	**N**	$\delta^{15}N$	**S.D.**	**N**	$\delta^{13}C$	**S.D.**	**N**	$\delta^{15}N$	**S.D.**	**N**	$\delta^{13}C$	**S.D.**	**N**	$\delta^{15}N$	**S.D.**	**N**
Copepods	-24.7	0.37	30	10.8	0.99	30	-25.6	0.59	33	10.3	0.56	33	-25.7	0.20	57	10.8	0.19	45
Euphausiids	-23.1	1.18	5	11.2	0.71	5	-24.2	0.85	5	11.0	0.29	5	-23.7	0.32	21	9.2	0.57	18
Chaetognaths	-23.2	0.32	11	12.8	0.81	11	-23.5	0.18	4	12.3	0.75	4	-23.4	0.53	5	13.5	0.60	5

Table 6. $\delta^{13}C$ and $\delta^{15}N$ values of bowhead whale tissues for 1997-1999 whales. Baleen (0 cm) represents the most recently formed baleen from the baleen plates.

Whale	**Muscle**		**Baleen 0 cm**		**Skin**		**Blubber**
	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
97B8			-18.36	13.70			
97B11			-19.96	13.89			
97B12			-20.66	13.55			
97B14	-19:87	13.65					
97B16	-20.80	14.91					
97B18	-20.83	12.85					
97B20	-20.62	13.00					
97B21	-20.98	12.31					
97B22	-21.38	12.68					
97B23	-20.46	12.58					
97B24	-20.70	12.91					
97B25	-21.37	12.97	-19.56	13.49			
97B26	-21.41	12.80					
97B27	-21.53	12.64					
97B28	-19.99	13.78					
97B29	-20.00	13.46					
97B30	-21.78	14.45					
97KK1	-20.79	12.85	-20.83	13.64	-21.72	13.00	-27.00
97KK2	-20.42	12.94	-20.33	13.09	-20.74	13.41	-26.13
97KK3	-20.44	14.67	-20.70	13.38	-21.50	13.51	-25.77
97KK4	-20.01	13.62	-19.91	13.94	-19.66	14.42	-25.50
98KK1	-20.47	12.40	-19.60	12.49	-21.17	13.80	-26.25
98KK2	-19.80	12.84	-19.33	13.14	-20.94	13.71	-26.16
98KK3	-21.30	12.54	-19.54	13.23	-21.29	13.30	-25.40
99KK1	-20.91	13.72	-20.04	15.61	-19.56	14.95	-26.71
99KK2	-20.49	12.60	-20.53	14.25	-20.86	13.62	-25.52
99KK3	-20.87	12.66	-20.93	13.65	-21.16	13.86	-26.88

Table 7. $\delta^{13}C$ and $\delta^{15}N$ values of muscle tissue for 1986-1988 whales (from Schell, 1992).

Whale	Muscle	
	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
86B1	-19.43	15.24
86B2	-20.10	14.63
86B3	-20.56	12.64
86B4	-19.55	15.56
86B5	-19.10	14.42
86B6	-19.73	13.30
86B7	-20.11	15.56
86KK1	-21.45	13.91
86KK2	-19.12	13.86
86KK3	-21.38	14.97
86WW1	-18.84	14.38
86WW2	-19.35	13.62
87B5F	-18.94	14.23
87B6	-19.20	13.27
87B7	-20.83	13.85
87N1	-20.85	12.89
88B1	-20.16	14.55
88B2	-19.43	14.80
88B3	-19.24	
88B4	-19.28	14.54
88B5	-19.43	13.80
88B6	-19.94	14.30
88B8	-19.52	13.97
88G2	-19.06	13.90

Table 8. Average $\delta^{13}C$ and $\delta^{15}N$ values, standard deviation, and number of whales for baleen grown while feeding in the Bering and Chukchi Seas by year. Each baleen plate spans several years and was sampled at 3-5 points for each year. Standard deviations are for all points in a given year.

Year	Number of Whales	$\delta^{13}C$ (‰)	Std. Dev.	$\delta^{15}N$ (‰)	Std. Dev.
1946	1	-18.07			
1947	1	-17.61		14.19	
1948	1	-17.34		14.43	
1949	1	-17.61		13.48	
1950	2	-17.68	0.02	13.36	0.39
1951	2	-17.70	0.34	14.04	0.45
1952	2	-17.92	0.45	15.21	0.62
1953	3	-17.27	0.17	15.57	0.33
1954	4	-17.68	0.51	15.41	0.92
1955	4	-17.63	0.42	15.07	1.26
1956	4	-17.92	0.73	14.93	1.19
1957	4	-17.63	0.83	15.49	0.94
1958	4	-17.66	0.52	14.86	0.49
1959	4	-17.68	0.65	14.99	0.55
1960	4	-17.65	0.68	15.09	0.35
1961	4	-17.70	0.43	15.52	0.48
1962	4	-17.52	0.31	15.60	0.24
1963	4	-17.46	0.43	15.01	0.47
1964	3	-17.19	0.31	15.37	0.67
1965	2	-16.54	1.04	15.24	0.40
1966	4	-16.85	0.24	15.05	0.67
1967	5	-16.69	0.41	15.15	0.25
1968	5	-17.05	0.60	15.35	0.33
1969	8	-17.66	0.37	14.41	0.67
1970	10	-17.77	0.80	14.62	1.06
1971	12	-17.99	0.40	15.32	0.59
1972	13	-17.71	0.60	15.02	0.20
1973	14	-17.50	0.41	15.00	0.54
1974	14	-17.16	0.23	14.40	0.46
1975	14	-17.18	0.41	14.89	1.08
1976	14	-17.57	0.31	15.05	0.85
1977	14	-17.46	0.52	14.61	0.65
1978	14	-17.72	0.49	14.23	0.35
1979	14	-17.84	0.42	14.51	0.43
1980	14	-17.91	0.46	14.32	0.50
1981	14	-18.23	0.42	14.17	0.42

1982	14	-18.23	0.41	14.48	0.59
1983	14	-18.39	0.39	14.38	0.45
1984	14	-18.79	0.36	14.52	0.61
1985	15	-17.78	0.28	15.01	0.48
1986	13	-18.47	0.28	14.25	0.56
1987	9	-18.27	0.26	13.87	0.41
1988	4	-18.56	0.36	14.27	0.62
1989	3	-18.01	0.30	14.20	0.30
1990	4	-17.94	0.34	14.36	0.45
1991	4	-18.03	0.26	14.33	0.78
1992	4	-18.09	0.22	14.83	0.36
1993	4	-19.07	0.56	14.09	0.29
1994	4	-19.33	0.56	14.34	0.09
1995	10	-18.55	0.38	14.49	0.54
1996	10	-19.11	0.46	13.80	0.38
1997	4	-19.30	0.18	14.09	0.22
1998	2	-19.47	0.21	14.23	0.13

Decadal shifts in $\delta^{13}C$ in bowhead muscle and baleen

Fall muscle for 1997-1999 exhibits a unimodal distribution in $\delta^{13}C$ with a range from - 22 to -19.5 ‰, centered about a mode of -20.5 ‰. By comparison, the spring muscle for 1986-1988 falls between -21 and -18.5 ‰ with a maximum frequency at -19.5 ‰ (Figure 7). There is an apparent shift of 1.0 ‰ between fall muscle and spring muscle. In addition, average values of $\delta^{13}C$ were different by 1.2 ‰ with -20.75 ‰ for 1997-1999 and -19.58 ‰ for 1986-1988. Obviously, the whale muscle differs between spring and fall, which might mean the whales feed to a significant extent during summer in the eastern Beaufort Sea. This, however, is not the case, but is due to a temporal bias in the data over the intervening decade.

Figure 8 shows the interdecadal average $\delta^{13}C$ and $\delta^{15}N$ values in baleen laid down during feeding in the Bering and Chukchi seas from 1946 to 1998. A comparison of the average values for the years 1986-1988 with the averages for samples collected in 1997-1998 shows a decline of approximately 1‰ from -18.17 ‰ to -19.29 ‰ (Table 8 and Figs. 17 and 18). This is essentially the same as the 1 ‰ difference observed between spring and fall muscle samples over the same time span (Figure 7). If this correction is applied to the observed values in muscle samples, the spring muscle values are not significantly different from the fall muscle (t-Test, 2 tails, p=0.81) (Figure 9).

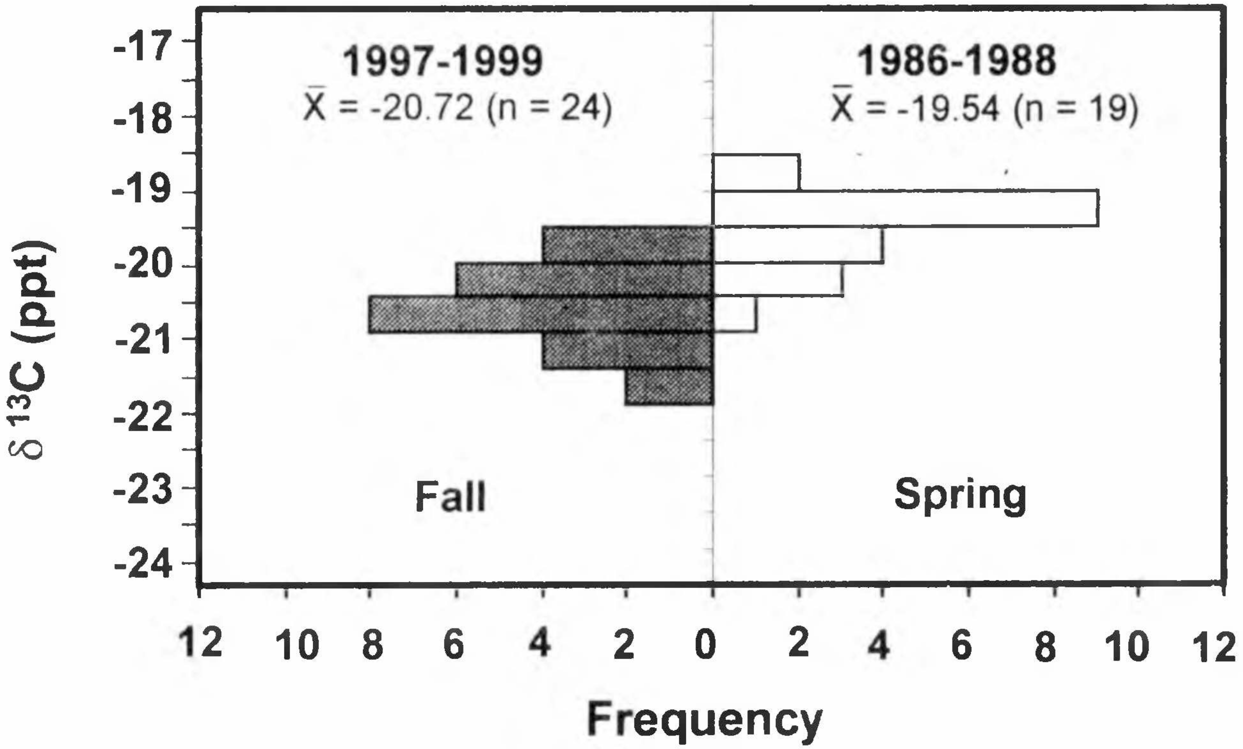


Figure 7. $\delta^{13}C$ values in bowhead whale muscle tissue taken in 1986-1988, compared to whales taken in 1997-1999.

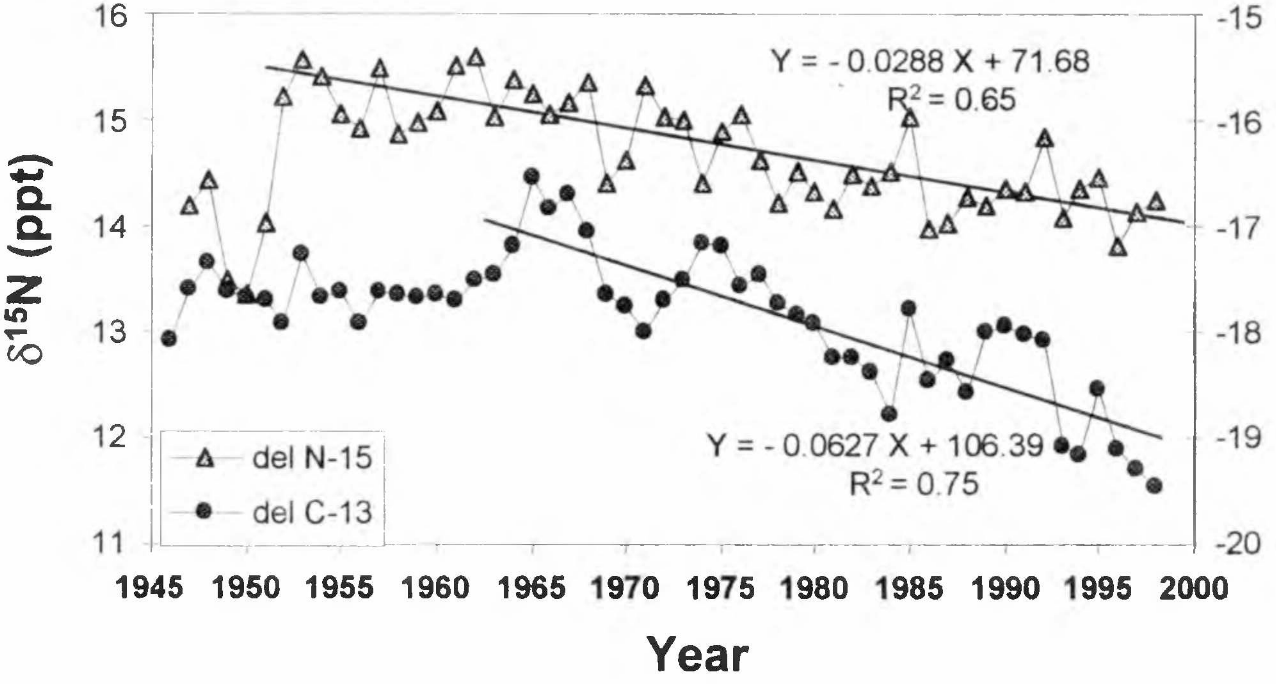


Figure 8. Average annual carbon and nitrogen isotope ratios in the portions of 39 whale baleen plates laid down during feeding in the Bering and Chukchi seas over the past five decades. Straight lines are least-squares linear fits from 1965 to 1998 for carbon and from 1952 to 1998 for nitrogen.

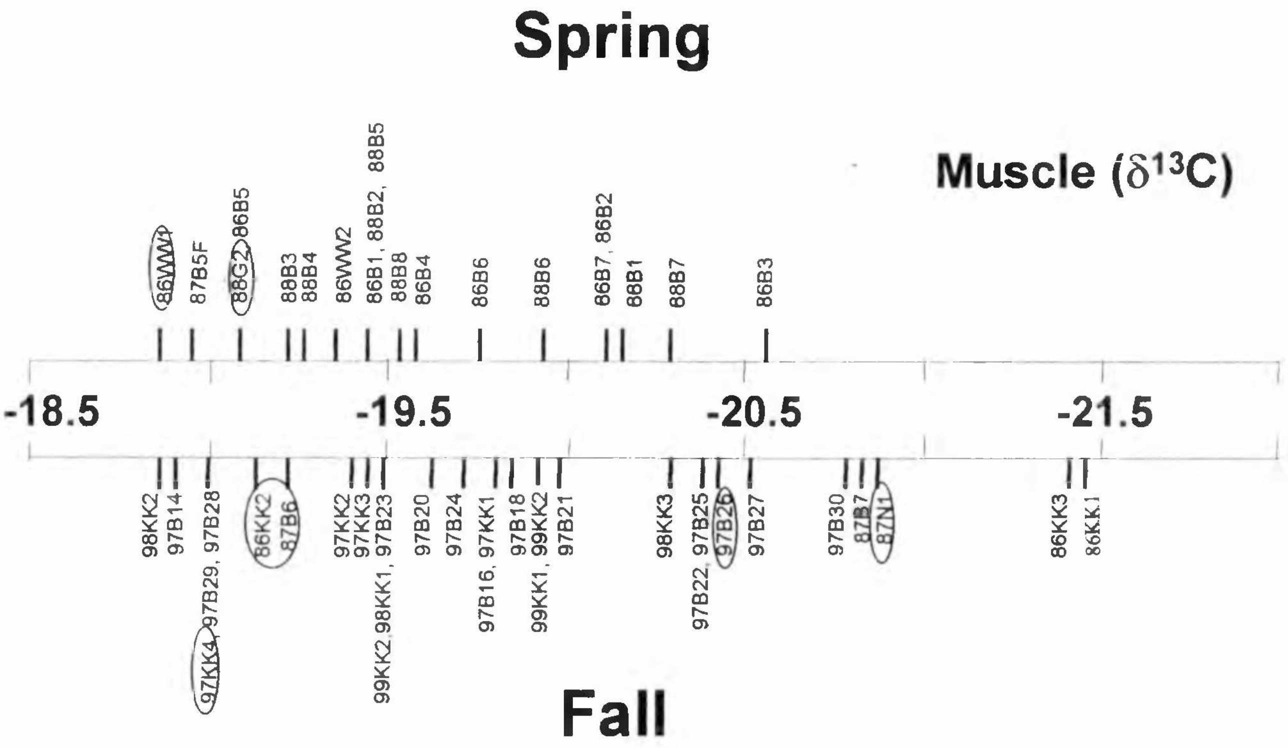


Figure 9. Comparison of $\delta^{13}C$ in whale muscle from spring and fall seasons. Data are normalized by adding 1‰ to 1997-99 whales to compensate for the decrease of 1‰ from 1986-1988 to 1997-1999 in Bering/Chukchi baleen. The whale numbers in circles are adults (body length ≥ 13.5 m).

Seasonal change in $\delta^{15}N$ of muscle and baleen

Whales taken in 1997-1999 have muscle with a mean $\delta^{15}N$ value of 13.16 ± 0.72 ‰ (Figure 10), whereas muscle samples for 1986-1988 have an average $\delta^{15}N$ of 14.32 ± 0.76 ‰ or an enrichment of 1.2‰. $\delta^{15}N$ values as well as $\delta^{13}C$ in muscle have decreased in the past decade (Figure 8). However, Bering/Chukchi baleen from the years 1997-1998 and 1986-1988 show similar average values. Therefore, the difference in $\delta^{15}N$ of muscle shown in Figure 10 is seasonal rather than decadal. The t-Test showed that the spring muscle is significantly different from the fall muscle ($p < 0.001$). The muscle samples from 1997-1999 are composed of 21 subadults and 3 adults and the 1986-1988 muscle samples are made up of 16 subadults and 3 adults.

Baleen from subadults decreased in both $\delta^{13}C$ and $\delta^{15}N$ but baleen from adult whales decreased only in $\delta^{13}C$, not in $\delta^{15}N$ (Figure 17-20). The ranges in $\delta^{15}N$ values for baleen from adults are almost identical for 1986-1988 and 1997 (Figure 19). The average $\delta^{15}N$ of adults for 1997 is 14.04 ± 0.68 ‰ and for 1986-1988, 14.00 ± 0.63 ‰. By comparison, the average for subadults decreased by about 0.5 ‰ and the number of high $\delta^{15}N$ values (above 15 ‰) decreased from 1986-1988 to 1997-1999 (Figure 20).

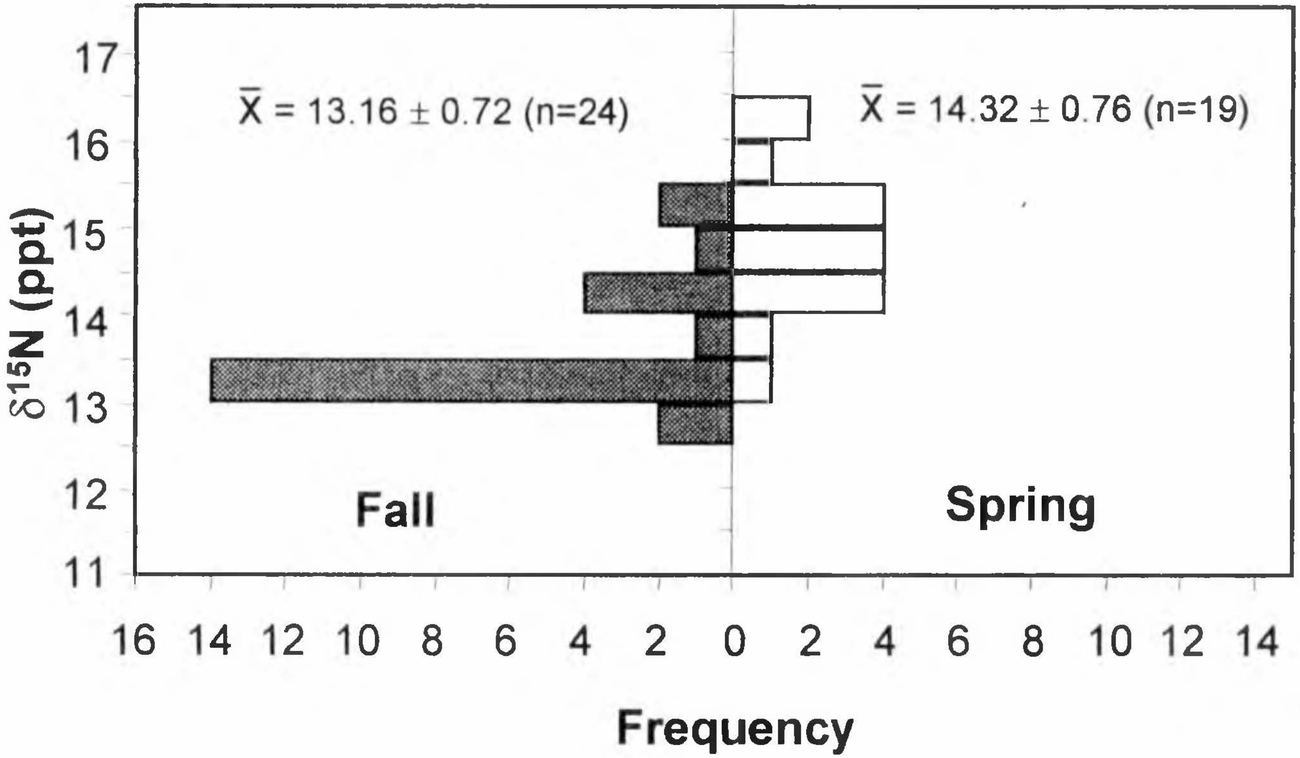


Figure 10. $\delta^{15}N$ values of fall and spring bowhead muscle (all whales). Fall muscle was taken in 1997-1999 and spring muscle was from 1986-1988.

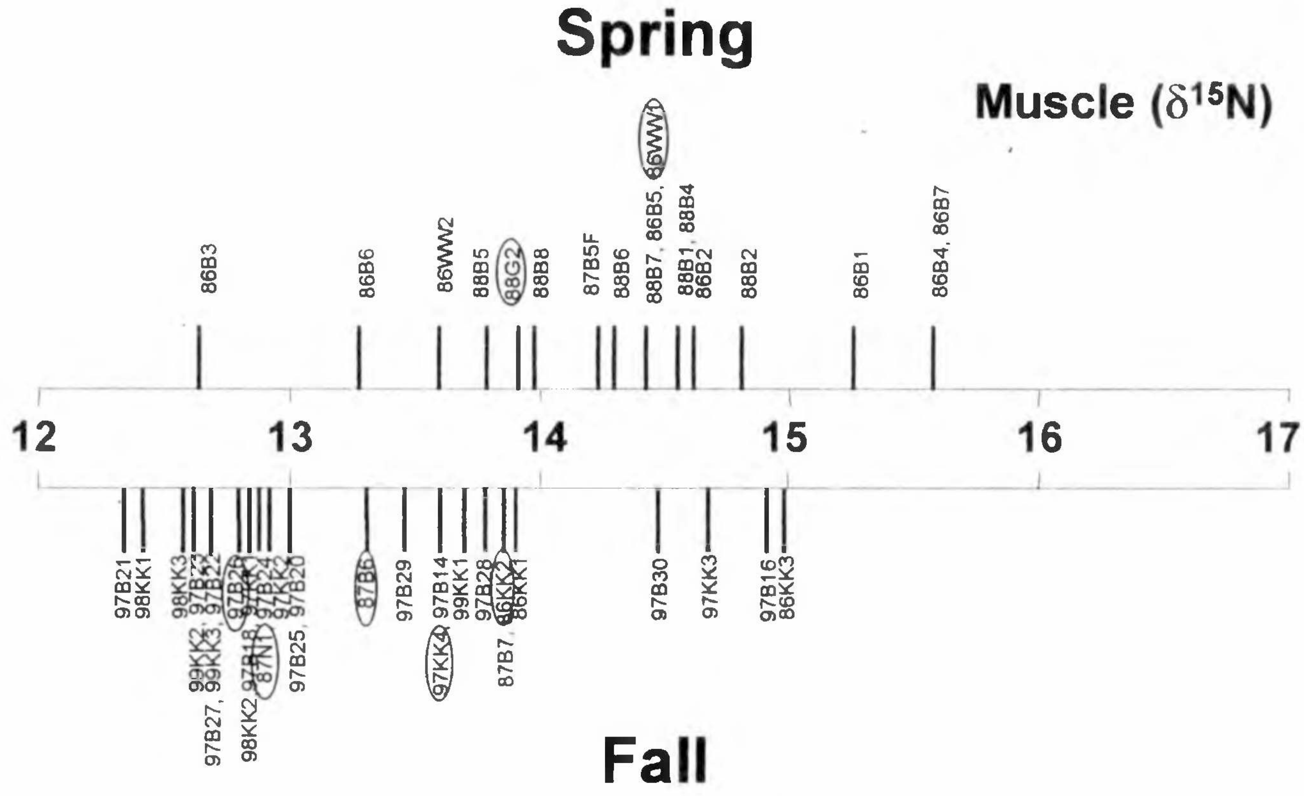


Figure 11. Comparison of $\delta^{15}N$ of subadults versus adults in muscle collected during spring and fall. The whale numbers in circles are adults (body length ≥ 13.5 m).

Temporal Variation of Isotope Ratios in Baleen

The baleen provides a continuous isotopic record over the temporal span required for its growth (Schell 1987; Schell et al. 1989; Hobson and Schell 1998). Figure 12 shows a highly significant correlation ($r^2 = 0.96$) between whale body length and baleen length in 14 whales for 1997-1999. Baleen length increases by about 26.9 cm for each 1m increase in whale body length. This increase in plate length is similar to the 27.5 cm for each 1m increase in whale length found by Lowry (1993).

Each major oscillation in $\delta^{13}C$ along the baleen plate reflects the annual movement of the whale between the eastern Beaufort Sea, with relatively ^{13}C-depleted zooplankton, to the Chukchi and Bering Seas, with more ^{13}C-enriched zooplankton (Schell et al. 1989; Schell and Saupe 1993). In contrast to $\delta^{13}C$, the interpretation of $\delta^{15}N$ oscillations is more difficult, because there is no marked geographic gradient of $\delta^{15}N$ in major prey from the eastern Beaufort Sea to the Bering and Chukchi Seas (Table 2).

$\delta^{13}C$ record along the baleen plates

Every plate harvested in the fall has new baleen (0 cm) depleted in ^{13}C except 97B8 (Figure 13). This is result of previous feeding on ^{13}C depleted zooplankton in the eastern Beaufort region during the summertime. Whale 97B8,

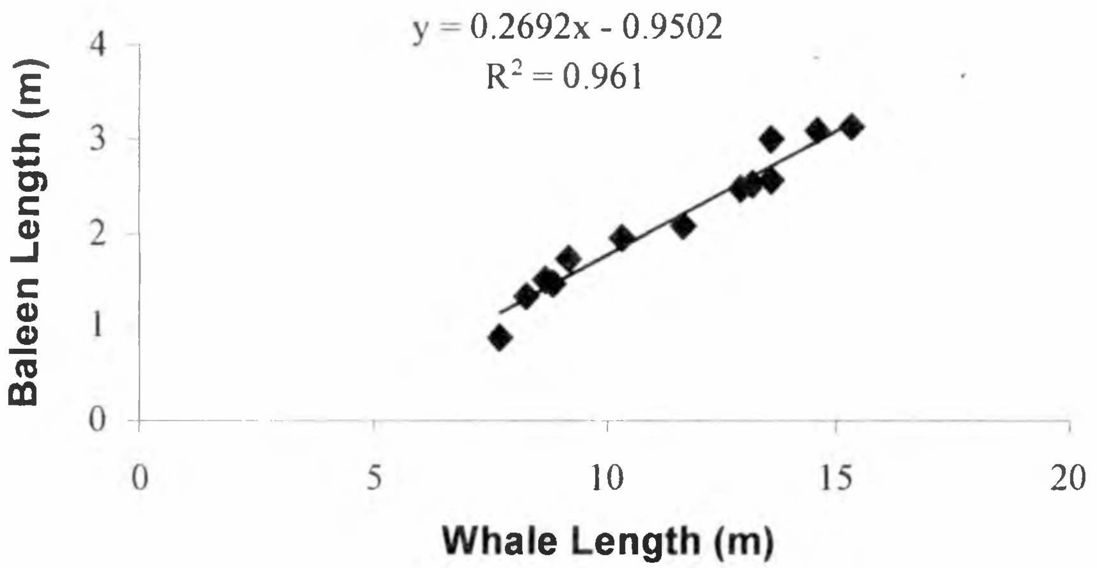


Figure 12. Relationship between baleen length (m) and whale length (m) for bowhead whales (n=14) landed at Kaktovik and Barrow, 1997-1999.

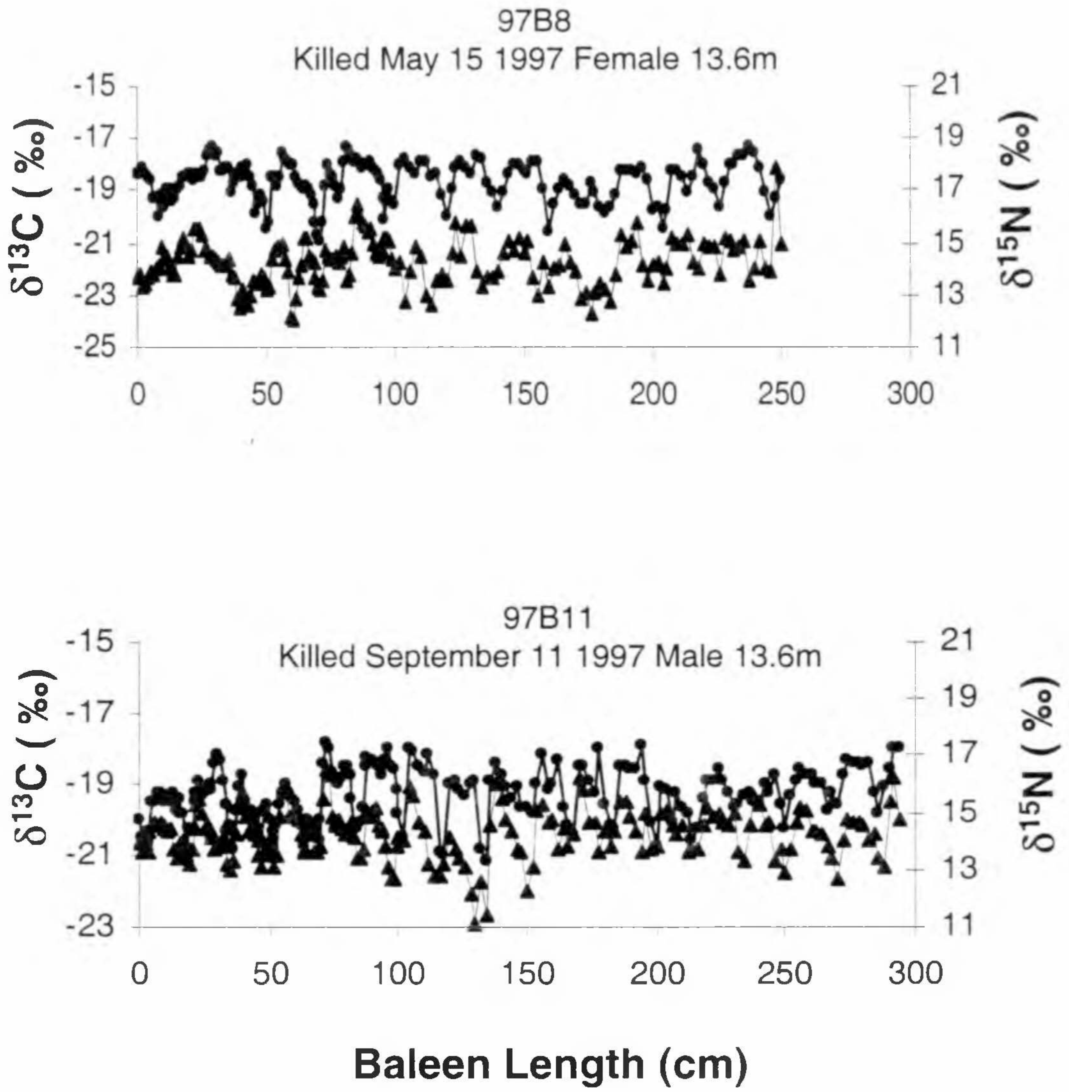


Figure 13. Carbon and nitrogen isotope ratios along the baleen plates from bowhead whales (*Balaena mysticetus*) killed between 1997 and 1999. Base of plate (newest baleen) is at left in all traces. Carbon trace (•—•), nitrogen trace (▲—▲).

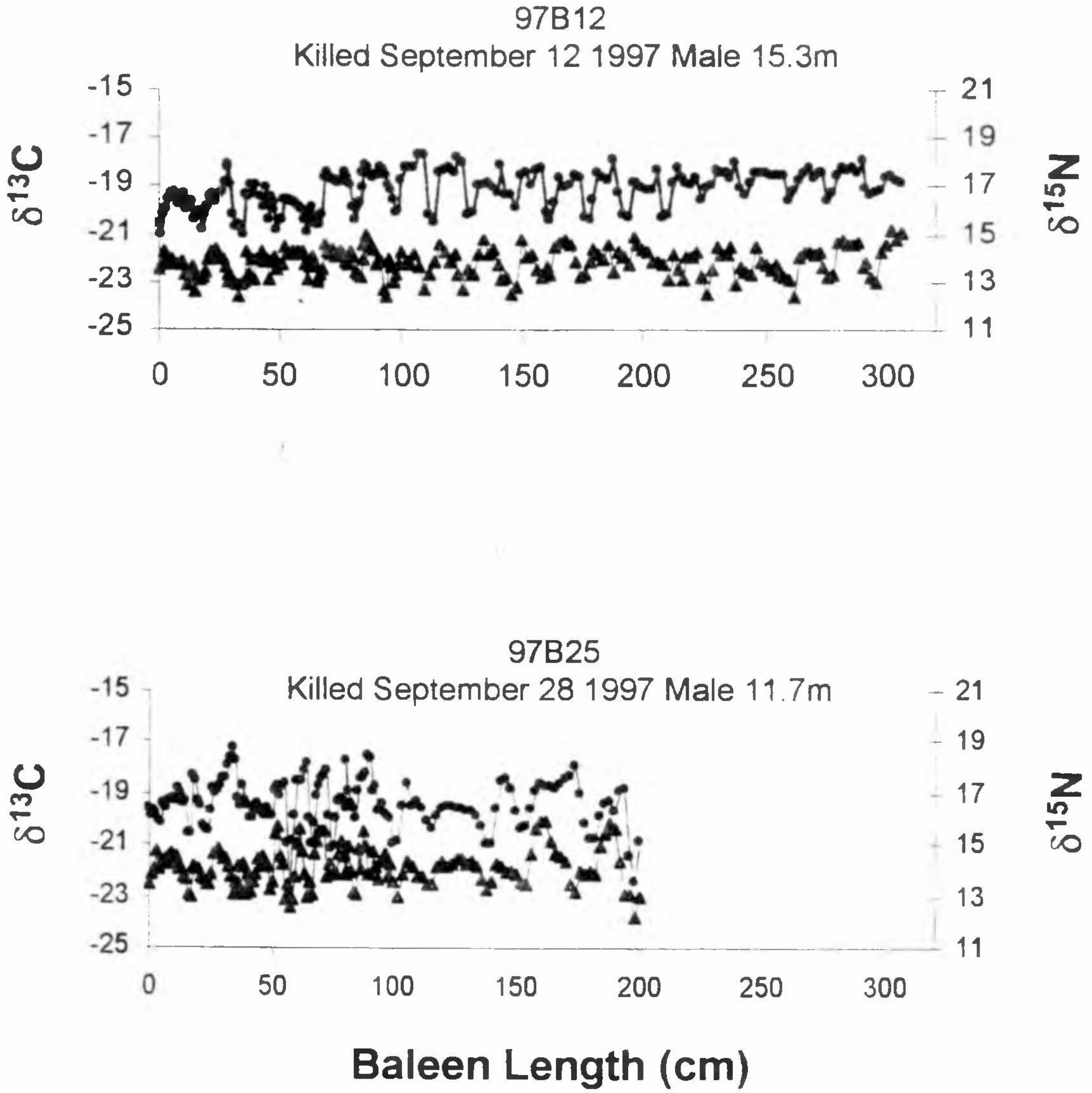


Figure 13. (continued).

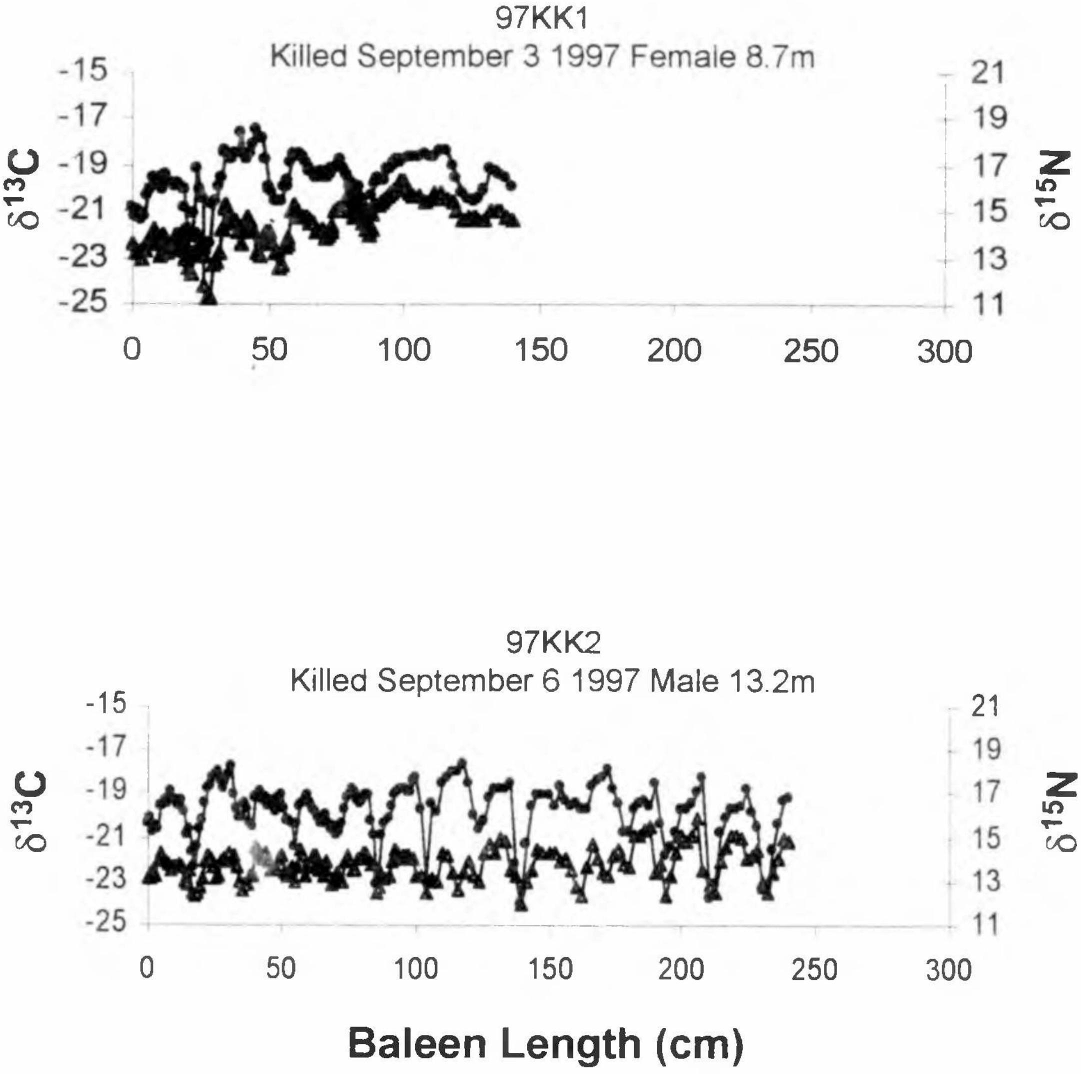
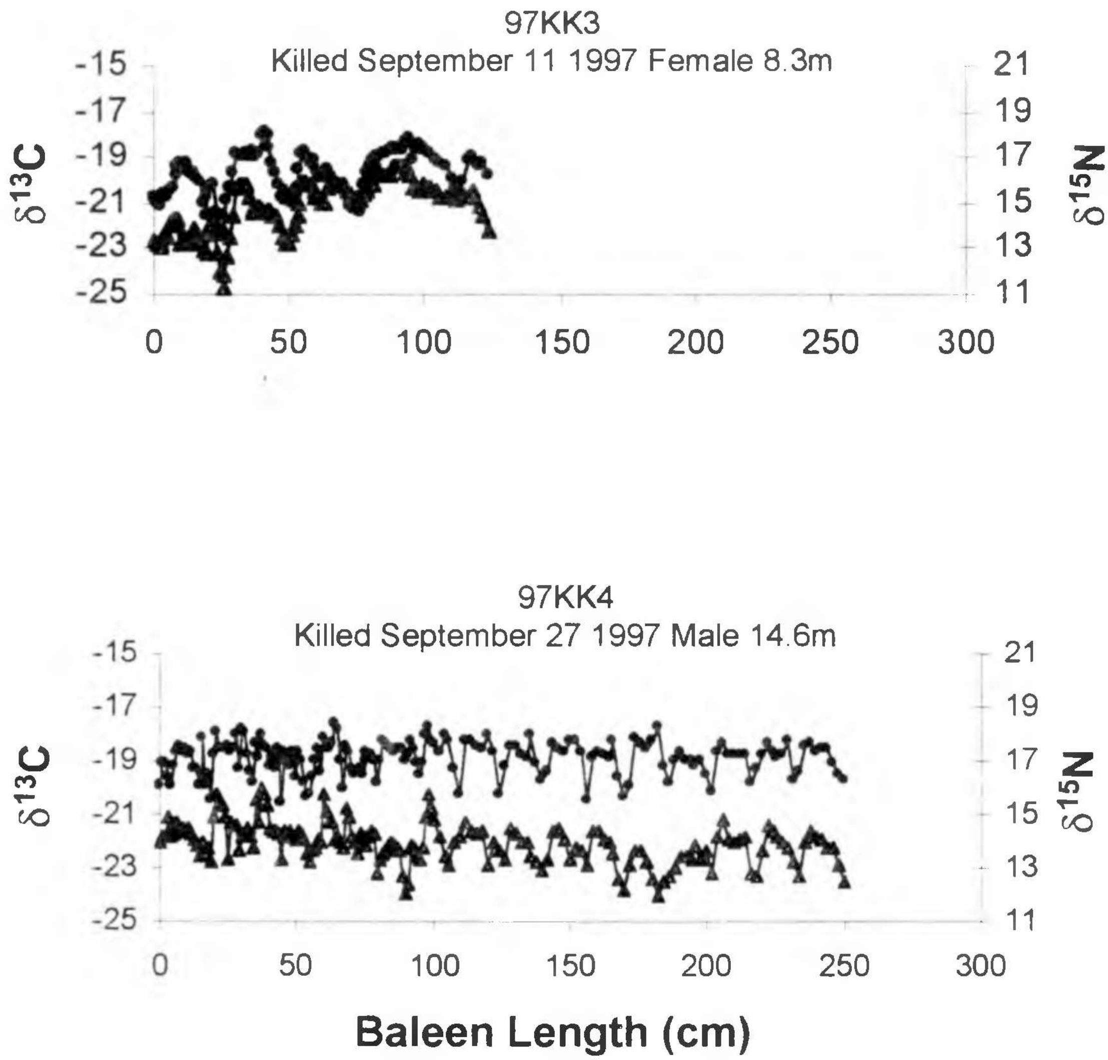


Figure 13. (continued).



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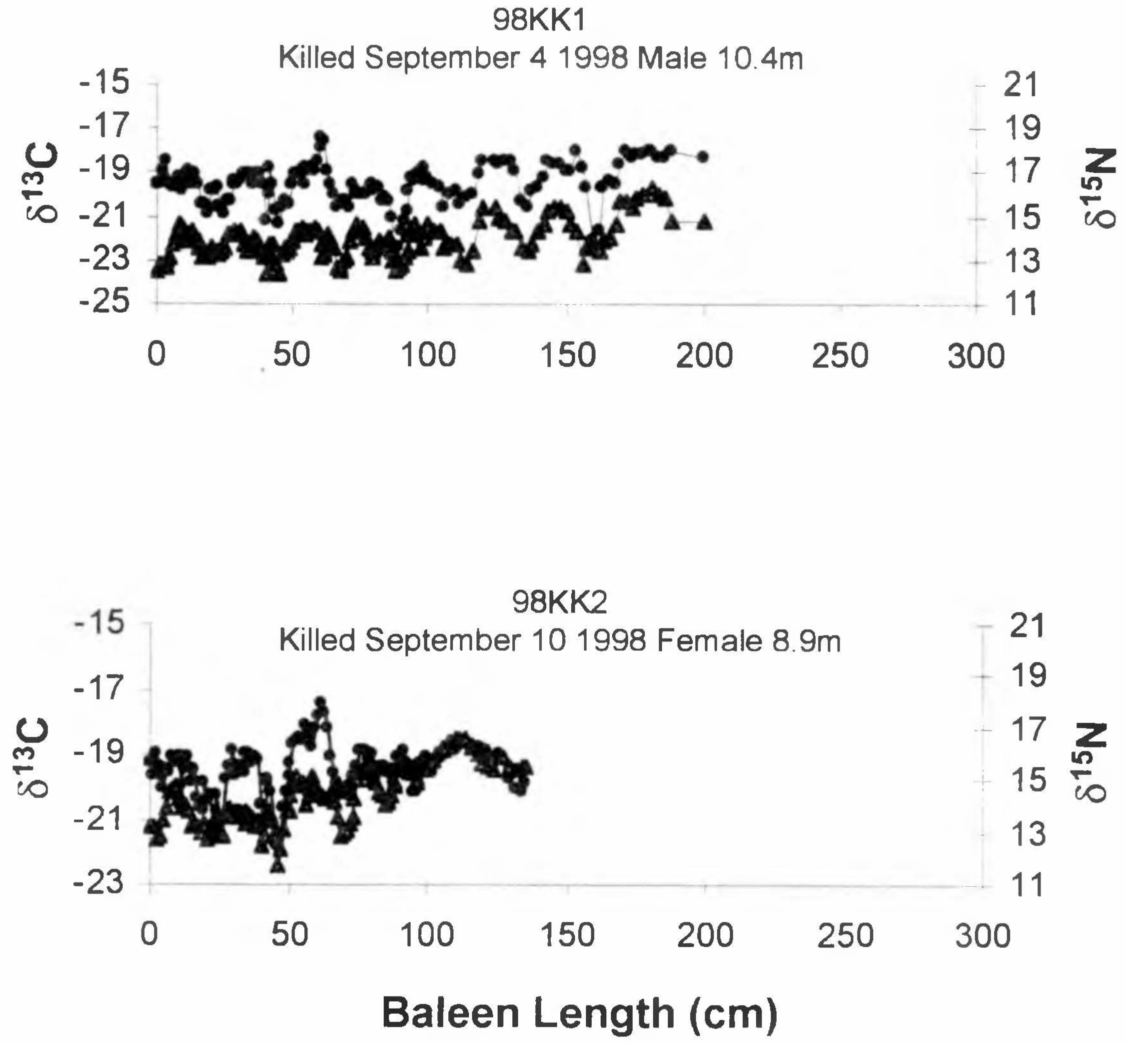
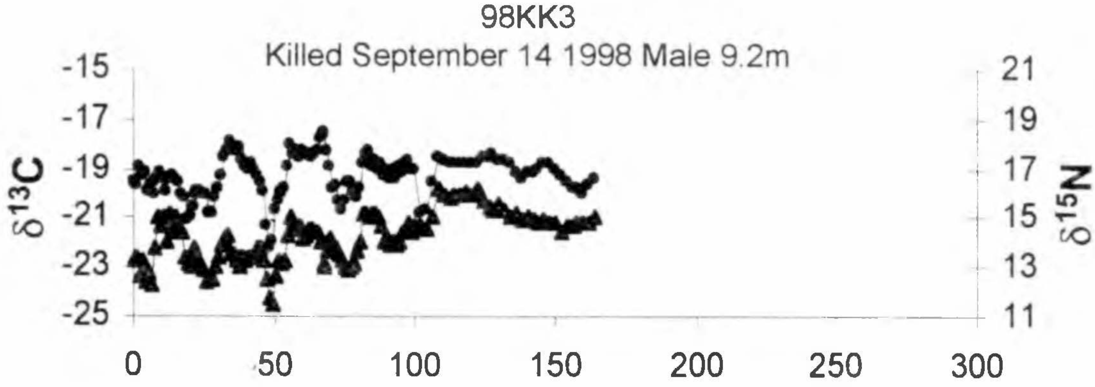


Figure 14. (continued).



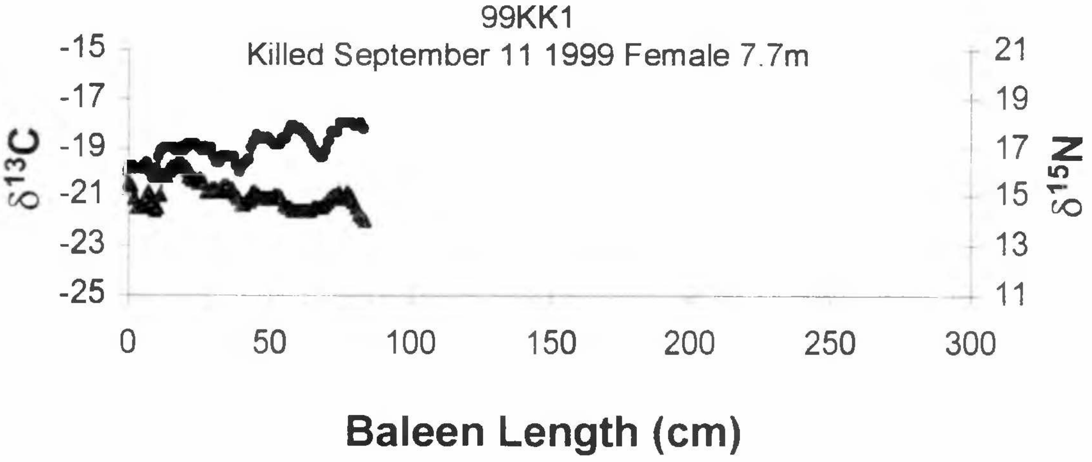


Figure 13. (continued).

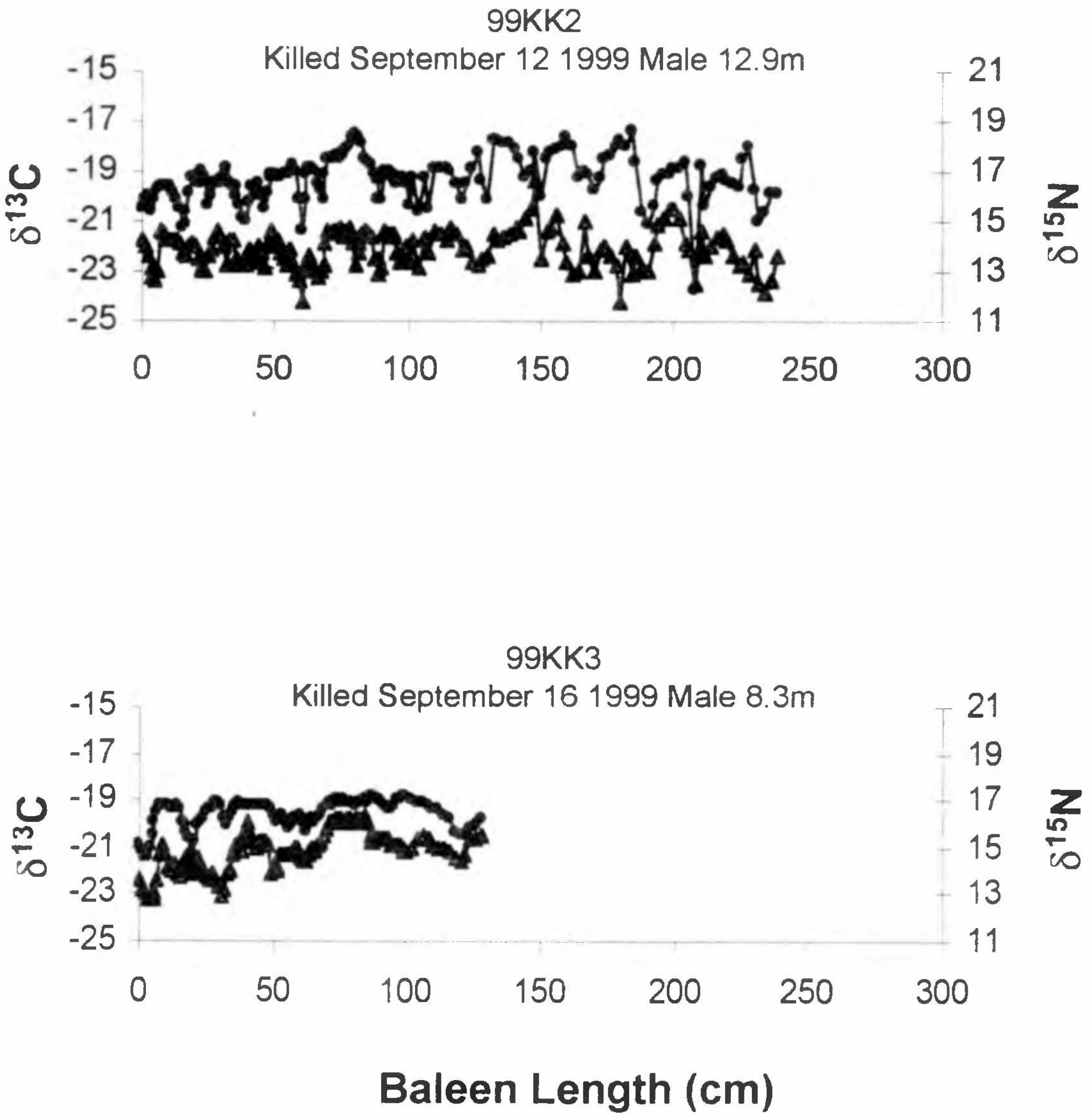


Figure 13. (continued).

killed in the spring, has ^{13}C-enriched baleen derived from food sources in the Bering and Chukchi seas. This provides evidence that baleen grows continuously throughout the year, not only in summer but also during winter (Schell et al. 1989).

Peaks (more enriched values) in the graph are believed to be formed during the fall and winter and the valleys in summer (Figure 13). Generally, fall-winter portions of the curves are wider than summer portions, especially for adult whales (≥13.5 m). The heights and widths of the peaks and valleys vary each year in response to changes in zooplankton composition, feeding grounds, and other environmental conditions (Schell et al. 1989; Schell 1992). The number of $\delta^{13}C$ peaks in each plate was highly correlated with both baleen length (r^2=0.94) and whale body length (r^2=0.96) (Figures 14 and 15).

The three whales killed at Kaktovik in 1998 and 97B25 killed at Barrow have relatively higher $\delta^{13}C$ in the new baleen laid down shortly before death than the 7 Kaktovik whales from 1997 and 1999. These whales are all subadults (< 13.5m). Generally, young whales taken at Kaktovik in the fall are more ^{13}C-depleted than adult whales (Schell et al 1989).

A young whale, 99KK1, shows subdued $\delta^{13}C$ oscillations and relative ^{13}C enrichment of the baleen. This whale is estimated at 1.5 years old using the

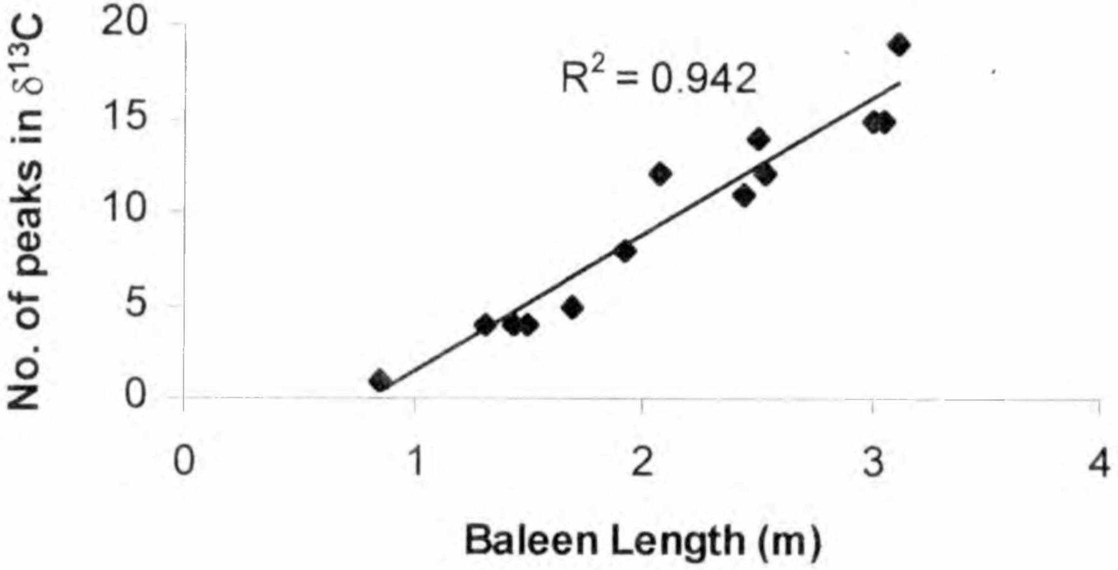


Figure 14. Relationship between the number of peaks in $\delta^{13}C$ along the baleen plates and baleen length (m) of bowhead whales (n=14) for 1997-1999 .

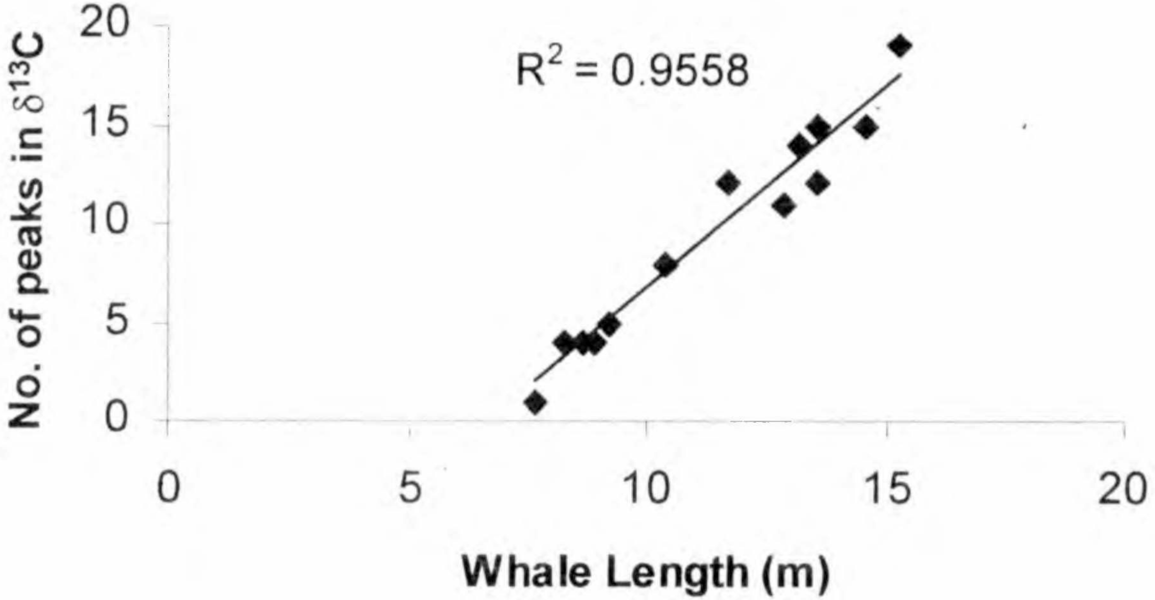


Figure 15. Relationship between the number of peaks in δ^{13}C along the baleen plates and whale length (m) of bowhead whales (n=14) for 1997-1999 .

equation for age in Schell and Saupe (1993). Because most young are assumed to be weaned at 9-12 months of age (Koski et al. 1993; Nerini et al. 1984), this whale is assumed to be recently weaned. Usually, the amplitudes of the oscillations in $\delta^{13}C$ in baleen increase as young whales become subadults and then tend to decrease as they become adults (Schell 1987).

Table 9 shows averages and ranges of stable carbon and nitrogen isotope values along the whole baleen plates for 1997-1999 whales. Generally, average $\delta^{13}C$ values of adult whales are more enriched than those of subadults, and $\delta^{13}C$ ranges of adults (except 97B11) are narrower than those of subadults.

$\delta^{15}N$ values of baleen plates

The seasonal oscillations of $\delta^{15}N$ along baleen plates are often as large as the $\delta^{13}C$ fluctuations in Figure 13. This is interesting because there were no observed large generalized gradients of $\delta^{15}N$ for zooplankton between the Beaufort and northern Bering and Chukchi seas (Table 2). The $\delta^{15}N$ oscillations are usually positively correlated with the changes in $\delta^{13}C$ along the plates. The $\delta^{15}N$ oscillations along the plates typically range from approximately 11.0 to 16.0 ‰ (Table 9). However, most subadults have greater fluctuations in $\delta^{15}N$ than adults.

Table 9. Average and range of stable carbon and nitrogen isotope values for all measurements along the baleen plates during the 1997-1999 period.

Whale (‰)	n	Average $\delta^{13}C$	Range (‰)	Average $\delta^{15}N$	Range
97B8	158	-18.69	-20.98 to -17.28	14.21	12.07 to 16.44
97B11	198	-19.32	-21.13 to -17.84	14.24	11.11 to 16.49
97B12	204	-19.22	-21.07 to -17.69	13.78	12.31 to 15.15
97B25	151	-19.51	-22.92 to -17.54	14.09	12.20 to 15.89
97KK1	121	-19.64	-22.83 to -17.44	14.31	11.20 to 16.36
97KK2	171	-19.80	-24.09 to -17.68	13.72	11.96 to 15.93
97KK3	103	-19.72	-22.50 to -17.87	14.79	11.30 to 16.67
97KK4	176	-18.95	-20.70 to -17.65	13.90	11.92 to 15.93
98KK1	145	-19.60	-22.70 to -17.41	13.93	12.34 to 16.31
98KK2	119	-19.50	-21.86 to -17.21	14.33	11.68 to 16.65
98KK3	133	-19.31	-22.19 to -17.49	14.14	11.56 to 16.21
99KK1	84	-19.02	-20.26 to -18.04	15.06	14.06 to 16.36
99KK2	170	-19.31	-23.79 to -17.35	13.87	11.76 to 16.63
99KK3	115	-19.58	-21.41 to -18.83	14.80	12.72 to 16.29

The $\delta^{15}N$ values along the baleen of 99KK1 increase from the apparent time of birth to near the time of death. This is also true for other young whales that retain the newly grown baleen from their birth (Figure 16). Adults and subadults do not have this baleen because of loss from wear of the tip.

The Feeding Pattern of Subadults vs. Adults

Figures 17-20 show $\delta^{13}C$ and $\delta^{15}N$ of values in frequency histograms from 0 to 50 cm of baleen (formed during the most recent 2 or 3 years) of subadults (n=9) and adults (n=4) for 1997-1999. These are compared with similar data from 1986-1988 whales. Subadults were separated by body length (<13.5 m) from adults (≥13.5 m). The range in $\delta^{13}C$ values of subadult whales is greater than that of adults for both time periods (Figures 17 and 18). The range of $\delta^{13}C$ for adults is from - 20 to -17 ‰ for 1986-1988 and from -20.5 to -17.5 ‰ for 1997. By comparison, $\delta^{13}C$ values of subadults range from -23 to -17‰ for 1986-1988 and - 22.5 to -17 ‰ for 1997-1999. The wider range for subadults is also found in $\delta^{15}N$ values (Figures 19 and 20). The range of $\delta^{15}N$ in adults is from 12.5 to 16 ‰ for both periods, and $\delta^{15}N$ of subadults ranges from 12.5 to 18 ‰ for 1986-1988 and 11.5 to 16.5 ‰ for the 1997-1999 period.

The differences that result from the feeding strategies of subadults versus adults are evident in Figure 21. The plots show $\delta^{13}C$ and $\delta^{15}N$ values for each

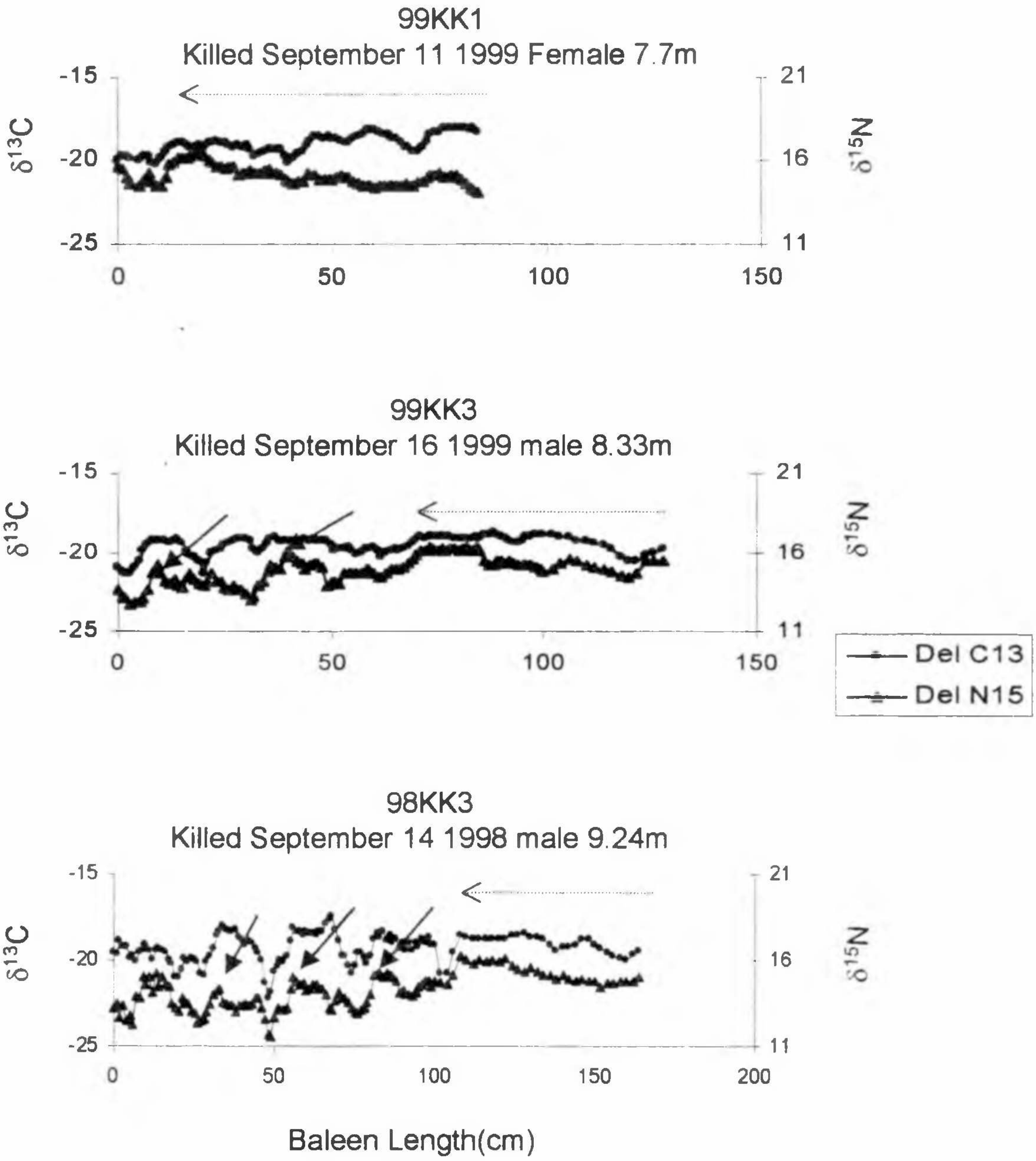


Figure 16. Estimated nursing period (←) and maximum $\delta^{15}N$ enrichments (↓) during the winter time along the baleen plates of young whales.

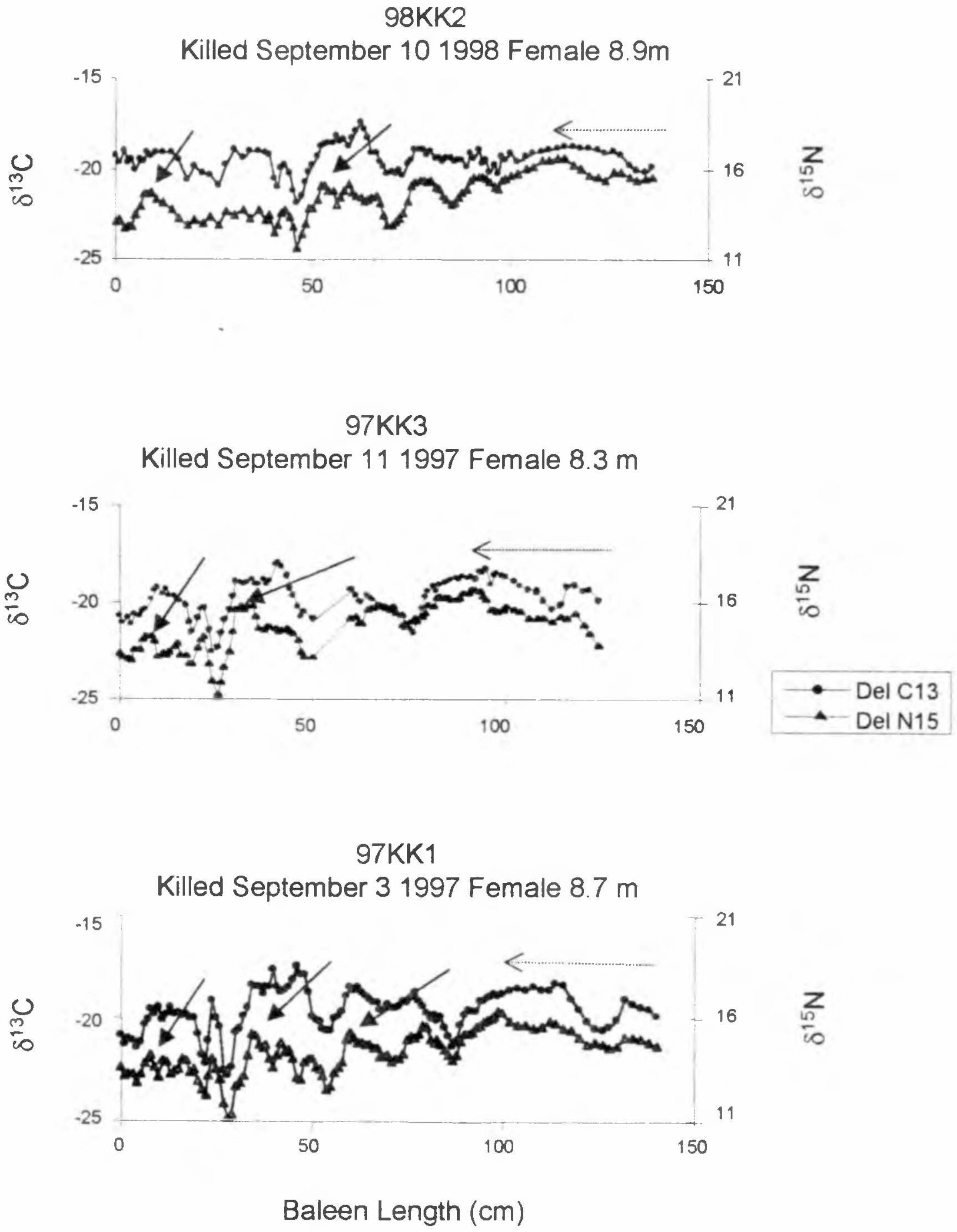
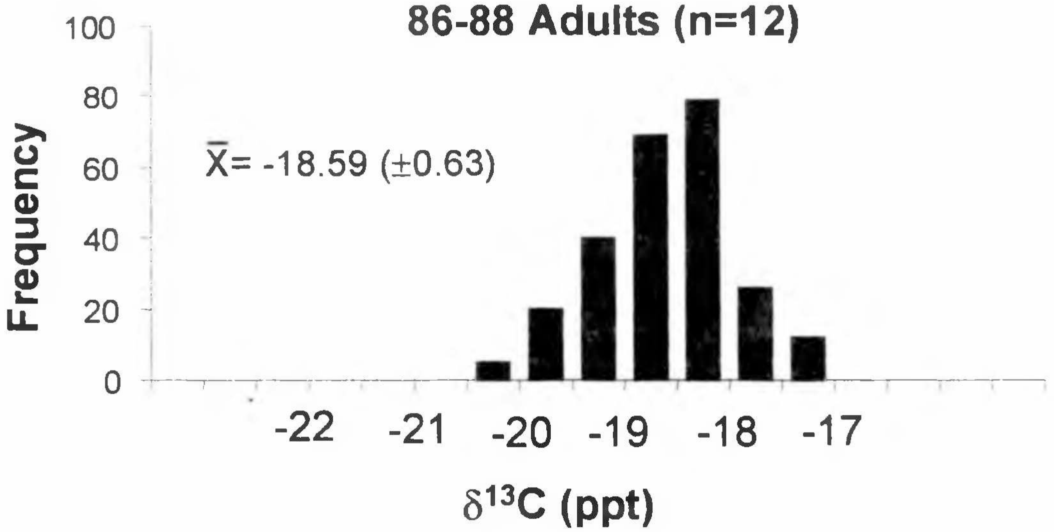


Figure 16. (continued).



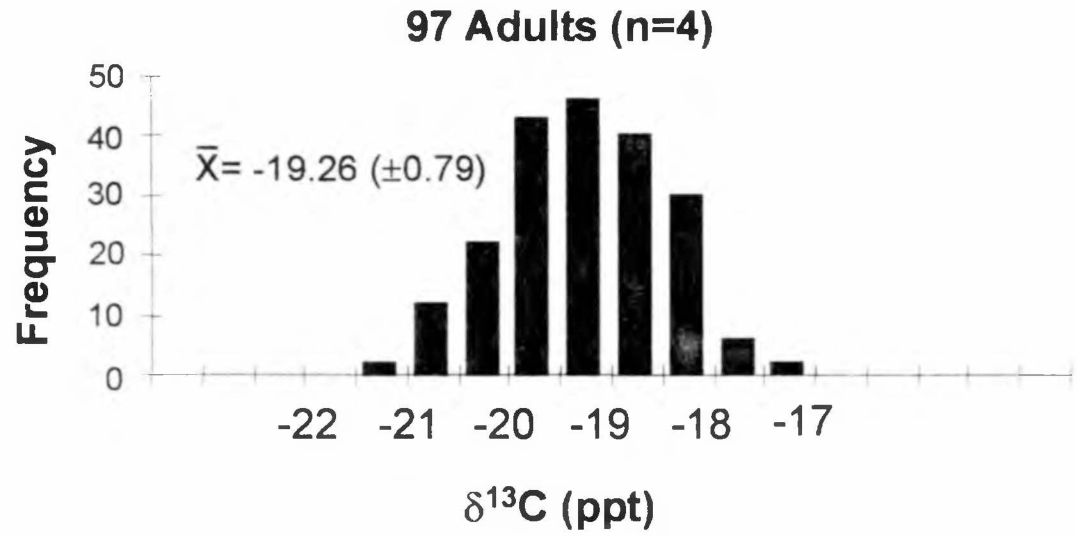


Figure 17. Frequency distribution of $\delta^{13}C$ values along the adult baleen from 0 cm to 50 cm between 1986-1988 and 1997.

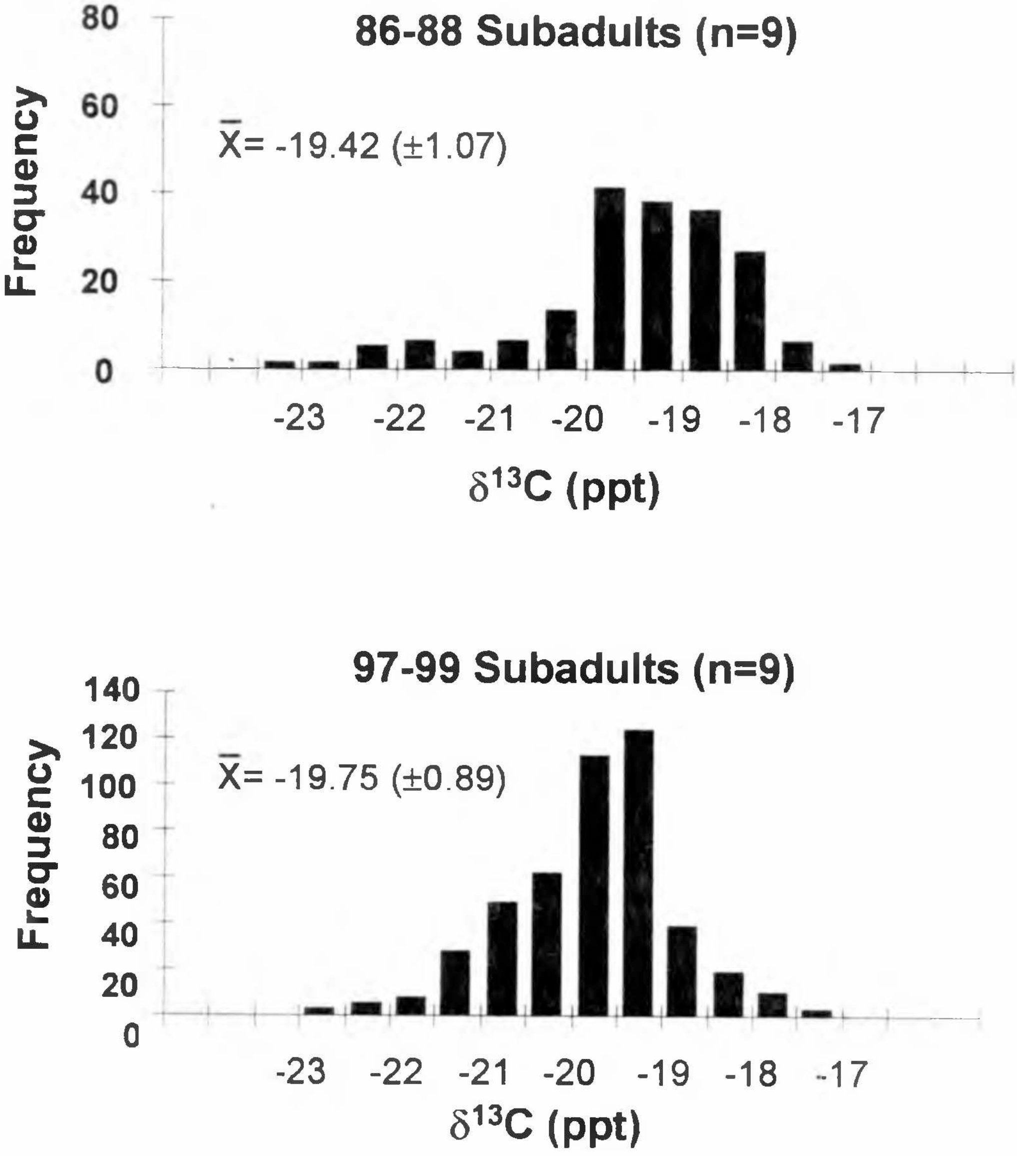
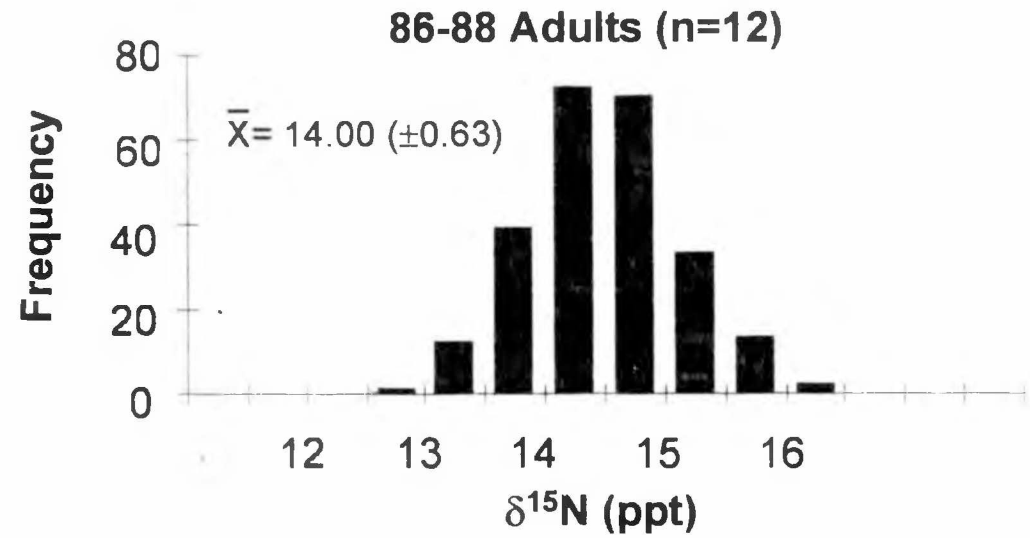


Figure 18. Frequency distribution of $\delta^{13}C$ values along the subadult baleen from 0 cm to 50 cm between 1986-1988 and 1997-1999.



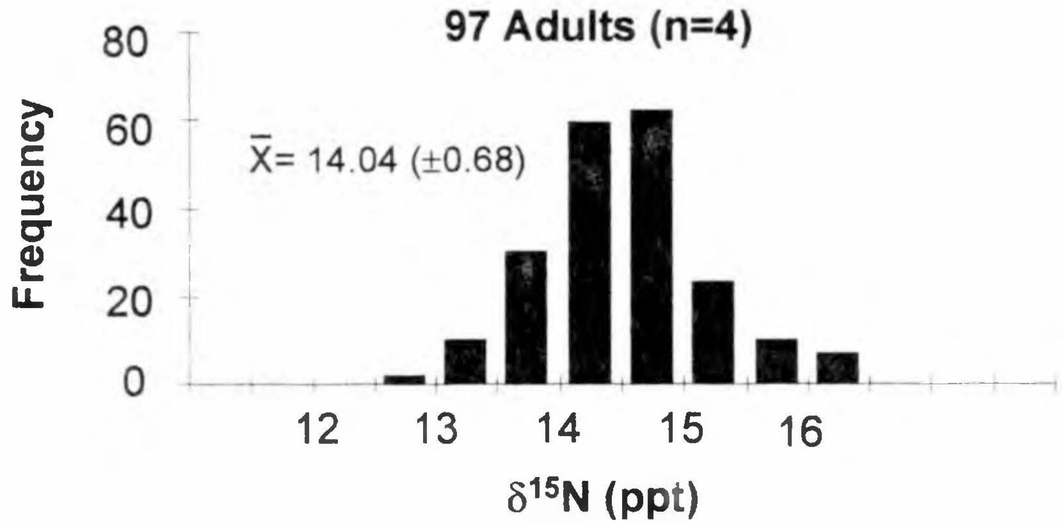
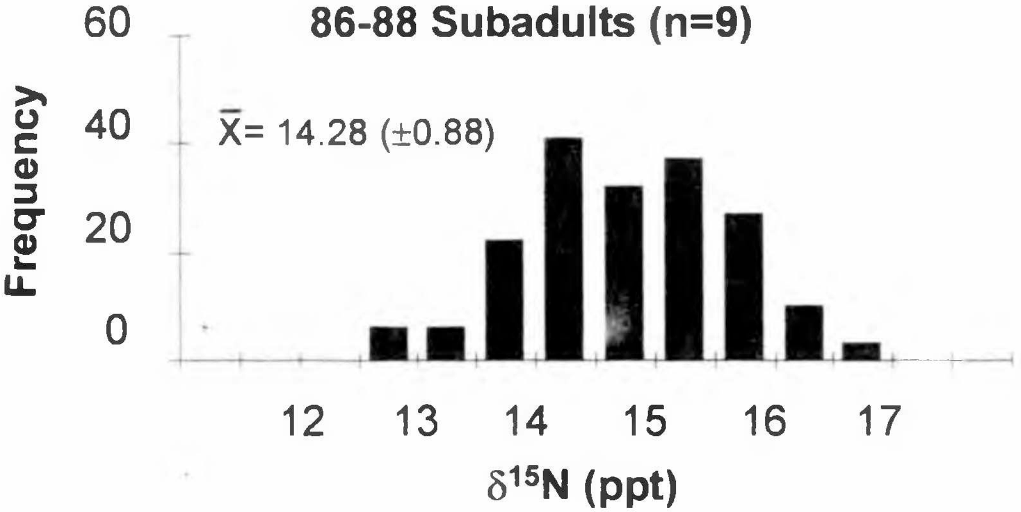


Figure 19. Frequency distribution of $\delta^{15}N$ values along the adult baleen from 0 cm to 50 cm between 1986-1988 and 1997.



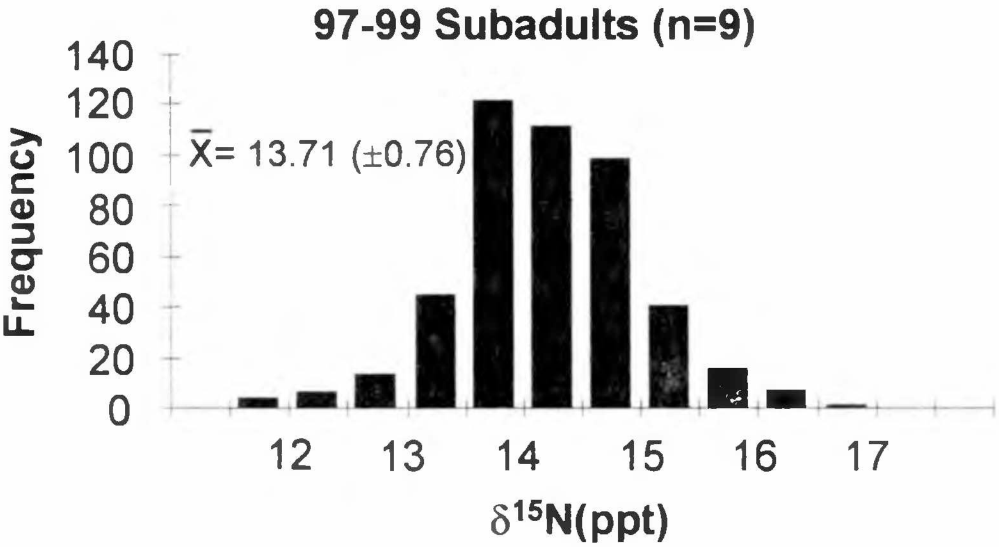
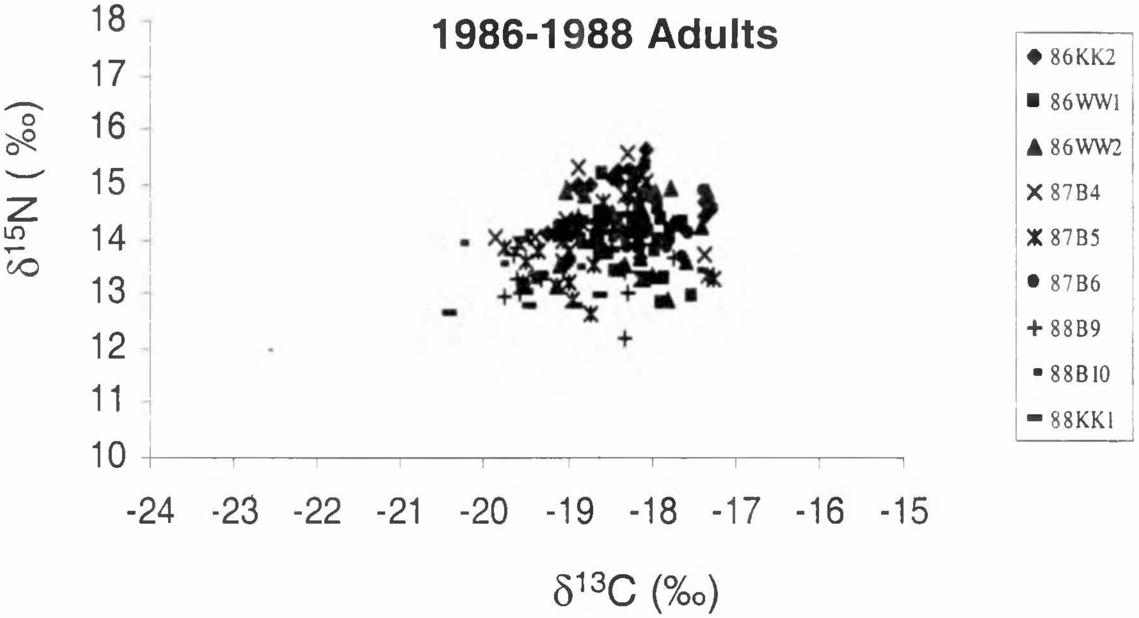


Figure 20. Frequency distribution of $\delta^{15}N$ values along the subadult baleen from 0 cm to 50 cm between 1986-1988 and 1997-1999.



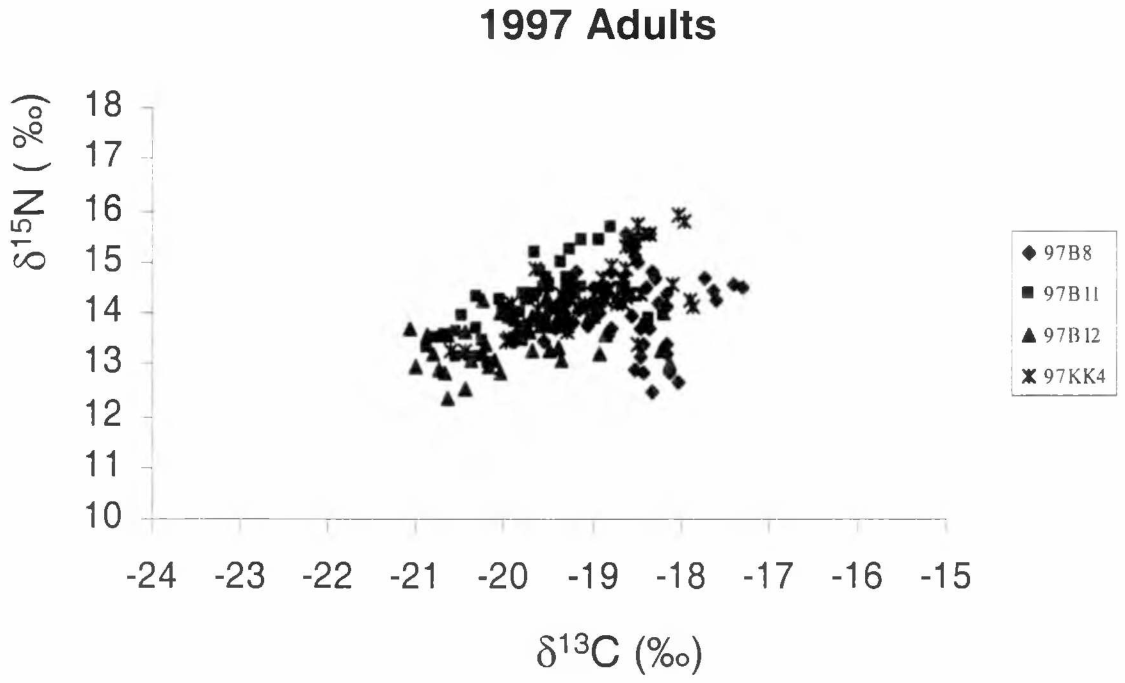
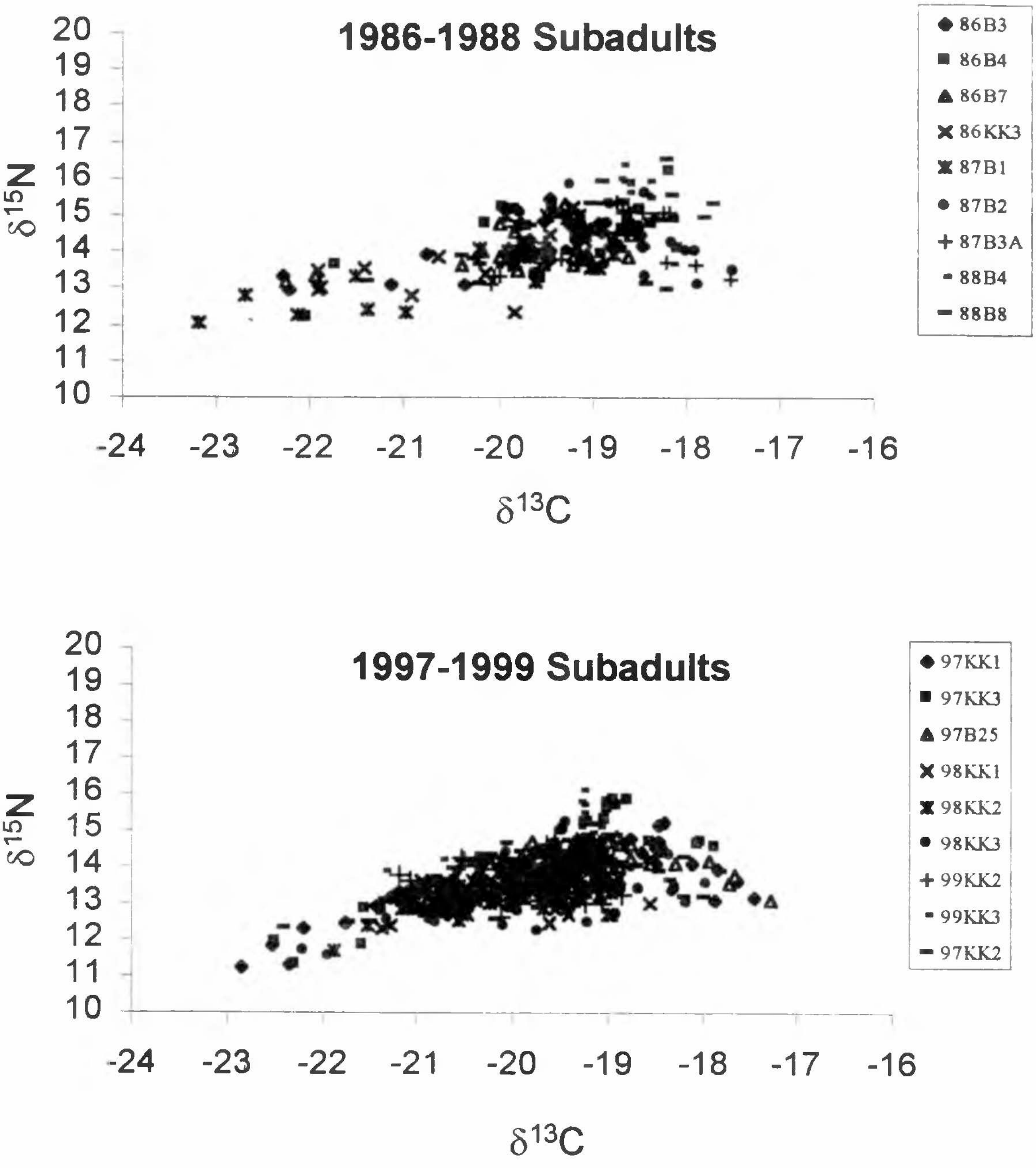


Figure 21. $\delta^{13}C$ and $\delta^{15}N$ for individual points from 0 to 50 cm along the baleen plates for 1986-1988 and 1997-1999.



(b) subadults

Figure 21. (continued)

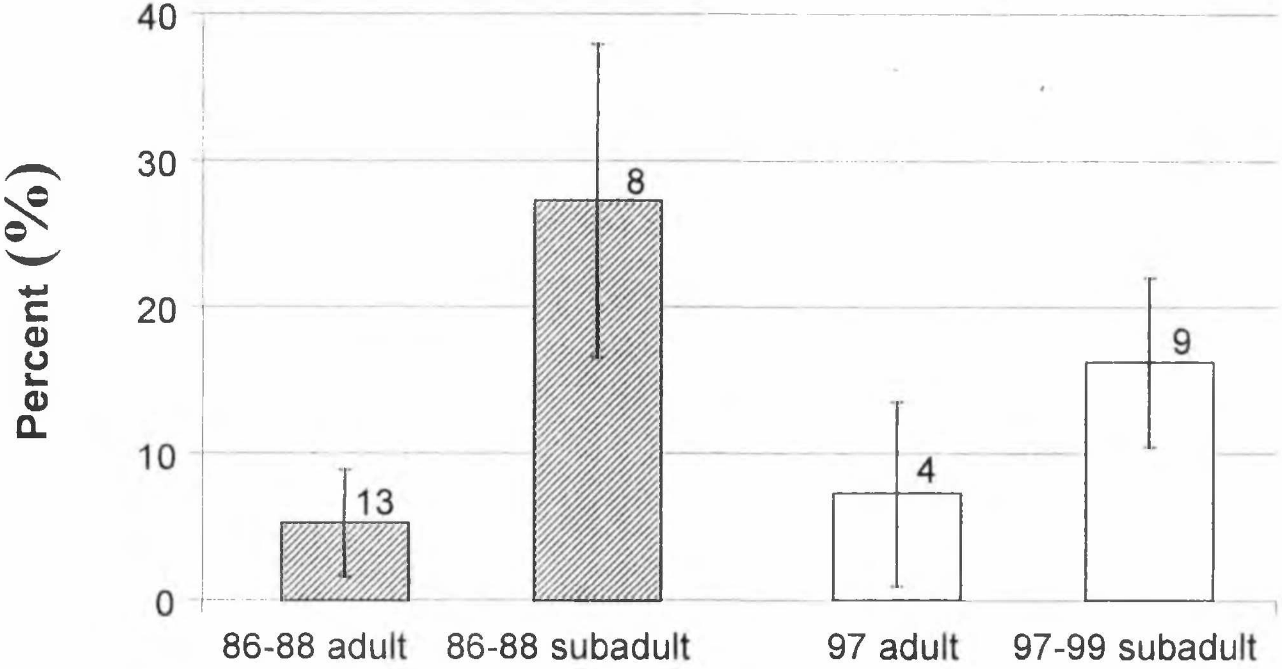


Figure 22. The estimated average percentage of lowered $\delta^{13}C$ values, indicating feeding activity in the eastern Beaufort Sea, for adults and subadults between the two periods. Vertical lines are standard deviations and numbers above bars the sample size.

point from 0 to 50 cm of the baleen plates. The pattern for adults from 1997 whales is identical to the pattern of adults from 1986-1988, except for the temporal decline in $\delta^{13}C$. It is apparent that the feeding patterns of adults and subadults in both time periods are quite different. It suggests that adult bowheads feed more intensively in one region, and values are consistent with isotope ratios from the Bering and Chukchi seas, whereas subadults apparently feed continuously while they are migrating across regions of different isotope ratios.

DISCUSSION

Inter-annual Variability of Zooplankton Carbon Isotope Ratios in the Eastern Beaufort Sea

The average $\delta^{13}C$ values of zooplankton in 1998 were higher than in 1999 and as reported in Schell et al. (1998) for years prior to 1990 (Table 5). The difference between 1998 and 1999 may have been caused by differing physical oceanography rather than changing zooplankton in the region. In 1998, nearshore water was uniformly cold and saline from surface to bottom. Over the inner shelf, surface temperatures were much warmer and the salinity was generally higher in 1998 than in 1986 (Griffiths 1999).

Muscle Tissue of Bowhead Whales

Muscle tissue $\delta^{13}C$ values provide a good overall indication of the bulk food sources that the whales have consumed over the seasonal feeding cycle. Since the estimated $\delta^{13}C$ values for total consumed prey are significantly different between the eastern Beaufort Sea (-24.8 ‰) and the Bering and Chukchi Seas (-21.6 ‰), muscle tissue should reflect the differences in $\delta^{13}C$ between spring-summer and fall-winter seasons, if whales feed to a significant extent in each region and the overall composition of the diets for bowhead whales as listed in

Table 1 is representative. However, the $\delta^{13}C$ values in fall muscle are not significantly different from those in the spring muscle after adjustment for the 1 ‰ long-term decline observed in Bering/Chukchi isotopic averages over the past 10 years (Figure 9). This indicates that almost all food for the whales came from the Bering and Chukchi seas.

By contrast, the $\delta^{15}N$ values in fall muscle are significantly different from those in the spring muscle (t-Test, 2 tails, $p < 0.001$). Although late winter prey of western Arctic bowhead whales is unknown, it is possible that they shift to a different prey during the winter. An alternative speculation is that nutritional stress caused substantial enrichment in $\delta^{15}N$ (Schell 1987). Hobson et al (1993) showed the enrichment of $\delta^{15}N$ in the tissues of birds under conditions of fasting and nutritional stress but $\delta^{13}C$ values in those tissues were unchanged.

There are no statistical differences in the $\delta^{13}C$ and $\delta^{15}N$ values in muscle between adults and subadults. However, the baleen plates do show significant differences in $\delta^{13}C$ between adults and subadults, with the latter indicating active feeding in the Beaufort Sea. Although the Bering and Chukchi seas provide most of the annual energy requirements to both adults and subadult whales, the eastern Beaufort Sea appears to support some of the energy needs for subadults.

Effects of Nursing on $\delta^{13}C$ and $\delta^{15}N$ in Baleen

Most calves are born during April, May, and early June (Koski et al. 1993), but some are born as late as early August (Davis et al. 1983). The time when weaning occurs in bowhead whales is not clear but is assumed to occur after 9-12 months (Nerini et al. 1984).

Variation in blubber thickness or blubber mass has been related to nutritional status in marine mammals (Aguilar and Borrell 1990; Read 1989). However, changes in body condition affect not only blubber thickness but also its lipid richness (Aguilar and Borrell 1990). Aguilar and Borrell (1990) found that all lactating female fin whales (*Balaenoptera physalus*) examined had low body-fat condition and the lowest mean lipid content of the blubber layers shortly before they weaned their young. Lactation of fin whales constitutes an extreme energy demand and must be accomplished partially during the nonfeeding season. This explains the poor nutrition of female fin whales near the end of lactation (Aguilar and Borrell 1990). In contrast, blubber thickness increases rapidly in nursing young of marine mammals (Schweigert 1993; Read 1989). Hobson and Clark (1992) found that nutritional stress causes substantial increases of $\delta^{15}N$ in the tissues of crows due to mobilization and redeposition of proteins elsewhere in the body, or amino acid composition changes in tissues. Thus, if nutritional stress occurs with lactating female bowhead whales, the nutritional stress would be expected to peak when the young whales are approaching the weaning point. Young whales receiving milk from their mother would be expected to show increasing $\delta^{15}N$ values up to the point of weaning, and a maximum $\delta^{15}N$ at that time, due to increasing nutritional stress and mobilization of protein by the mother. In Figure 16, the $\delta^{15}N$ values of baleen from all young whales having baleen grown while nursing increase from the tip of baleen plate, which was formed before or after parturition, to the estimated point that is believed to be concurrent with the start of the next spring migration (April to May).

Following weaning, young whales begin feeding by themselves and $\delta^{13}C$ values decrease after the estimated weaning points, suggesting the calves are consuming ^{13}C-depleted prey that is different from milk. However, nursing bowhead calves store sufficient fat to sustain themselves for several months after weaning (Schell et al. 1989). This may also explain the reduced $\delta^{13}C$ oscillations and relative enrichment observed in 98KK2 and 99KK3 whales in the first year after weaning.

Estimated Feeding Activity in the Eastern Beaufort Sea

Figure 22 indicates estimated percentage of feeding activity of whales in the eastern Beaufort Sea. The underlying assumption is that the whales feed in only two isotopic regimes, the Bering/Chukchi and eastern Beaufort seas, and that the changes in baleen isotope ratios are approximately proportional to food consumed. The estimated feeding time in the Canadian Beaufort and eastern Alaskan Beaufort Seas, as calculated from the simple mixing equation, is less than 7.3 % (± 6.3 %) for adults in 1997, for the most recent 2 or 3 years, and 5.3 % (± 3.7 %) from 1986-1988 adults. In contrast, the feeding activity for subadults in those areas is 16.2 % (± 5.8 %) for 1997-1999 whales and 27.3 % (± 10.7 %) for 1986-1988 whales. Bradstreet et al. (1987) estimated that subadult bowheads alone consumed about 10 % of total annual food requirements for the entire bowhead population from part of the southeastern Canadian Beaufort Sea during 1986. In addition, total consumption by all whales (adults and subadults) in the eastern Alaskan Beaufort Sea was estimated as < 1 % in 1985 or 1.4 % in 1986 of total annual population requirements. Therefore, the total consumption by the bowhead population in the eastern Beaufort Sea (Canadian Beaufort and eastern Alaskan Beaufort seas) is approximately 11 % of total annual population requirements. This percentage is lower than the feeding activity of 32.6 % calculated for adults plus subadults from the 1986-1988 period. However, the actual extent of feeding activity in the eastern Beaufort Sea is only an approximation, and may be overestimated due to the preponderance of copepods in the zooplankton biomass of the eastern Beaufort Sea (Saupe et al. 1989). Copepods have a high lipid content and a more depleted $\delta^{13}C$ value relative to euphausiids within a given region. Large amounts of copepods in the diet would result in decreased $\delta^{13}C$ values in the whale. The estimated percentage of feeding activity over the past decade has not significantly changed for adults, but has significantly changed (t-Test, 2 tails, p=0.04) for subadults. Subadults' feeding activity in the eastern Beaufort Sea (the eastern Alaskan Beaufort and Canadian Beaufort seas) appears to have decreased from 27.3 % to 16.2 %.

Difference in Utilization of Feeding Habitat between Adults and Subadults

There are no statistically significant differences in $\delta^{13}C$ and $\delta^{15}N$ values of muscle tissue between adults and subadults in spring and fall seasons (Figures 9 and 11), indicating that the predominance of food acquisition occurs in the same region. In contrast, $\delta^{13}C$ and $\delta^{15}N$ values of the baleen plates do show considerable differences, indicating variation in feeding patterns between subadult and adult (Figure 21). This variability is evident because each point along the plates records the isotopic value of the food source at the time of formation (Schell 1987), whereas muscle shows bulk isotopic composition of whales integrated over several months.

Observational evidence suggests that subadults and adults bowheads have different feeding patterns, with subadults spending more of the summer in coastal waters and actively feeding. Subadults have wider ranges of $\delta^{13}C$ and $\delta^{15}N$ than adults, also suggesting they may be feeding in different and wider areas or feeding on a larger variety of prey. Most whales in the coastal waters of the eastern Beaufort Sea were subadults and relatively higher numbers of adults spend much of the summer in offshore waters (Moore and Reeves 1993; Richardson et al. 1987). These large bowheads were observed to migrate through the eastern Alaskan Beaufort Sea in 1985 and 1986, not lingering to feed (Richardson et al. 1987). In addition, recent blubber composition of bowhead whales showed lower lipid contents of longer, and presumably older, whales in fall 1998 (Mau et al. 1999). These observations are in general agreement with the lack of summer feeding activity of adults indicated in the baleen isotopic ratios (Figure 22).

The consumption of different prey by adults versus subadults in summer could also account for the different isotopic compositions. However, no differences between the diet of small and large whales were found in stomach content samples collected from Kaktovik during 1976-1998 (Lowry and Sheffield 1999). Both adults and subadults probably feed on any species of zooplankton that is sufficiently concentrated to provide a reasonable energy source (Bradstreet et al. 1987).

In conclusion, the utilization of feeding habitats appears to be more diverse for subadults than adults, as indicated by the larger range in isotope ratios. The eastern Beaufort Sea is not an important feeding habitat for adults, but may be more important for subadults. The estimated feeding activity for subadults in the eastern Beaufort Sea, as approximated by the ratio of more depleted to enriched values along the baleen plates, is 16.2 % (± 5.8 ‰) in 1997-1999 and 27.3 % (± 10.7 ‰) for the 1986-1988 period.

Overall, the Bering and Chukchi regions are the preferred feeding areas for both adults and subadults, based on isotopic values in both bulk body tissues and the baleen plates. A rich pelagic community of large copepods and juvenile euphausiids, transported northward in the Anadyr water mass through the Bering Strait, supports large numbers of planktivorous fish, mammals and seabirds on the northern shelf (Springer 1988). The flux of zooplankton biomass into the Chukchi Sea is proportional to transport volumes (Springer 1988) which are usually maximal in summer and minimal in winter (Roach et al. 1995). The extremely high seasonal zooplankton biomass would be peaking as the bowheads return through this area during the fall migration southward (Schell and Saupe 1993).

Bowhead Whale Energetics

The energetic model of Thomson (1987) suggested that the carrying capacity in the eastern Beaufort Sea is not sufficient to provide the yearly requirement of food for the bowhead whale population, if they fed solely in that area (Bradstreet et al. 1987; Richardson 1987). In order to obtain their annual requirement of food, they would have to feed in waters containing at least 2,000 mg/m^3 of zooplankton biomass during the 130 day summer season in the region. However, the highest average zooplankton biomass found in the water column was 678 mg/m^3 (Griffiths 1999). They found less suitable habitats for feeding in the eastern Alaskan Beaufort Sea in 1998 than they had in a prior sampling in 1986. Moreover, the population of bowhead whales has increased at an estimated annual rate of 4.9 % from 1978 to 1993 (Zeh et al. 1995). The most recent estimate of the size of this stock is around 8,000 (95 % CI 6,900 - 9,200) (Zeh et al. 1995). Therefore, the trophic competition among themselves, or with other species such as arctic cod, might also have increased in the eastern Beaufort Sea in recent years. The arctic cod (*Boreogadus saida*) is a pivotal species in the trophic ecology of the Beaufort Sea (Craig et al. 1982; Frost and Lowry 1984; Lowry 1993; Crawford and Jorgenson 1993; Tynan and DeMaster 1997). It is the major consumer of zooplankton (93.1 % of diet) in the Beaufort Sea north of Alaska, with lesser amounts eaten by bowheads (5.9 %) (Lowry 1993). Arctic cod consume locally abundant prey such as amphipods and mysids (Bradstreet et al. 1987), as well as large numbers of small copepods, which have only occasionally been found in bowhead stomachs (Lowry 1993). Total biomass of zooplankton in the eastern Alaskan Beaufort Sea in 1998 and 1999 was lower compared with 1985 and 1986 (Griffiths 1999; W. B. Griffiths, pers. comm.) and trophic competition between arctic cod and bowheads may have increased in recent years. In addition, the Arctic Ocean has shown a trend of decreasing sea ice extent during the past decades (Maslanik et al. 1996; Johannessen et al. 1995). However, more recent trends in sea ice extent are nonuniform (Tynan and DeMaster 1997) and the effects on arctic cod could vary geographically. The distribution and diet of arctic cod may vary with the amount and location of ice cover (Crawford and Jorgenson, 1993; Tynan and DeMaster 1997). Moreover, arctic cod exhibit an r-selection reproductive strategy, unlike that typified by many other arctic fish populations, which tend to be slow growing, late maturing and long-lived (k-selection) (Craig et al. 1982). Their population and seasonal distributions would respond quickly to changes in the environment. However, nothing is known of concurrent changes in the population of arctic cod and their feeding strategy in the eastern Beaufort Sea or of interactions with feeding bowhead whales, especially subadults.

The Bering Sea ecosystem also has changed during the past three decades. In the early 1980s, several populations of marine birds and mammals in the western N. Pacific and Bering Sea were declining rapidly, probably due to a lack of forage fishes resulting from commercial fisheries and climate change (Springer 1998). There is no evidence on how these changes may have affected the whales or the relative importance of different feeding habitats to the whales.

Decadal Trends in $\delta^{13}C$ of Baleen Plates Laid Down in the Wintering Ground

The average winter values in baleen samples for 1985-1987 compared with the averages for samples collected in 1996-1998 showed a decrease in $\delta^{13}C$ from -18.17 ‰ to -19.29 ‰ or 1.12 ‰ (Figure 8). This observed decline of $\delta^{13}C$ in the Bering and Chukchi Seas almost exactly matches the decline observed in the whale muscle tissue over the same time period (Figure 7).

One possible interpretation is that the whales have changed their feeding ground in the Bering Sea to areas in which zooplankton are more depleted in ^{13}C. However, the distribution of adult whales does not seem to have changed. This decline is assumed to be in response to an overall decline in phytoplankton isotope ratios in the Bering Sea (Schell 2000). According to Schell (2000), the Bering Sea ecosystem may have undergone a decrease of up to 30-40 percent in average seasonal primary productivity during the past three decades. The major assumptions are that phytoplankton species compositions have not changed over the years and that seasonal concentrations of dissolved free CO_2 in the euphotic zone have remained nearly constant in the Bering Sea. Recently, Laws et al. (1995) and Bidigare et al. (1997) demonstrated linear relationships between cell growth rate and carbon isotope ratios in phytoplankton in the laboratory and in the marine environment. Lowered cell growth rates would lead to a decrease in the

$\delta^{13}C$ of phytoplankton, which would subsequently lead to decreases in $\delta^{13}C$ value of zooplankton and tissues of whales (Schell 2000).

Decadal Trends in $\delta^{15}N$ in the Bering and Chukchi Seas

Stable isotope ratios of nitrogen can be used as a tracer for dietary analysis (Minagawa and Wada 1984; Owens 1987; Schell 1987). The $\delta^{15}N$ of an organism reflects both the primary producer $\delta^{15}N$ and the trophic level (Wainright et al. 1993). Therefore, the $\delta^{15}N$ of a carnivore can be altered by a change in the $\delta^{15}N$ of the primary producer and/or its trophic position. However, a carnivore's $\delta^{15}N$ values can also be changed through physiological processes such as nutritional stress (Schell 1987; Hobson et al. 1993; Hobson and Schell 1998).

Within the marine environment, $\delta^{15}N$ values of phytoplankton vary as a result of changes in the relative amounts of upwelled nitrate and recycled ammonia (Wada et al. 1987; Schell 1987), and nitrogen fixation (Mariotti, 1983). The upwelled nitrate has a $\delta^{15}N$ value near 6-7 ‰ (Michener and Schell 1994), whereas the phytoplankton nourished primarily by recycled nitrogen or fixation of atmospheric N_2 have lower $\delta^{15}N$ values (Checkley et al. 1989). Recently, Freeland et al. (1997) found that mixed layer depths and nitrate supply to the euphotic zone have decreased over the past four decades at Ocean Station Papa (50 °N and 145 °W) in the North Pacific Ocean. If this is true, then N-fixation could be an increasingly important nitrogen source for the phytoplankton. Hence, as the nitrate supply declines, $\delta^{15}N$ of phytoplankton in the North Pacific Ocean would be expected to decrease due to increased utilization of N-fixation. This decline in average euphotic zone $\delta^{15}N$ values in primary producers could shift the isotopic composition of the whole food web downward in the Bering Sea and subsequently in the Chukchi Sea. This is because the North Pacific is connected to the Bering Sea through Aleutian passes that allow transport of water, and, potentially, significant amounts of nutrients northward. The Anadyr current then transports large zooplankton communities as well as abundant nutrients through the Bering Strait and into the Chukchi Sea (Springer 1988).

Another possibility is that fishery harvests in the Bering Sea are removing the heavier isotope. Fish have high $\delta^{15}N$ values compared with phytoplankton and zooplankton. If a significant fraction of the total nitrogen is removed from the Bering Sea via harvesting of fish and shellfish, there would be a decline in $\delta^{15}N$ value in the Bering Sea ecosystem. It is not known if the current harvest rate is indeed removing a sufficient quantity to contribute to the observed decline in biological $\delta^{15}N$.

The other sources of change in whale $\delta^{15}N$ are a shift to a different prey or a change arising from physiological processes such as changing of nutritional status. Hobson and Clark (1992) and Hobson et al. (1993) found that nutritional stress could cause substantial increases of $\delta^{15}N$ in the tissues of birds, without changing $\delta^{13}C$, due to mobilization and redeposition of proteins elsewhere in the body, or amino acid transamination during replacement of tissues. Although physiological processes of whales and birds may be different, nutritional stress is a possible reason for the observed increase in $\delta^{15}N$ over winter. Best and Schell (1996) noted that southern right whales (*Eubalaena australis*) increase in $\delta^{15}N$ with no change in $\delta^{13}C$ during the northward migration. This was ascribed to fasting and metabolism of body proteins.

The maximum enrichments of $\delta^{15}N$ occur during the late winter period before the start of the spring migration (Figure 16). Most of the whales taken at Point Hope and Wainwright had empty stomachs during the early spring migration (Lowry 1993). However, the stomach of a bowhead whale killed at Gambell, Alaska, in May 1982 contained benthic prey (Hazard and Lowry 1984). Hence, it is possible that a change in diet is causing the enrichments of $\delta^{15}N$ during the winter, especially the late winter.

SUMMARY

1. The Bering and Chukchi Seas provide most of the annual energy requirements to both adult and subadult whales, as indicated by carbon isotope ratios in whale muscle. However, the feeding habitats appear to be more diverse for subadults than adults, as shown by the larger range in isotope ratios that indicates the eastern Beaufort Sea may supply some of the annual energy to subadults.

2. The decrease in the estimated feeding activity for subadults in the eastern Beaufort Sea between 1986-88 and 1997-99 may be caused by changes in ecosystem productivity of the eastern Beaufort and Bering/Chukchi Seas during the last decade.

3. The average $\delta^{15}N$ values of baleen plates grown during feeding in the Bering and Chukchi Seas have decreased from 1952 to 1998. This decrease may derive from a decrease in the $\delta^{15}N$ of phytoplankton in the North Pacific Ocean, perhaps due to an increasing role of N-fixation or removal of the heavier isotope via fisheries harvest in the Bering Sea.

SUGGESTIONS FOR FUTURE RESEARCH

1. Use an alternate tracer, such as mercury or $\delta^{18}O$, in addition to carbon and nitrogen isotope ratios in order to better define the time spent feeding in Canadian versus Alaskan waters during the fall migration across the Beaufort Sea.

2. Analyze and determine the seasonal changes in the metabolism of the western Arctic Bowhead whales in the eastern Beaufort Sea, to better understand how much energy the whales acquire from the eastern Beaufort Sea.

3. Study the population size and distribution of Arctic cod in the eastern Beaufort Sea in order to see if they compete directly with bowhead whales.

4. Calculate the total biomass of zooplankton and the amount of lipid available to bowheads while feeding in the eastern Beaufort Sea during summer, and in the Bering/Chukchi Seas during the fall migration, to determine if energy availability affects the timing and pathways of their migration.

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