A RETROSPECTIVE ASSESSMENT OF PRIMARY PRODUCTIVITY

ON THE BERING AND CHUKCHI SEA SHELVES USING

STABLE ISOTOPE RATIOS IN SEABIRDS

By

Grace Elizabeth Abromaitis

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Dean, School of Fisheries and Ocean Sciences

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A

THESIS

Presented to the Faculty

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By

Grace Elizabeth Abromaitis, B.S.

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Abstract

Recent declines of marine mammal and seabird populations in the Bering Sea have raised the question of whether the changes are caused by fishing pressure or a decrease in ecosystem carrying capacity. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios in Thick-billed Murre muscle and feathers were used as indicators of changing seasonal primary production. $\delta^{13}C$ values in phytoplankton vary directly with growth rates and are passed up the food web to consumers. Muscle and feather $\delta^{13}C$ values decreased over the period 1976-1998 suggesting a decline in Bering/Chukchi continental shelf primary production. Carbon isotope ratios in murres were correlated with bowhead whale baleen isotope ratios and to some climate indices. In contrast, $\delta^{15}N$ values in the birds showed no significant change indicating no concurrent shifts in trophic status.

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Introduction

Recent declines of marine mammal and seabird populations in the Bering Sea may have been linked to a decline in regional carrying capacity over the past several decades. Red-legged Kittiwakes (*Rissa brevirostris*) on the Pribilof Islands decreased by as much as 50% between the mid-1970's and mid-1980's (Byrd et al. 1999). The numbers of Steller sea lions (*Eumetopias jubatus*) and northern fur seal (*Callorhinus ursinus*) pup production decreased by as much as 90% for the former and as much as 50% for the latter between the 1950's and the 1980's (Loughlin et al. 1984; Trites and Larkin 1989; Merrick et al. 1997).

These declines of marine mammal and bird populations raised inquiries as to whether the causes were "top down", due to fishing pressure, or "bottom-up", driven by climate change effects. One indication that the declines were from a bottom-up effect was found using stable isotopes in bowhead whale (*Balaena mysticetus*) baleen. Stable isotope ratios of carbon in bowhead whale baleen over the last 53 years suggested that primary productivity, and thus carrying capacity on the northern Bering/southern Chukchi continental shelf, may have decreased in the past 34 years (Schell 2000). This Thick-billed Murre (*Uria lomvia*) study used samples collected over the years 1931-1998 to look for additional evidence of a change in carbon isotope ratios that might support the hypothesis of a drop in primary productivity on the Bering/Chukchi shelf.

Thick-billed Murres are piscivorous seabirds that breed in Alaska coastal regions and on islands from southeastern Alaska to Cape Lisburne (Gabrielson and Lincoln 1959; Service 2000). Thick-billed Murres nest on steep seaward-facing cliffs near areas of high

food availability and pursue prey underwater at depths up to 180 meters (Gabrielson and Lincoln 1959; Tuck 1961; Piatt and Nettleship 1985). Murres in the Bering and Chukchi Seas usually forage within about 50-60 km of their colonies, feeding primarily on arctic cod (*Boreogadus saida*) and sculpin (Family *Cottidae*), but with a significant consumption of invertebrates (Swartz 1966; Hunt et al. 1981).

The breeding sites at Cape Lisburne and Cape Thompson (Figure 1) in the Chukchi Sea, sources of the bird tissue utilized in this study, support an estimated 500,000 murres and are the northernmost colonies of Thick-billed Murres (Springer et al. 1984). The birds typically arrive in complete breeding plumage at Cape Thompson and Cape Lisburne for summer breeding during the first week of May (Swartz 1966). Little is known about the wintering grounds of Thick-billed Murres at these colonies, but it is thought that they winter in open water or loose ice south of Bering Strait (Gabrielson and Lincoln 1959). Smaller numbers may winter in open leads near the Cape Thompson region (Swartz 1966).

Environment of the Northern Bering and Southern Chukchi Seas

Although the Chukchi Sea is geographically part of the Arctic Ocean, it is dominated physically, chemically, and biologically by water flow from the Bering Sea northward through the Bering Strait (Fleming and Heggarty 1966; Shuert and Walsh 1993). Maximal flow of approximately 1 Sv ($10^6 m^3 s^{-1}$) typically occurs in summer and the residence time of water in the southeastern Chukchi Sea is approximately ten days (Fleming and Heggarty 1966; Roach et al. 1995). The majority of the water being

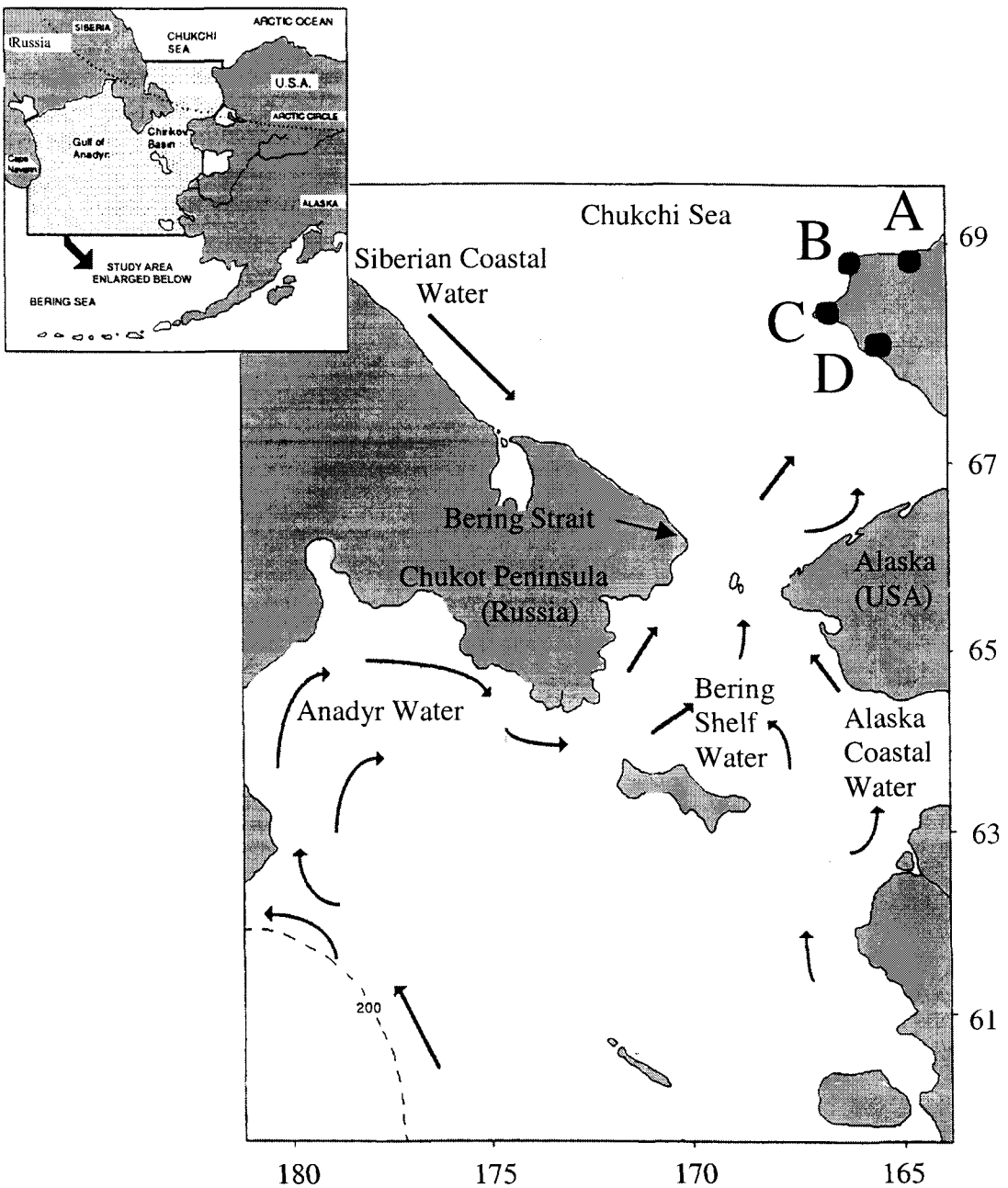

Figure 1. The northern Bering/southern Chukchi shelf region. Sampling locations in the Chukchi region are marked, as well as currents transporting water through Bering Strait in to the Chukchi Sea. A = Cape Sabine, B = Cape Lisburne, C = Point Hope, D = Cape Thompson

advected into the Chukchi from the Bering Sea is derived from the Bering Slope Current of the northern Bering Sea (Coachman and Shigaev 1988).

Nutrients, phytoplankton, and zooplankton are transported through Bering Strait into the southern Chukchi Sea, but more importantly, most of the nutrients are being transferred from the northwestern Bering shelf region, through the Bering Strait , and into the southern Chukchi shelf region by the Anadyr Current (Springer and McRoy 1993). In areas where the Anadyr water slows and phytoplankton stay above the critical depth (especially on the shallow shelf), these nutrients lead to areas of exceptionally high phytoplankton production (Springer and McRoy 1993).

For that reason, biological production is closely tied to the chemical and physical properties of the region. Climate change would cause pronounced shifts in the carrying capacity of the Bering Sea through changes in meteorology over the North Pacific as characterized by the Pacific Decadal Oscillation (Mantua et al. 1997), changes in wind patterns that may affect flow through Bering Strait, or other factors that may affect primary productivity.

Stable Isotopes in Ecological Studies

Stable isotope ratios of carbon and nitrogen were used as tools in this study to infer changes in seasonal primary productivity. Most elements have two or more stable isotopic forms. Stable carbon and nitrogen are found in the forms ^{12}C and ^{13}C and ^{14}N and ^{15}N, respectively. Primary producers are the source of carbon and nitrogen into the food web as they convert inorganic nitrogen (99.63% ^{14}N and 0.037% ^{15}N) and carbon (98.89% ^{12}C and 1.11% ^{13}C) into organic matter. Fractionation of carbon and nitrogen

during fixation, respiration, and metabolism alter these ratios slightly as they are passed through different trophic levels, resulting in different isotopic compositions. Isotope ratios are typically described in terms of difference from a standard in parts per thousand. This difference (δ) is the ratio of $^{13}C/^{12}C$ in the sample compared to the same ratio in the standard. Enriched tissues have a larger $^{13}C/^{12}C$ ratio than the standard (referred to as "heavy") and depleted tissues have a smaller ratio than the standard ("lighter"). As carbon and nitrogen are passed up through the food web, beginning with the primary producers, ^{12}C and ^{14}N are discriminated against, leading to an enrichment of ~0.5‰ for carbon and ~3.4‰ for nitrogen per trophic level (DeNiro and Epstein 1978; Wada et al. 1987).

Apex consumers, such as seabirds, reflect the stable isotope ratios of primary producers after they have passed through several trophic levels. Isotope ratios have been used in avian dietary studies to assess the relative contributions of marine and terrestrial food sources (Hobson 1986; Hobson 1990; Mizutani et al. 1990; Hobson and Sealy 1991; Wainright et al. 1998). Both $\delta^{15}N$ and $\delta^{13}C$ have been used in establishing trophic relationships and food sources in birds, and $\delta^{13}C$ has been used in seabirds as an indicator of inshore vs. offshore feeding preferences (Hobson 1990; Hobson et al. 1994; Thompson et al. 1995; Bearhop et al. 1999; Hobson 1999). Isotopic fractionation of both carbon and nitrogen between diet and avian tissues has been investigated by using a variety of tissues with fast or slow turnover rates to assess short and long-term dietary effects on fractionation (Tieszen et al. 1983; Mizutani et al. 1991; Hobson and Clark 1992; Hobson and Clark 1992).

Relationship Between Primary Production and Carbon Isotope Ratios

Phytoplankton $\delta^{13}C$ values are dependent on the amount and initial composition of aqueous CO_2, cell geometry, cell size, and growth rate (Laws et al. 1995; Bidigare et al. 1997; Popp et al. 1998). Fast phytoplankton growth rates and low cell surface area to volume ratios yield higher $\delta^{13}C$ values due to reduced fractionation (Laws et al. 1995). Slower phytoplankton growth rates and/or high surface area to volume ratios yield lower $\delta^{13}C$ values resulting from increased fractionation (Laws et al. 1995).

Study Rationale

Schell (2000) reported a decrease of 2.7‰ in the $\delta^{13}C$ values of bowhead whale baleen from 1966 to present, and ascribed the decrease to changes in phytoplankton $\delta^{13}C$ values. If this change were indeed due to a decline in productivity, then it should be evident in other species as well. Isotope ratios in Thick-billed Murres were analyzed in an attempt to independently observe changes in $\delta^{13}C$ values in the same geographic region. This study consisted of three tasks. First, stable isotope ratios in different tissues of individual birds were analyzed. Thick-billed Murre muscle and feather tissues were collected from birds in the summer season over several years. Avian muscle carbon has a half-life of approximately 30 days, whereas a feather is inert once it has completed growth (Hobson and Clark 1992). Isotope ratios in feathers and muscle were thought to represent food assimilation from different geographic locations, times, and/or prey bases. The second task was to follow isotopic labeling in Pigeon Guillemots (*Cepphus columba*) to determine if diet was immediately incorporated into feather synthesis or stored in body

reserves and later mobilized. This information was to be used in the Thick-billed Murre work to understand the temporal and geographic information represented by isotope ratios along a feather. Diet/feather fractionation, incorporation of new diet into new feather growth, and variability within an individual feather were considered. The last task was to compare the temporal trends in Thick-billed Murre muscle and feather $\delta^{13}C$ to assess indications of changes in primary productivity in response to climatic effects.

Goal and Objectives

Hypotheses:

(1) Isotope ratios in Thick-billed Murre tissues can be used as a proxy to assess changes in isotope ratios in primary producers in the northern Bering Sea/southern Chukchi Sea area correlated to climatic effects.

(2) The dietary and trophic shifts in a Thick-billed Murre colony over time could be assessed using long-term changes in average $\delta^{15}N$.

Specific objectives were:

1. Sample muscle tissue from as many years as possible to assess whether trophic positions were shifting, whether $\delta^{13}C$ ratios were changing, and whether concurrent shifts in $\delta^{15}N$ were occurring.
2. Compare carbon and nitrogen isotope ratios in tissues from birds to assess differences in fractionation between tissues, variability within a feather, and variability along a feather.

3. Analyze feathers from archived birds in museums to extend the timeline of isotope ratios back in time.
4. Through use of captive birds, measure the rate of incorporation of ^{15}N-labeled amino acids into blood, feces, and feathers.

Materials and Methods

This study consisted of two phases - a temporal analysis of stable isotope ratios in recently collected birds and archived samples from the Bering and Chukchi Seas and a study on the distribution of isotope ratios in captive birds with known diets. The first phase used samples of Thick-billed Murre tissues from the University of Alaska or from museum study skins. The second phase (a captive study on Pigeon Guillemots) took place at the Alaska SeaLife Center in Seward, AK.

Thick-billed Murre Tissue Analyses

Tissues from Thick-billed Murres collected at Cape Lisburne, Cape Thompson, Cape Sabine, and Point Hope during the period 1931-1998 were analyzed for $\delta^{13}C$ and $\delta^{15}N$ (Figure 1). Birds were sampled from archived collections at the University of Alaska Museum (UA), the University of California Museum of Vertebrate Zoology (UCMVZ), and Institute of Marine Science University of Alaska Fairbanks research collection held by Dr. Alan Springer (IMS). Breast muscle, feathers from the back, breast, chin, secondary, primary, covert, and under wing, and stomach contents from Thick-billed Murres, were collected when available from all birds in the IMS collection. Back feathers were sampled from archived study skins at the UA and UCMVZ museum.

Muscle Sampling

Pectoral muscle was cut out from along the breastbone and then oven dried to constant weight at 60°C. Muscle samples were ground in a Wig-L-Bug grinder (Crescent

Dental Corporation) for homogeneity and stored in glass vials until weighed for stable isotope analysis. Muscle samples were weighed on a microbalance and analyzed to examine interannual and geographical variability of $\delta^{13}C$ and $\delta^{15}N$.

Feather Sampling

Feathers were plucked out at the base, rinsed with mild soap, tap water, and deionized water to eliminate any residues from storage, and then oven dried to constant weight at 60°C.

Feathers were used for three purposes. Temporal changes were determined by analyzing feathers from under the wing and chin (1976-1998) or back (1931-1966) to assess interannual variability in $\delta^{13}C$ and $\delta^{15}N$ (Table 1). For small feathers from under the wing and back, the whole feather with the exclusion of the rachis (shaft) was sampled. Whole chin feathers were used, due to minimum weight limitations and difficulty in separating the barbs from the rachis. In most cases, two chin feathers were required to provide 0.8-1.1 mg for mass spectrometry. For each bird, two samples per body region were prepared.

Variability in isotope ratios between feathers of individual birds was assessed by using feathers from seven areas on the bodies of 6 birds collected in 1998 from Cape Lisburne. The following feathers were sampled: primaries, secondaries, coverts, back, chin, contour under the wing, and breast. For all feathers, excluding the primaries, secondaries, and chin feathers, the whole feather excluding the shaft was sampled. For each primary and secondary feather only the tip was used (excluding the shaft). As before, two samples per body area were prepared for each bird.

Table 1. Thick-billed Murre tissues sampled. The number of birds sampled for each tissue is shown along with year and location of collection. Multiple tissue types were taken from the same bird in some years. CL = Cape Lisburne, CT = Cape Thompson, PH = Point Hope, CS = Cape Sabine, n/a = not available.

Year	Location	Muscle	Feather	Collagen	Stomach Contents
1998	CL	10	10	0	10
1997	CL	10	2	0	10
1993	CL	10	n/a	0	10
1992	CL	10	n/a	0	10
1987	CL	9	n/a	0	9
1986	CL	10	n/a	0	10
1985	CL	10	n/a	0	10
1984	CL	10	n/a	0	10
1983	CL	20	n/a	0	20
1983	PH	10	n/a	0	10
1980	CL	10	n/a	0	10
1978	CL	6	6	4	6
1977	CL	9	9	1	9
1977	CT	10	10	0	10
1976	CT	10	10	2	10
1966	CT	n/a	1	0	n/a
1964	CT	n/a	1	0	n/a
1960	CT	n/a	4	0	n/a

Table 1 continued.

1960	PH	n/a	1	0	n/a
1959	CT	n/a	6	0	n/a
1958	CS	n/a	2	0	n/a
1931	PH	n/a	5	0	n/a
1931	CT	n/a	5	0	n/a

Variability within an individual feather was also assessed. Primary feathers were sectioned from two different birds (29-76 and 37-76) to assess variability in isotope ratios between sections of the same feather. Each feather was sectioned in 1-cm increments down the anterior and posterior vanes, and the shaft in 0.2-1.5 cm increments from tip to base (Figure 2). The vanes and shaft were sampled at different locations along the feather because larger areas of vanes were required to provide an adequate sample for the mass spectrometer.

Pigeon Guillemot Captive Bird Isotope Labeling Experiment

Pigeon Guillemots were hatched at the Alaska Sealife Center and raised in individual enclosures. Chicks were fed monotonous diets of either pollock or herring until fledging at approximately 5 weeks. At approximately 24 days of age, 12 birds were fed ^{15}N-glycine (Cambridge Isotope Laboratories, Andover, MA) in amounts based on their weights (average = 366 grams) to equate 158 ‰ addition to normal levels of ^{15}N. At approximately 26 days of age, the same 12 birds were given ^{13}C-glycine in amounts based on their weights to equate 15 ‰ addition to normal levels of ^{13}C (Table 2). Each capsule was inserted into a piece of fish and then hand fed to each chick during their morning feeding. The appearance of labeled nitrogen and carbon was then measured in feces, blood, and feather samples. Samples of muscle tissue were also collected from 5 pollock (*Theragra chalcogramma*) and 5 herring (*Clupea pallasi*) that were being fed to the chicks to determine the isotope ratios of the chick diet (Figure 3).

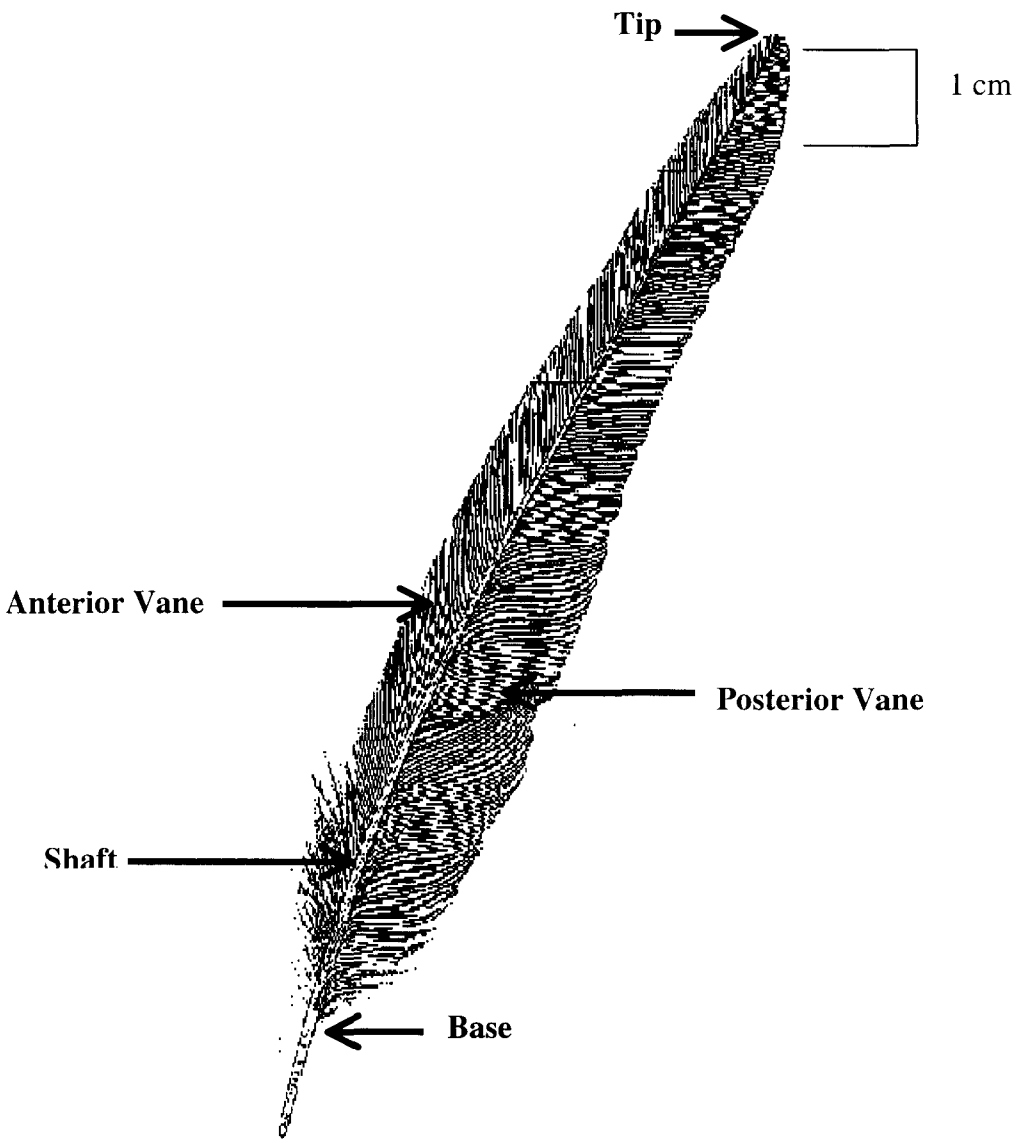

Figure 2. Feather sectioning protocol for a Thick-billed Murre primary feather. The posterior and anterior vanes were sampled every 1 cm and the shaft was sampled every 0.2-1.5 cm. Feathers on average were 9.5 cm long.

Table 2. Pigeon Guillemot ^{15}N-glycine and ^{13}C-glycine dosage. The birds dosed, diet, weight, and actual dosage amount of labeled glycine. Dosage of ^{15}N occurred on day 1 and ^{13}C on day 3.

Bird ID	Diet	Initial mass (g)	^{15}N-glycine dosage amount (g)	^{13}C-glycine dosage amount (g)
6	Herring	363	0.0299	0.2398
7	Herring	361	0.0301	0.2700
9	Herring	381	0.0301	0.2699
10	Herring	382	0.0299	0.2702
22	Herring	410	0.0349	0.2701
23	Pollock	347	0.0302	0.2400
24	Pollock	340	0.0299	0.2400
25	Herring	355	0.0299	0.2398
26	Pollock	345	0.0301	0.2398
32	Herring	400	0.0350	0.2703
42	Pollock	363	0.0299	0.2400
43	Pollock	344	0.0299	0.2401

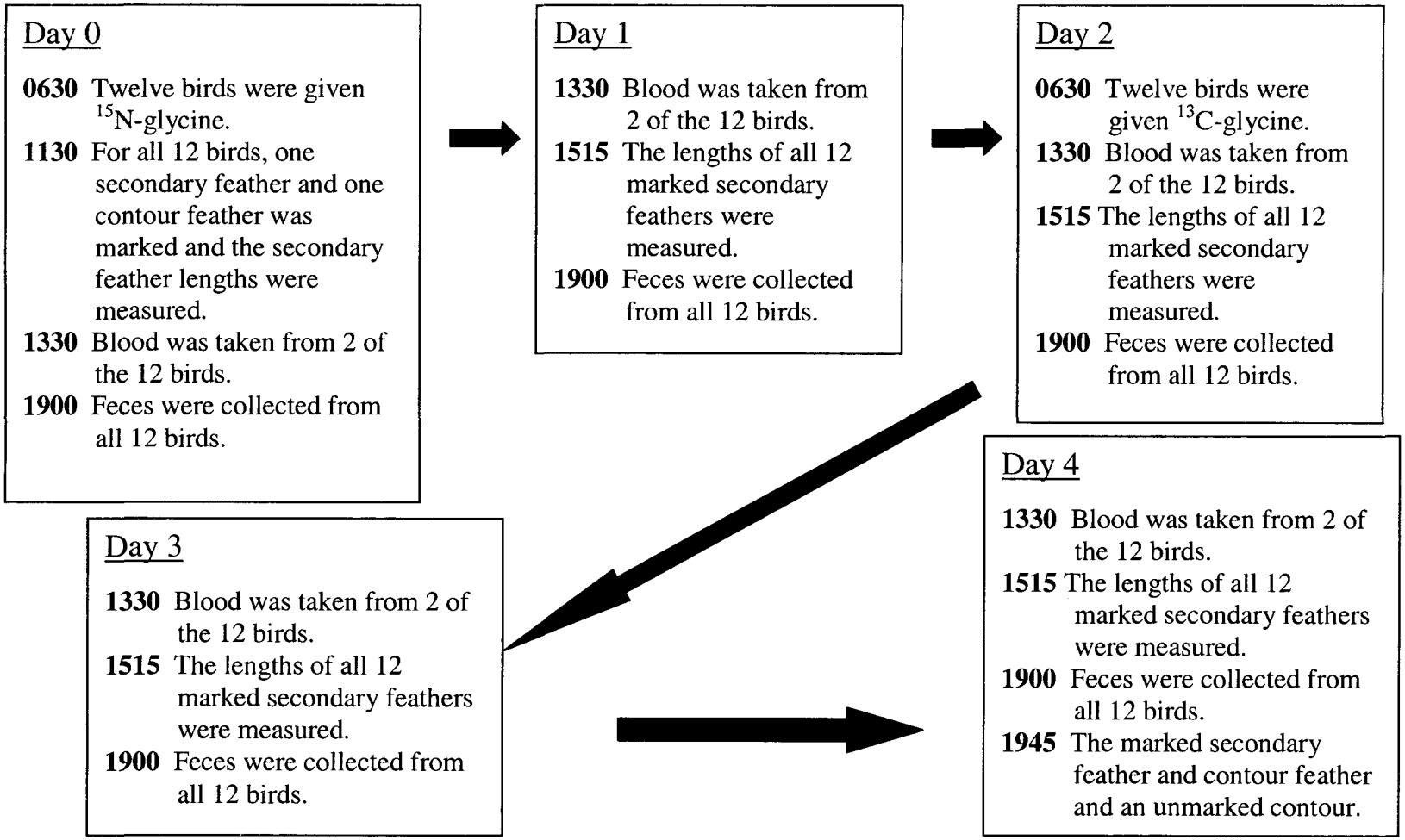

Figure 3. Methods for the ^{15}N-glycine and ^{13}C-glycine dosage and subsequent tissue sampling of twelve Pigeon Guillemot chicks. All twelve birds were treated to the same methods except for blood sampling. Two of the twelve birds were sampled on each particular day and considered representative of the twelve.

Sampling of Pigeon Guillemot Blood, Feces, and Prey Items

The experiment ran for five days from dosage to fledging. Feces were collected from all 12 chicks in the morning, and blood was collected from two birds a day. The two chicks sampled for blood were considered representative of the twelve. Immediately after collection, the blood was centrifuged for 15 minutes at 3000 rev·min^{-1}. The serum and blood cells were separated and dried in an Eppendorf Vacufuge for 3.5 hours at 60°C. Samples were stored in cryovials until later weighing on a microbalance for mass spectrometer analysis.

Fish muscle and feces were oven dried at 60°C to constant weight (48 hours for feces / 60 hours for fish muscle). Subsamples were ground to a fine powder and 0.80 mg weighed into tin cups for analysis.

Sampling of Pigeon Guillemot Feathers

From each Pigeon Guillemot the second secondary feather was selected for collection and identified by notching a neighboring secondary feather. Each day the secondary feather length was measured for growth and the feather was then plucked on day 4 of the experiment. Feathers were washed and dried as previously described and then sectioned to assess variability in isotope ratios along their length. The feathers were 4.9 cm long on average and were sampled at 4 intervals along the length of the feather. Each feather was sectioned at 0-0.5 cm from the tip, 1-1.5 cm from the tip, 0-0.5 cm from the base, and 1-1.5 cm from the base meaning a lengthwise cross section spanning 0.5 cm

was sampled (Figure 4). For each section, the posterior vane, anterior vane, and shaft were sampled. Each sample was then weighed and prepared for mass spectrometry.

At the beginning of the experiment, day 0, one Pigeon Guillemot body feather located on the lower abdomen was marked by coloring all visible feather barbs with a red marking pen. The red feather and one adjacent body feather were pulled on day 4. New unmarked growth on the body feather was identified at the base under the red portion. The tip of an adjacent feather was sampled to establish pre-label values.

Each marked body feather was washed, dried, and then sampled in the portion of new barb growth below the marker. The barbs located at the base of the feather were removed from the shaft and weighed for mass spectrometry. The barbs located at the tip of the adjacent unmarked feather were sampled for comparison.

Mass Spectrometry and Statistical Tests

Duplicate subsamples of muscle, red blood cells, serum, and feces (0.8 - 1.2 mg) were combusted and analyzed for stable isotope ratios using a Europa 20/20 continuous flow mass spectrometer. For feathers, two different mass spectrometers were used. The larger samples from shaft and multiple smaller feathers were analyzed on the Europa mass spectrometer. For museum specimens where only one feather was available, duplicate subsamples of feathers (0.1-0.3mg) were combusted and analyzed for stable isotope ratios using a Finnegan Delta+ mass spectrometer with a Conflo inlet.

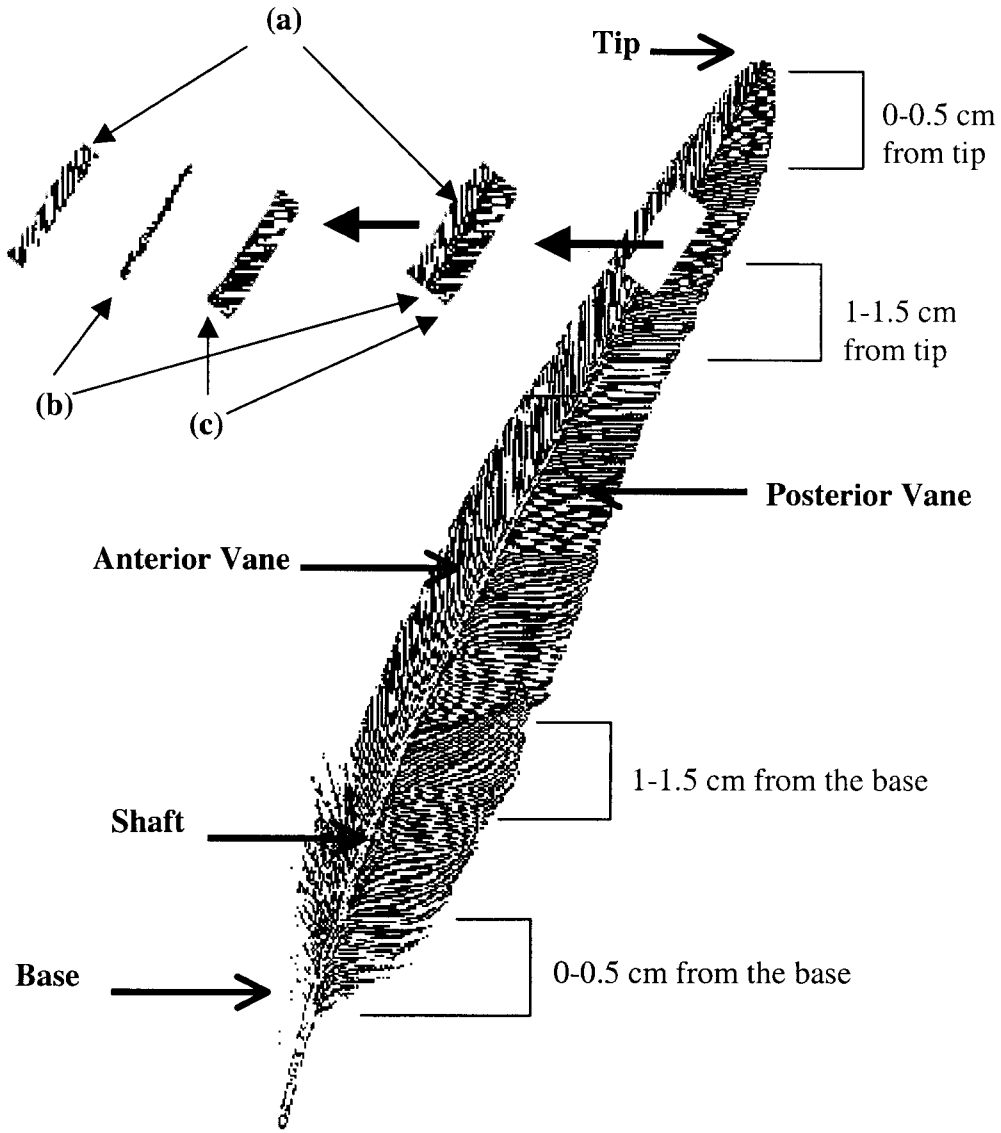

Figure 4. Feather sectioning protocol for a Pigeon Guillemot secondary feather. The anterior vane (a), shaft (b), and posterior vane (c) were each sampled 0-0.5 cm from the tip, 1-1.5 cm from the tip, 0-0.5 cm from the base, and 1-1.5 cm from the base. Feathers on average were 4.9 cm long.

Sample results are expressed in terms of $\delta^{13}C$ and $\delta^{15}N$ as defined by the following equation:

$$\delta^{13}C \text{ or } \delta^{15}N = [(R_{sample}/R_{standard})-1] \times 1000(‰)$$

where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio, and the Peedee belemnite (PDB) carbonate and atmospheric N_2 are used as standards. Samples were reanalyzed if the replicates differed by more than 0.5‰. Overall analytical precision of the Europa was $\pm$ 0.25‰ (standard deviation, n=84) for nitrogen and $\pm$ 0.15‰ for carbon. Overall analytical precision of the Finnigan Delta+ was $\pm$ 0.13‰ (standard deviation, n=41) for nitrogen and $\pm$ 0.12‰ for carbon.

Interannual differences in mean muscle and feather isotope ratios were tested using a Kruskal-Wallis Test, which accounts for non-homogenous errors. For pairwise comparisons of years for both muscle and feather, Tukey Tests were used because of deviations from population normality and homogeneity (Keselman 1976). For variability among body regions, 95% confidence intervals were calculated and compared. Linear regressions were done on both the $\delta^{13}C$ and $\delta^{15}N$ timeline to test for trends over time.

Thick-billed Murre muscle isotope ratios were tested for correlation to possible climatic factors that may affect primary productivity. The climatic factors considered were the Pacific Decadal Oscillation, annual flow through the Bering Strait, and annual sea ice extent over the time period 1976-1999 (Roach et al. 1995; Mantua et al. 1997; Niebauer 1998). The climatic factors were tested with different time lags ranging from

no lag to a lag of 2 years. Additionally, $\delta^{13}C$ values in Thick-billed Murre muscle were compared to $\delta^{13}C$ values in bowhead whale baleen (Schell 2000). All muscle data for each year (all locations) was pooled when calculating these correlations.

Results

Thick-billed Murre Tissue Analyses

Interannual Variability

Carbon isotope ratios of Thick-billed Murre muscle over the period 1976-1998 ranged between -16.5‰ and -20.7 ‰ and nitrogen isotope ratios ranged between 14.9‰ and 18.4‰ (Figure 5, Table 3). From 1976-present, annual mean carbon isotope ratios were significantly lower ($p \leq 0.0001$) in 1977 (Cape Lisburne birds), 1985, and 1998 and significantly higher in 1976 and 1992 (Tukey pairwise, alpha=0.05) when compared to means in all other years. The mean carbon isotope ratios from all locations showed a decreasing trend of 0.04‰ yr^{-1} over the 1978-1998 time period. The mean nitrogen isotope ratios from all locations showed a decreasing trend of 0.03‰ yr^{-1} over the time period 1978-1998.

Nitrogen isotope ratios were not correlated with carbon isotope ratios in muscle indicating that changes in $\delta^{13}C$ were not linked to changes in trophic status of the birds. If changes in $\delta^{13}C$ values were linked to trophic level, a correlation with trends in nitrogen should be evident. Mean annual nitrogen isotope ratios were significantly lower in 1992 and 1997 and significantly higher in 1987 and 1983 when compared to all other years. In 1977, stable nitrogen isotope ratios were not different between Cape Thompson and Cape Lisburne birds. Also, in 1983, nitrogen isotope values were not statistically

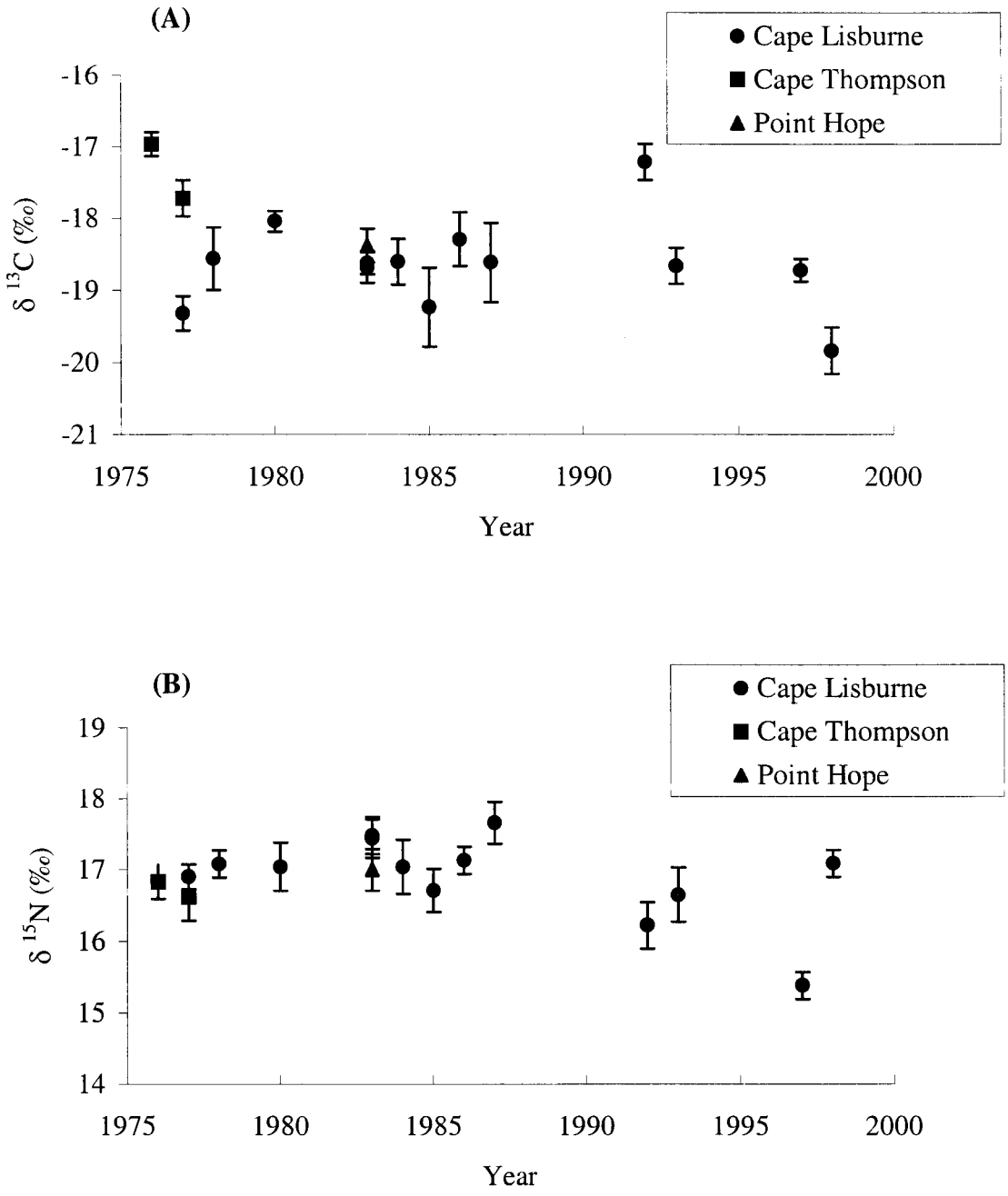

Figure 5. $\delta^{13}C$ **(A)** and $\delta^{15}N$ **(B)** values in Thick-billed Murre muscle during the time period 1976-1998. Error bars represent 95% confidence intervals.

Table 3. Mean $\delta^{13}C$ and $\delta^{15}N$ values for each year in Thick-billed Murre muscle and 95% confidence intervals. n is number of birds sampled in each year.

Year	Location	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	n
1998	Cape Lisburne	-19.83 ± 0.32	17.09 ± 0.19	10
1997	Cape Lisburne	-18.72 ± 0.16	15.38 ± 0.19	10
1993	Cape Lisburne	-18.65 ± 0.25	16.65 ± 0.38	10
1992	Cape Lisburne	-17.21 ± 0.25	16.22 ± 0.32	10
1987	Cape Lisburne	-18.61 ± 0.55	17.66 ± 0.29	9
1986	Cape Lisburne	-18.29 ± 0.38	17.13 ± 0.19	10
1985	Cape Lisburne	-19.23 ± 0.54	16.71 ± 0.30	10
1984	Cape Lisburne	-18.6 ± 0.32	17.04 ± 0.38	10
1983 (June)	Cape Lisburne	-18.62 ± 0.16	17.44 ± 0.27	10
1983 (August)	Cape Lisburne	-18.68 ± 0.21	17.48 ± 0.26	10
1983	Point Hope	-18.38 ± 0.24	17.00 ± 0.30	10
1980	Cape Lisburne	-18.04 ± 0.14	17.04 ± 0.34	10
1978	Cape Lisburne	-18.56 ± 0.44	17.08 ± 0.19	6
1977	Cape Lisburne	-19.32 ± 0.24	16.90 ± 0.17	9
1977	Cape Thompson	-17.72 ± 0.25	16.62 ± 0.34	10
1976	Cape Thompson	-16.96 ± 0.17	16.83 ± 0.24	10

different between birds collected from Point Hope in May, Cape Lisburne in June, and Cape Lisburne in August.

Carbon isotope ratios of Thick-billed Murre chin and under the wing contour feathers over the period 1976-1998 ranged between -15.47‰ and -20.38‰ and nitrogen isotope ratios ranged between 16.13‰ and 19.72‰ (Figure 6). Overall, $\delta^{13}C$ values in feather were depleted in 1997 and 1998 with respect to the rest of the years sampled and enriched in 1978 (Tukey pairwise, alpha=0.05, Figure 6). Both enrichment and depletion were observed between 1931-1978 with peak enrichment in 1978 (Figure 6). In contrast, there were no significant annual differences in $\delta^{15}N$ values.

The diet of Thick-billed Murres varied between years (Springer 1984; Springer pers. comm.)(Table 4). Arctic cod and sculpin were present in the diet in almost every year. The only exceptions to this were in 1976 when cod were absent and 1992 when sculpin were absent. Sand lance (*Ammodytes hexapterus*) were also a part of the diet. Invertebrates were present in the diet in every year except 1998 and 1986, when none were found in any of the stomachs sampled.

Mean annual Thick-billed Murre muscle $\delta^{13}C$ values were correlated with the Pacific Decadal Oscillation values (Mantua et al. 1997) of the previous year (Spearman's Test, $p = 0.0015$, Figure 7). However, they were not correlated with annual sea ice extent nor to annual flow through Bering Strait (Roach et al. 1995; Niebauer 1998). Thick-billed Murre $\delta^{13}C$ values followed trends seen in bowhead whale baleen (Schell 2000) (Spearman's Test, $p = 0.03$, Figure 8).

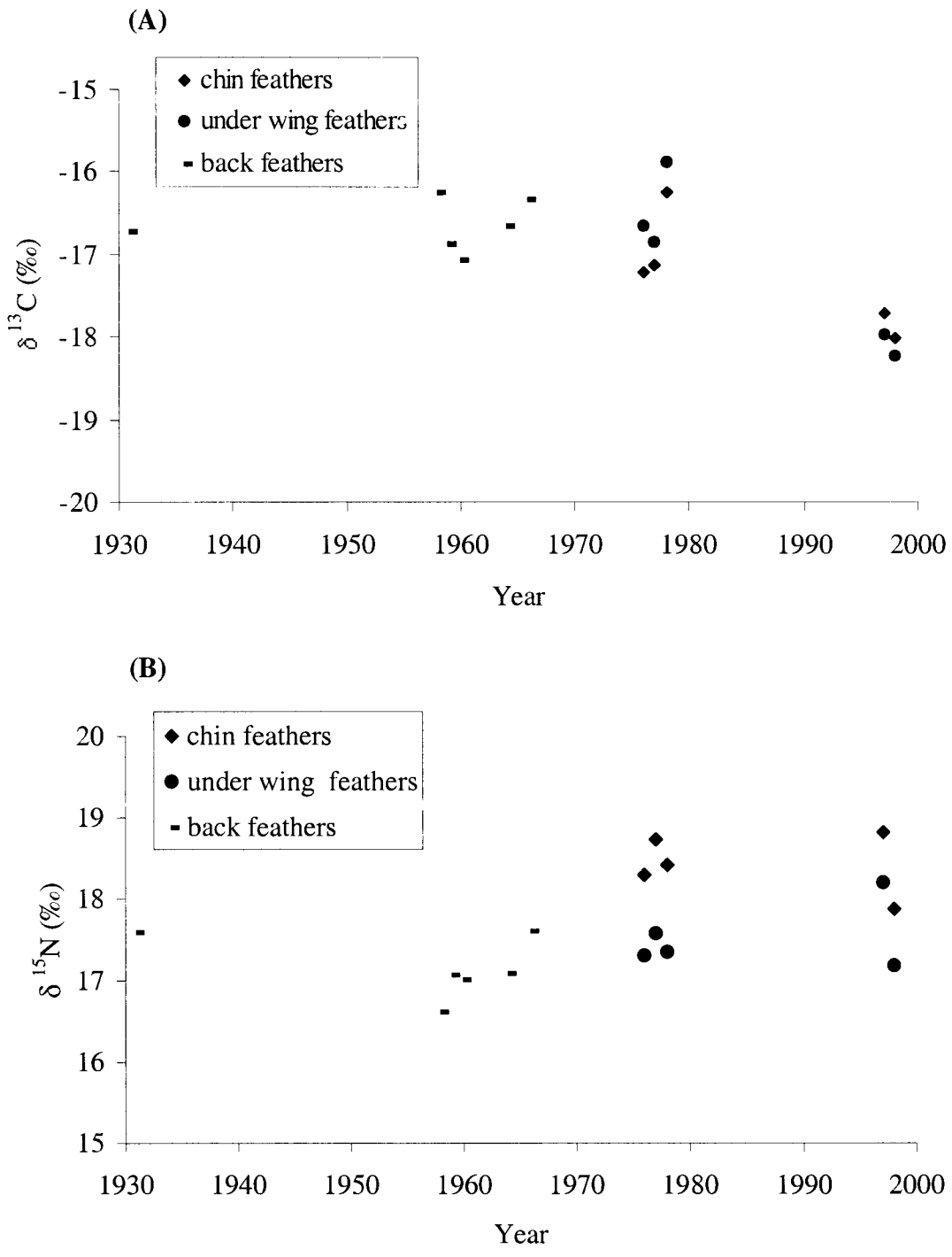

Figure 6. Mean $\delta^{13}C$ **(A)** and $\delta^{15}N$ **(B)** values in Thick-billed Murre chin feathers, back feathers, and feathers located under the wing during the time period 1931-1998.

Table 4. Thick-billed Murre dietary components. Number of birds (n) are those with measurable amounts of prey in their stomach, stomach contents are expressed as frequency of occurrence, and values in parentheses are biomass in grams - only available for vertebrate prey. All years that do not have colony markings are from Cape Lisburne. (Springer, unpub.)

* Birds collected at the Cape Thompson colony
** Birds collected at the Point Hope colony
• Birds collected at the Cape Lisburne colony in July
• • Birds collected at the Cape Lisburne colony in August

Year	n	Arctic cod	Saffron Cod	Cod	Sculpin	YOY flatfish	Sand lance	Capelin	Amphipods	Mysids	Polychaetes	Crustaceans	Snails	Euphausiids	Crab	Shrimp
76*	7	0	0	0	3 (38)	2 (4)	0	0	3	0	1	1	0	0	0	0
77*	6	0	0	2 (6)	1 (35)	0	0	0	1	0	0	0	0	0	0	1
77	8	1 (76)	0	1 (5)	2 (30)	4 (54.9)	1 (.5)	0	1	0	0	0	0	1	0	0
78	5	0	1 (4.5)	1 (10)	2 (12.8)	2 (17.5)	2 (29)	0	1	0	0	0	0	0	0	0
80	9	3 (464)	2 (28)	1 (20)	5 (79)	0	5 (51.6)	1 (29)	0	0	0	0	0	1	0	0
83•	9	6 (1034)	2 (25)	0	3 (8.6)	2 (1)	0	0	1	1	2	0	0	0	2	2
83• •	10	8 (669.2)	3 (1.7)	0	6(100.1)	4 (4.5)	3 (56.6)	1 (2.7)	4	0	2	0	1	0	4	3
83**	6	4 (287)	0	0	0	0	0	0	0	0	0	0	1	0	2	0
84	8	1 (42)	0	0	3(133.3)	6 (25)	1 (6.4)	0	0	2		2	1	0	0	1
85	9	8 (943.4)	1 (7.7)	0	2 (7.9)	0	0	0	0	0	0	7	0	0	0	1

Table 4 continued.

86	10	2 (49)	0	3 (44.7)	8(398.4)	1 (17)
87	9	1 (5)	0	0	3 (40.5)	2 (95)
92	7	1 (14)	0	0	0	0
93	10	5 (506)	1 (4.8)	0	6(203.9)	9 (92.3)
97	8	3 (73.4)	2 (8.6)	0	8 (41.2)	0
98	5	2 (79)	3(247)	1 (30)	1 (25.3)	0

2 (116)	0	0	0	0	0	0	0	0	0
7 (376)	0	0	0	0	0	0	0	0	4
0	0	0	0	0	0	0	3	0	0
2 (18.7)	0	1	3	0	2	0	0	0	0
2 (25)	1 (4.3)	2	5	1	1	0	0	0	5
3 (10.8)	0	0	0	0	0	0	0	0	0

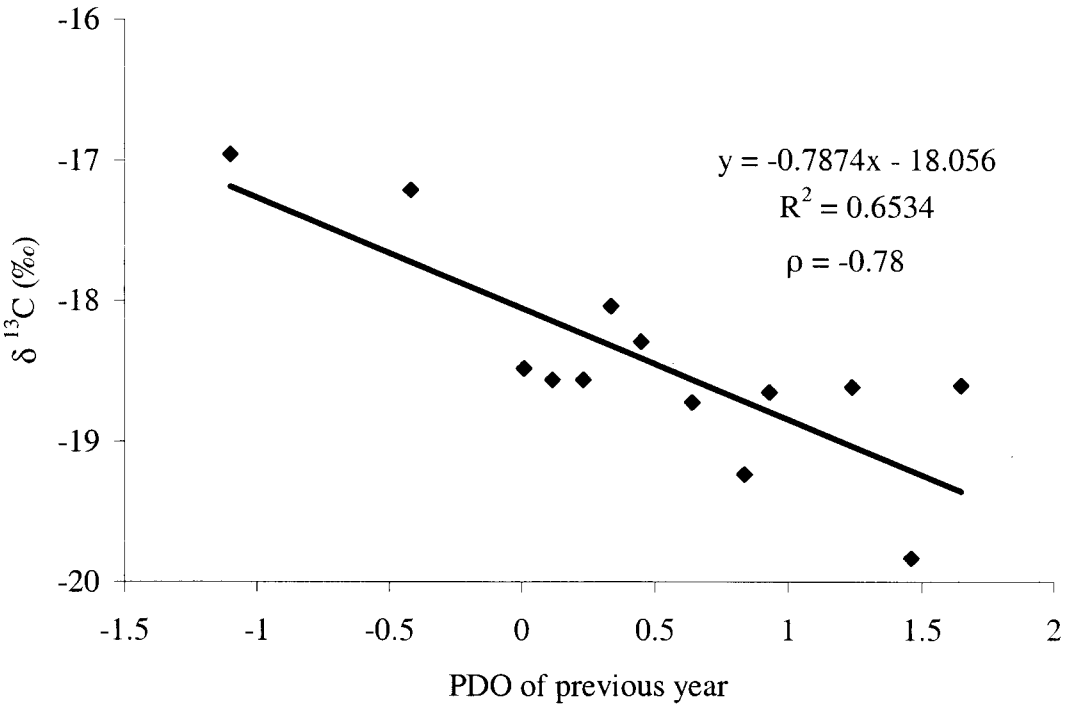

Figure 7. Regression of $\delta^{13}C$ values in Thick-billed Murre muscle on the Pacific Decadal Oscillation of the previous year. ρ = Spearman correlation coefficient

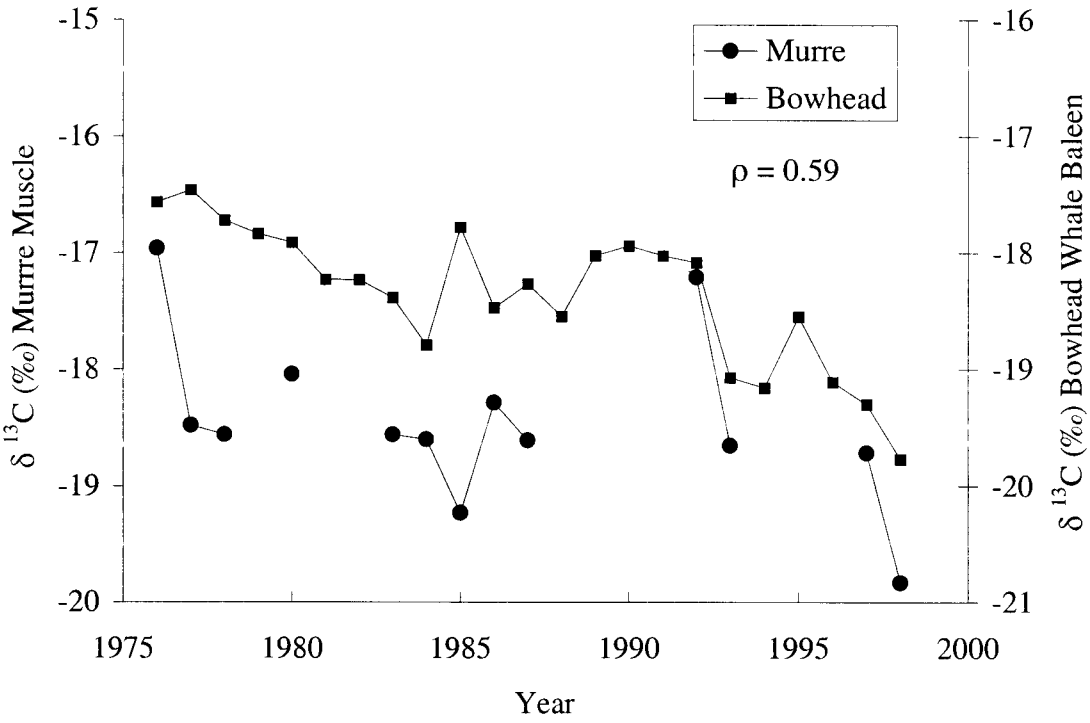

Figure 8. $\delta^{13}C$ values in Thick-billed Murre muscle (left axis) and bowhead whale baleen (right axis) over the time period 1976-1999 (Schell 2000). Axes are offset by 1‰ for comparison. The Thick-billed Murre line used averages of all birds from all locations in 1983 and 1977. ρ = Spearman correlation coefficient.

Seasonal and Geographic Variability in Thick-billed Murre Isotope Ratios

Geographic variability in $\delta^{13}C$ was apparent in muscle samples from Cape Thompson and Cape Lisburne birds, with the former being significantly higher than the birds from Cape Lisburne by 1.6 ‰ (Tukey Test, $p \leq 0.05$)(Figure 5). In contrast the $\delta^{13}C$ values in birds collected in 1983 from Point Hope in May, Cape Lisburne in June, and Cape Lisburne in August, were not significantly different.

Variability Between Tissues

Feathers are comprised of keratin and enriched in ^{13}C and ^{15}N over muscle samples for the same bird. Chin feathers compared to muscle for the period 1976-1998 ranged from -0.71‰ to 3.14‰. Chin feathers averaged over all years were enriched by 0.87 ± 0.33‰ (95% CI) in carbon and by 1.09 ± 0.31‰ in nitrogen relative to muscle (Table 5). Contour feathers located under the wing averaged over all years were enriched by 0.98 ± 0.30‰ in carbon and by 0.31 ± 0.27‰ in nitrogen (Table 5). Feather enrichment over muscle varied between years for carbon but not nitrogen, resulting in no direct correlation between feather values and muscle.

Feathers from different body regions did not differ significantly in either the $\delta^{13}C$ or $\delta^{15}N$ values for the birds collected in 1998 (Figure 9). However, chin feather $\delta^{13}C$ values were statistically distinct relative to values in feathers from under the wing for birds sampled in 1976 (Figure 10). Chin feathers $\delta^{15}N$ values were also statistically distinct relative to values from under the wing in birds sampled from Cape Thompson in

Table 5. The difference in $\delta^{13}C$ and $\delta^{15}N$ between Thick-billed Murre feathers and muscle. Chin = feathers from the chin region, under wing = contour feathers taken from the region underneath the wing.

Bird ID	Location	Chin feather minus muscle		Under wing feather minus muscle	
		$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
CL20598	Cape Lisburne	0.06	0.03	0.60	0.46
CL20698	Cape Lisburne	0.01	0.11	0.37	0.85
CL20798	Cape Lisburne	0.16	0.73	0.49	1.81
CL20898	Cape Lisburne	0.27	0.05	0.24	0.19
CL20998	Cape Lisburne	0.03	0.02	0.54	0.01
CL22998	Cape Lisburne	0.17	0.69	0.19	0.44
CL25798	Cape Lisburne	0.18	0.01	0.23	0.37
CL25998	Cape Lisburne	0.34	1.09	0.09	0.29
CL29298	Cape Lisburne	0.16	0.06	0.57	1.01
CL30098	Cape Lisburne	0.01	0.08	0.19	0.08
CL-27-97	Cape Lisburne	0.08	0.79	1.17	0.76
CL-28-97	Cape Lisburne	0.12	0.38	0.18	0.10
LAMS 59-78	Cape Lisburne	0.33	0.04	0.17	0.05
LAMS 63-78	Cape Lisburne	0.34	1.43	0.67	0.10
LAMS 57-78	Cape Lisburne	0.19	0.8	1.04	1.38
LAMS 58-78	Cape Lisburne	0.24	0.06	1.08	0.08
LAMS 67-78	Cape Lisburne	0.03	0.01	0.63	0.93
LAMS 62-78	Cape Lisburne	0.01	0.21	0.14	1.20
AMS-19-77	Cape Thompson	0.07	0.08	0.05	0.35
AMS-20-77	Cape Thompson	0.21	0.15	0.13	0.36
AMS-21-77	Cape Thompson	0.31	0.01	0.1	0.12

Table 5 continued.

AMS-22-77	Cape Thompson	0.18	1.13	0.55	1.60
AMS-23-77	Cape Thompson	0.26	0.09	0.14	0.09
AMS-25-77	Cape Thompson	0.06	0.94	0.43	1.35
AMS-28-77	Cape Thompson	0.2	1.2	0.31	0.71
AMS-31-77	Cape Thompson	0.04	0.18	0.3	0.11
AMS-35-77	Cape Thompson	0.38	0.15	0.91	2.45
AMS 174-77	Cape Lisburne	0.31	0.02	0.11	1.77
AMS 178-77	Cape Lisburne	0.24	0.13	0.06	0.44
AMS 170-77	Cape Lisburne	0.05	0.5	0.92	0.24
AMS 177-77	Cape Lisburne	0.17	1.03	0.26	2.08
AMS 172-77	Cape Lisburne	0.01	0.19	0.12	0.29
AMS 175-77	Cape Lisburne	0.08	0.43	0.19	0.37
AMS 171-77	Cape Lisburne	1.24	0.14	0.16	0.04
AMS 173-77	Cape Lisburne	0.47	0.29	0.89	2.69
AMS 176-77	Cape Lisburne	0.06	0.12	0.6	0.24
AMS 13-76	Cape Thompson	0.23	0.56	1.41	0.10
AMS 39-76	Cape Thompson	0.13	0.14	0.82	2.36
DGR 37-76	Cape Thompson	0.27	0.6	0.4	0.40
AMS 10-76	Cape Thompson	0.01	0.35	0.79	1.68
AMS 8-76	Cape Thompson	0.12	0.4	0.07	0.24
DGR-29-76	Cape Thompson	0.26	0.02	0.02	0.73
AM 1-76	Cape Thompson	0.4	0.64	0.27	0.00
AM 2-76	Cape Thompson	0.14	0.49	0.03	0.15
AMS 11-76	Cape Thompson	0.15	0.07	0.04	0.14
AMS 6-76	Cape Thompson	0.06	0.15	1.1	0.45

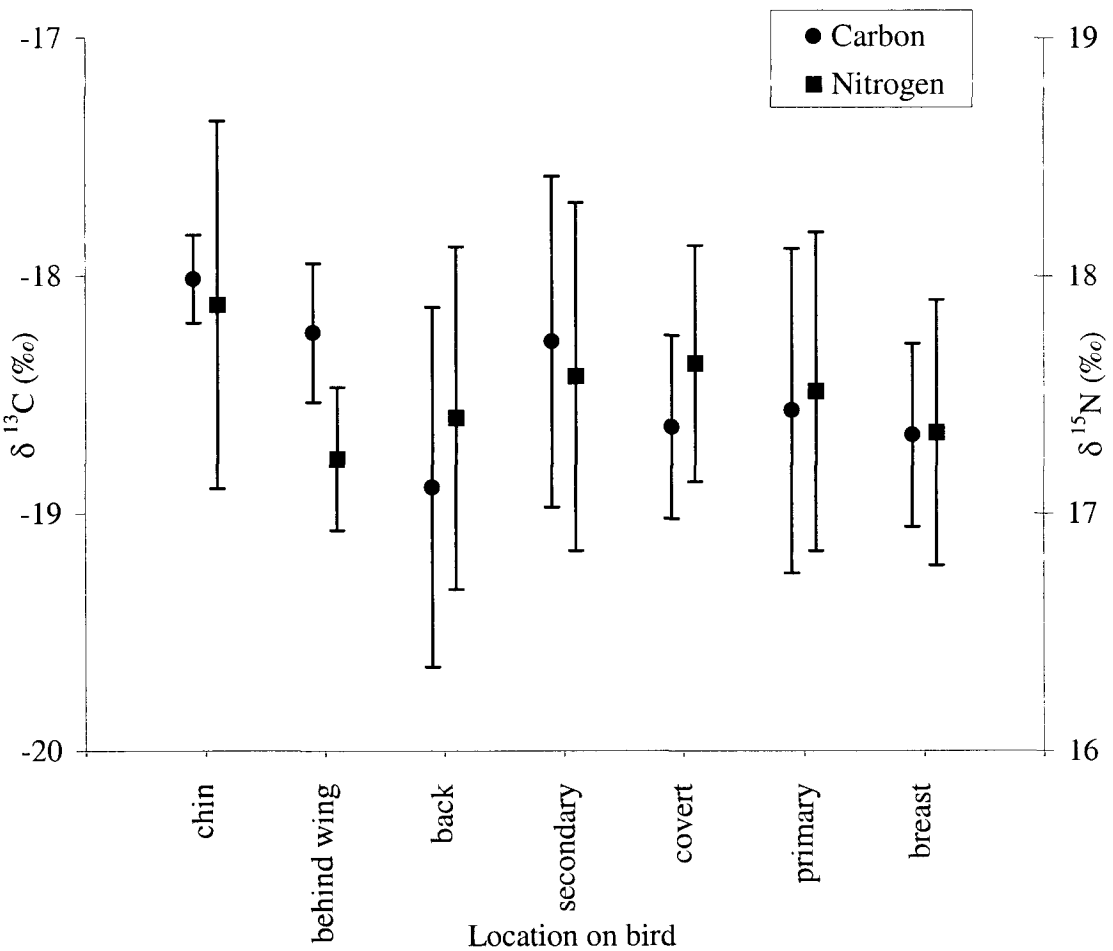

Figure 9. Average $\delta^{13}C$ and $\delta^{15}N$ values in each feather region sampled on the Thick-billed Murres. Birds were collected from the Cape Lisburne colony in 1998. Error bars represent 95% confidence intervals.

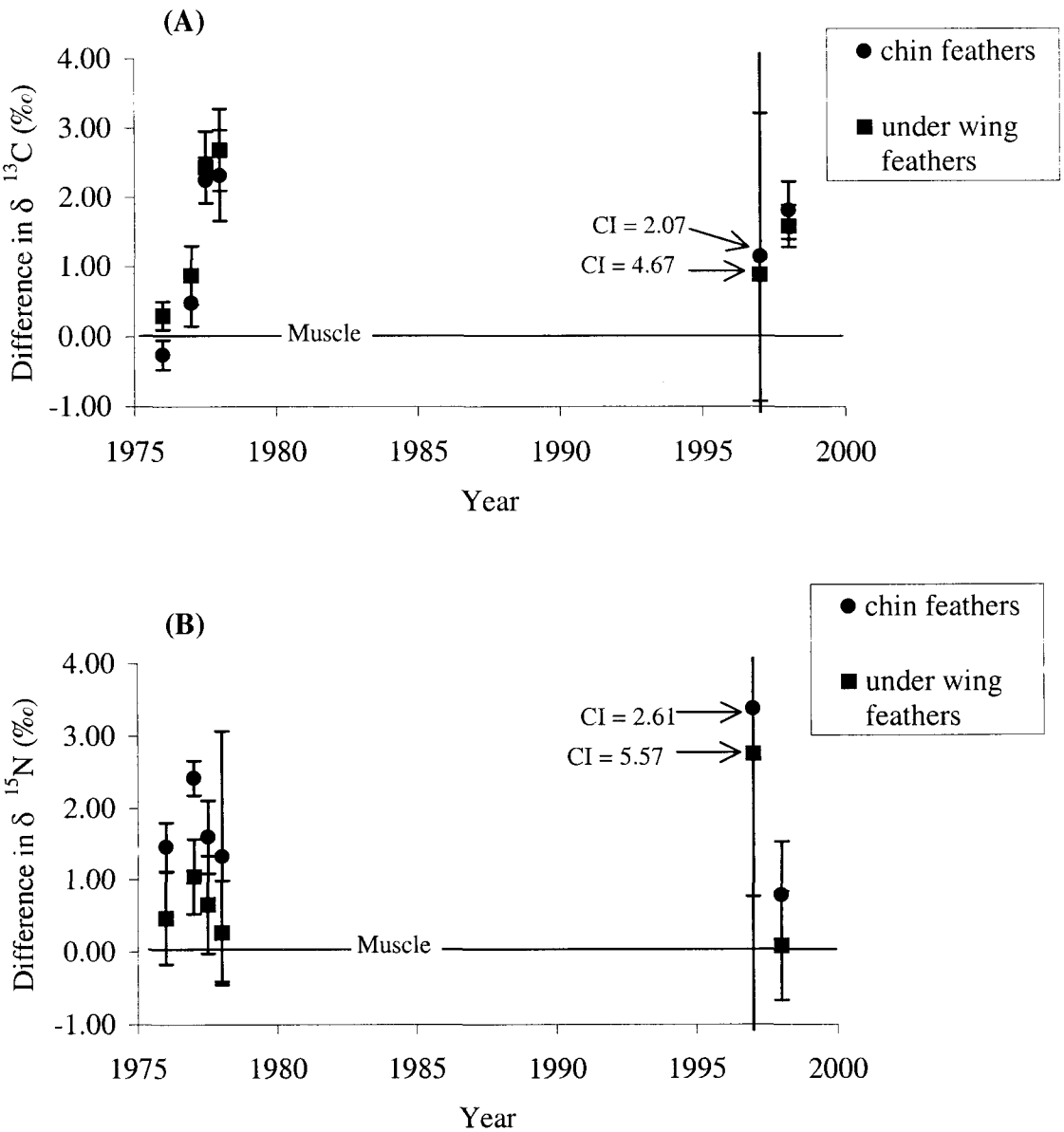

Figure 10. $\delta^{13}C$ **(A)** and $\delta^{15}N$ **(B)** values in Thick-billed Murre chin feathers and feathers located under the wing normalized to muscle. Error bars represent 95% confidence intervals. CI = confidence interval.

1977 (Figure 10). $\delta^{13}C$ and $\delta^{15}N$ values in the two feathers sampled within the same area on the same bird differed on average by 0.29 ‰ and 0.46 ‰, respectively.

In two Thick-billed Murre primary feathers, the posterior vane appeared slightly enriched in relation to the anterior vane. However, in one primary, the shaft was highly variable in both stable carbon, ranging 0.08 ‰ to 1.47 ‰ and nitrogen ranging 0.06 ‰ to 3.63 ‰ isotope ratios (Figure 11, Figure 12). Vanes derived from a given shaft location were in most cases greater than values of the shaft.

Fractionation between posterior vane, anterior vane, and shaft was determined on 12 Pigeon Guillemot feathers. Two segments of unlabeled feather were analyzed, the tip 0.5 cm and 1-1.5 cm from the tip. No consistent differences were noted between each vane and shaft. The average difference between $\delta^{13}C$ values in the posterior vane, anterior vane, and shaft was 0.20 ± 0.05‰ and in $\delta^{15}N$ was 0.43‰ $\pm$ 0.14‰. The anterior vane was, however, consistently depleted in $\delta^{13}C$ relative to the posterior vane and shaft at 1-1.5cm from the tip (Figure 13). However, the depletion in anterior vane $\delta^{13}C$ values was not statistically significant and was not evident in the tip segments. Although the $\delta^{15}N$ values in the tip segments of 3 feathers differed by up to 3.34‰ between posterior vane, anterior vane, or shaft, the differences were not consistent between segments or feather components (Figure 14).

Pigeon Guillemot Isotope Labeling Experiment

^{15}N-glycine was given to the birds on day 0 and ^{13}C-glycine was given to the same birds on day 2 of the experiment. The largest immediate enrichment of nitrogen

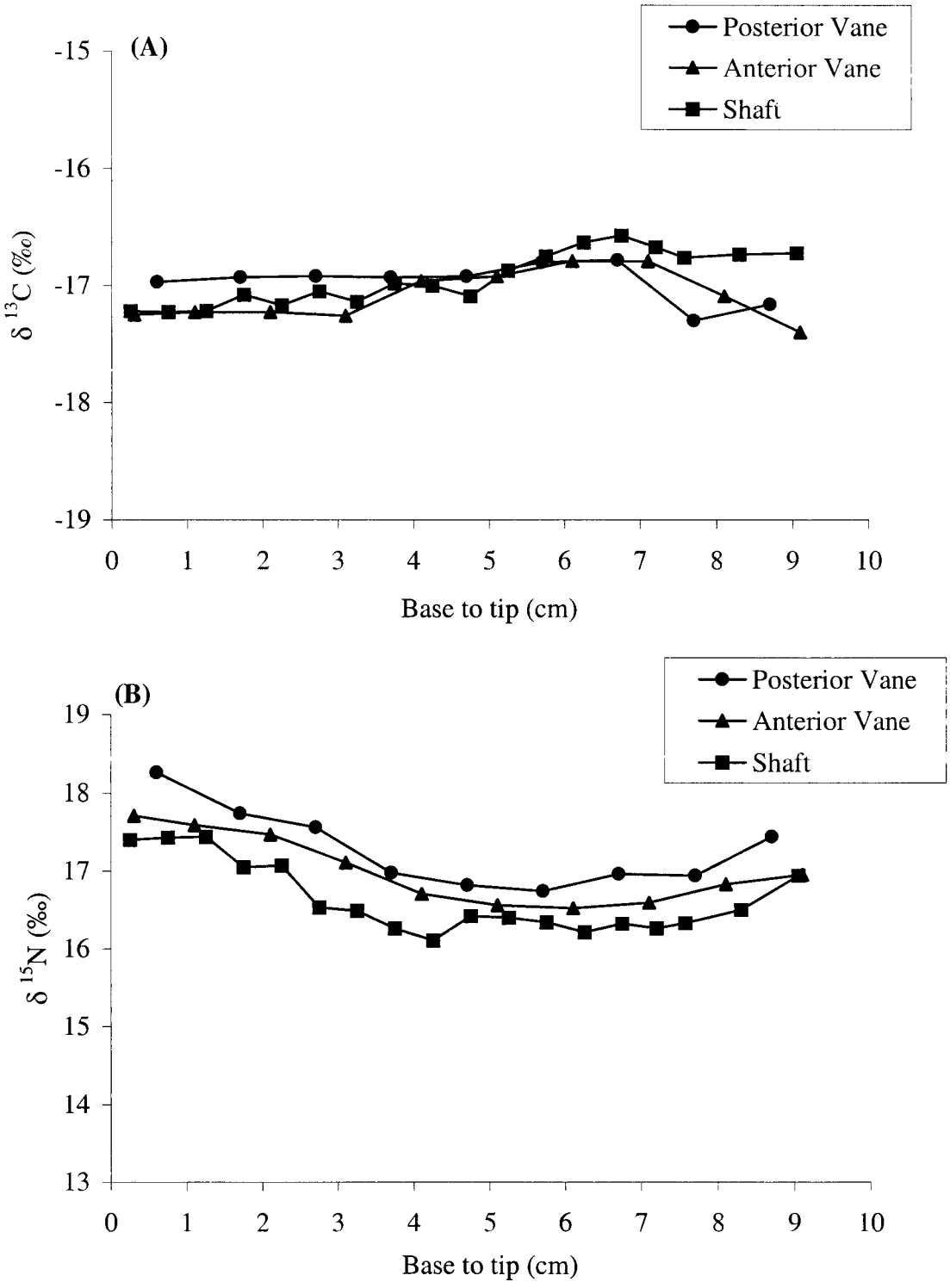

Figure 11. $\delta^{13}C$ **(A)** and $\delta^{15}N$ **(B)** values (weighted means) along a sectioned primary feather in a Thick-billed Murre (Bird ID: 29-76).

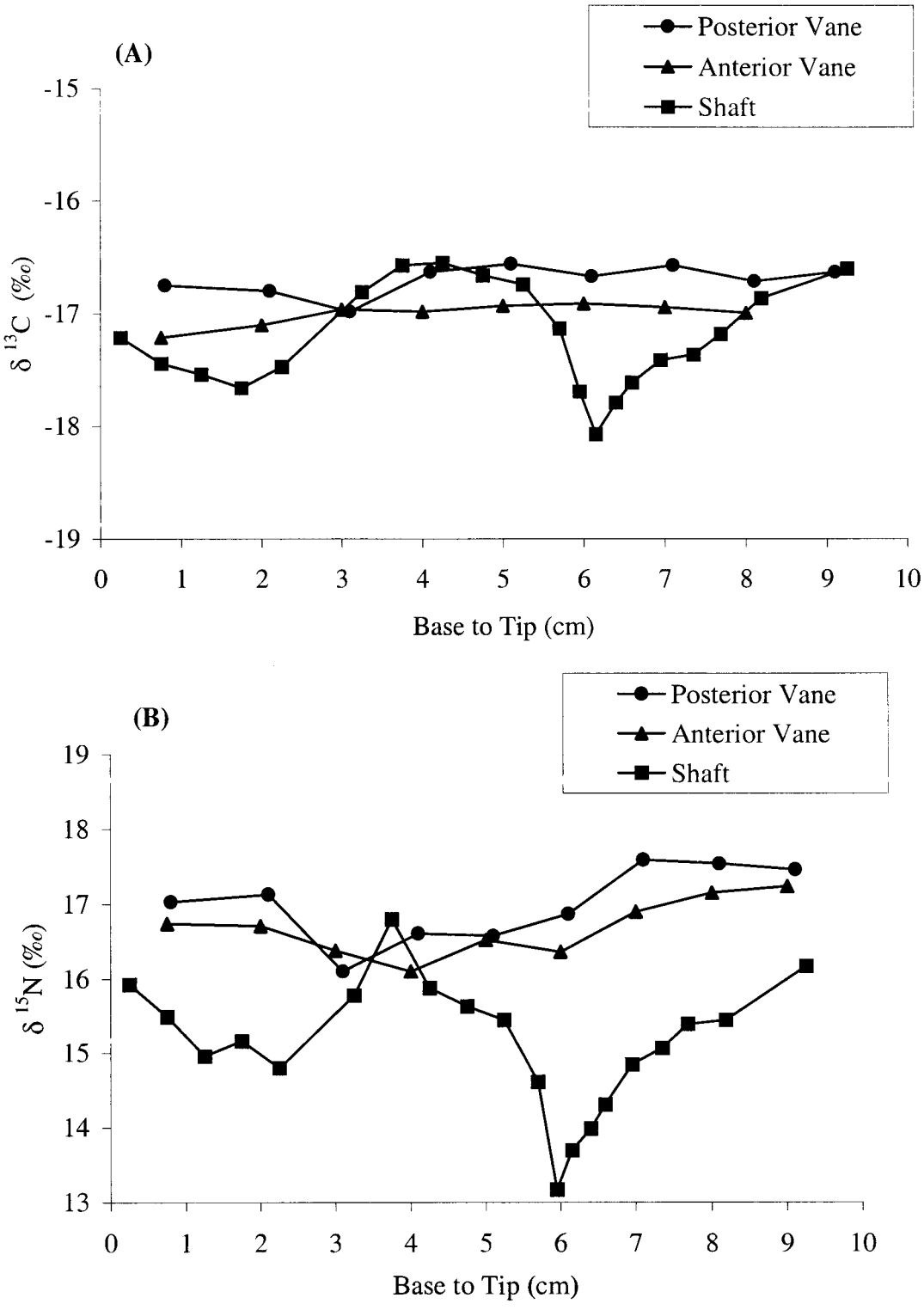

Figure 12. $\delta^{13}C$ **(A)** and $\delta^{15}N$ **(B)** values (weighted means) along a sectioned primary feather in a Thick-billed Murre (Bird ID: 37-76).

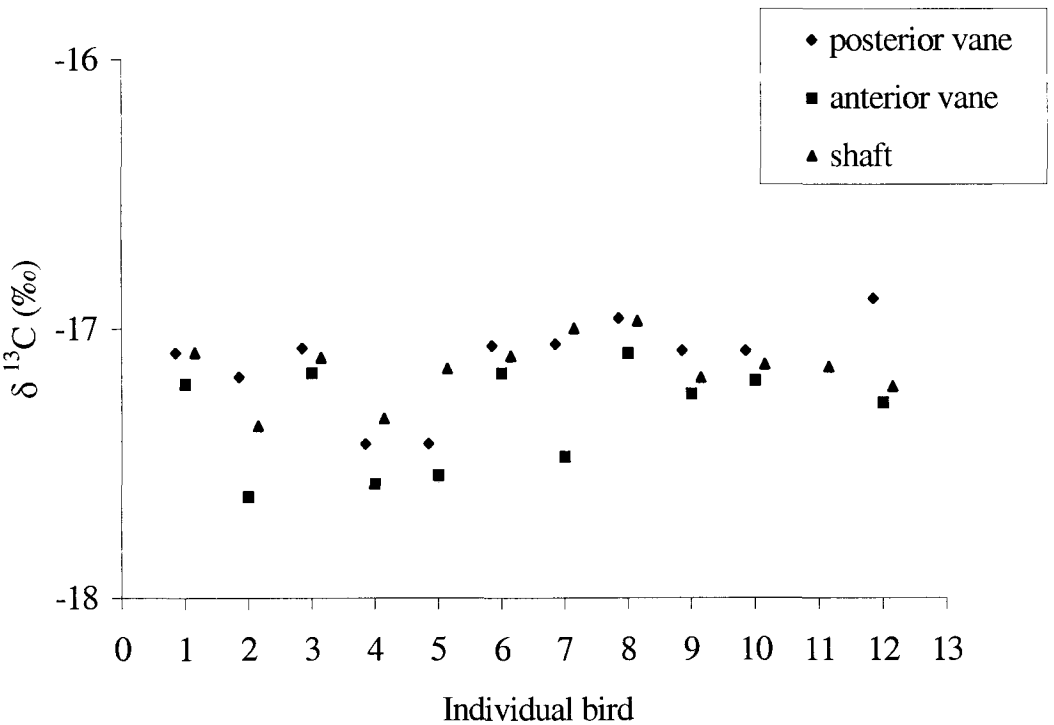

Figure 13. $\delta^{13}C$ values in the feather section located 1-1.5 cm from the tip of a secondary in each Pigeon Guillemot. For each section the posterior vane, anterior vane, and shaft were sampled.

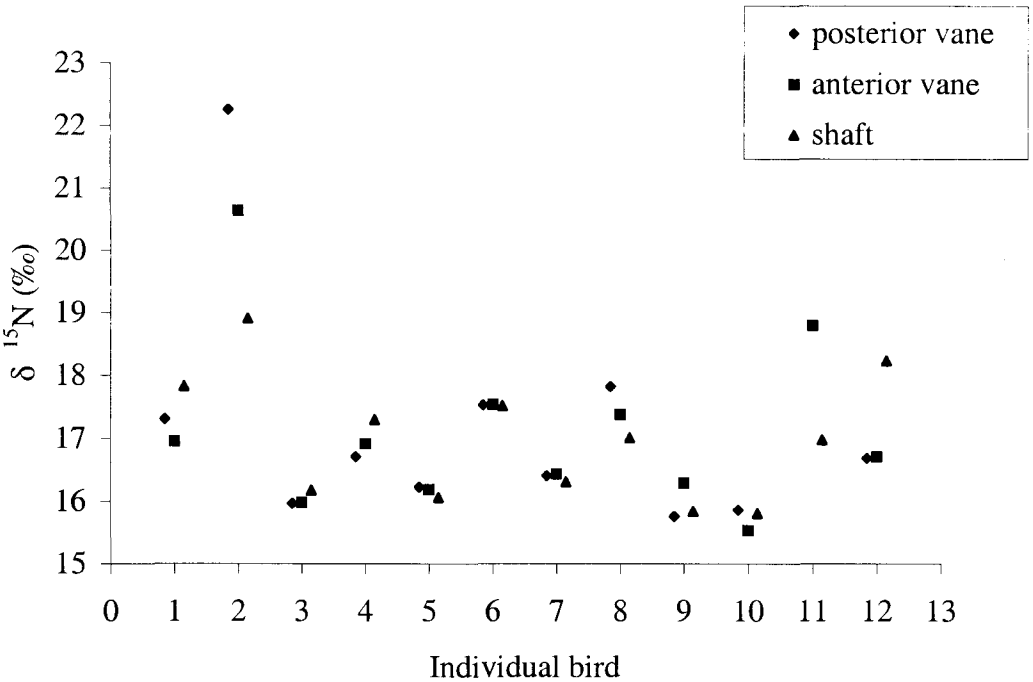

Figure 14. $\delta^{15}N$ values in the feather section located 0-0.5 cm from the tip of a secondary in each Pigeon Guillemot. For each section the posterior vane, anterior vane, and shaft were sampled.

was seen in the feces (birds were dosed at 0630hr and feces was collected at 1900hr), as compared to blood and feather (Figure 15). The $\delta^{15}N$ values returned to non-enriched values on day 3 of the study and in 3 cases were back to non-enriched values in 2 days, indicating the labels were eliminated from the gut. On day 4 of the experiment, $\delta^{13}C$ values in feces of the same birds were still slightly enriched with respect to values on day 0 and 1 (before $\delta^{13}C$ label was introduced) (Figure 15).

For both nitrogen and carbon, enrichments were seen in the bloodstream within seven hours after dosing. In both red blood cells and the serum, the $\delta^{13}C$ values were enriched on day 2 of the experiment (^{13}C-glycine dosage was fed to the chicks that morning) and were still enriched on day 4 of the experiment (Figure 16). Enrichment in the serum was higher than in the red blood cells. For nitrogen there were no pre-enrichment values because no controls were taken prior to dosing. The red blood cells did not change much due to their turnover rate of ~30 days.

The base of the Pigeon Guillemot secondary feathers were highly enriched relative to the tip in both $\delta^{15}N$ and $\delta^{13}C$ indicating that the labeled glycine had been incorporated into the feathers (Figure 17). The feather segment sampled at 1-1.5cm from the base also showed enrichment in $\delta^{15}N$ values and showed enrichment in $\delta^{13}C$ for 3 birds (Figure 17). In two of those three birds, the enrichment in $\delta^{13}C$ was present in the shaft but was not evident in either anterior or posterior vane, implying that the shaft was still forming after the vanes were completed. In six of the twelve birds sampled, the enrichment in $\delta^{15}N$ in the segment 1-1.5cm from the feather base was much higher in the

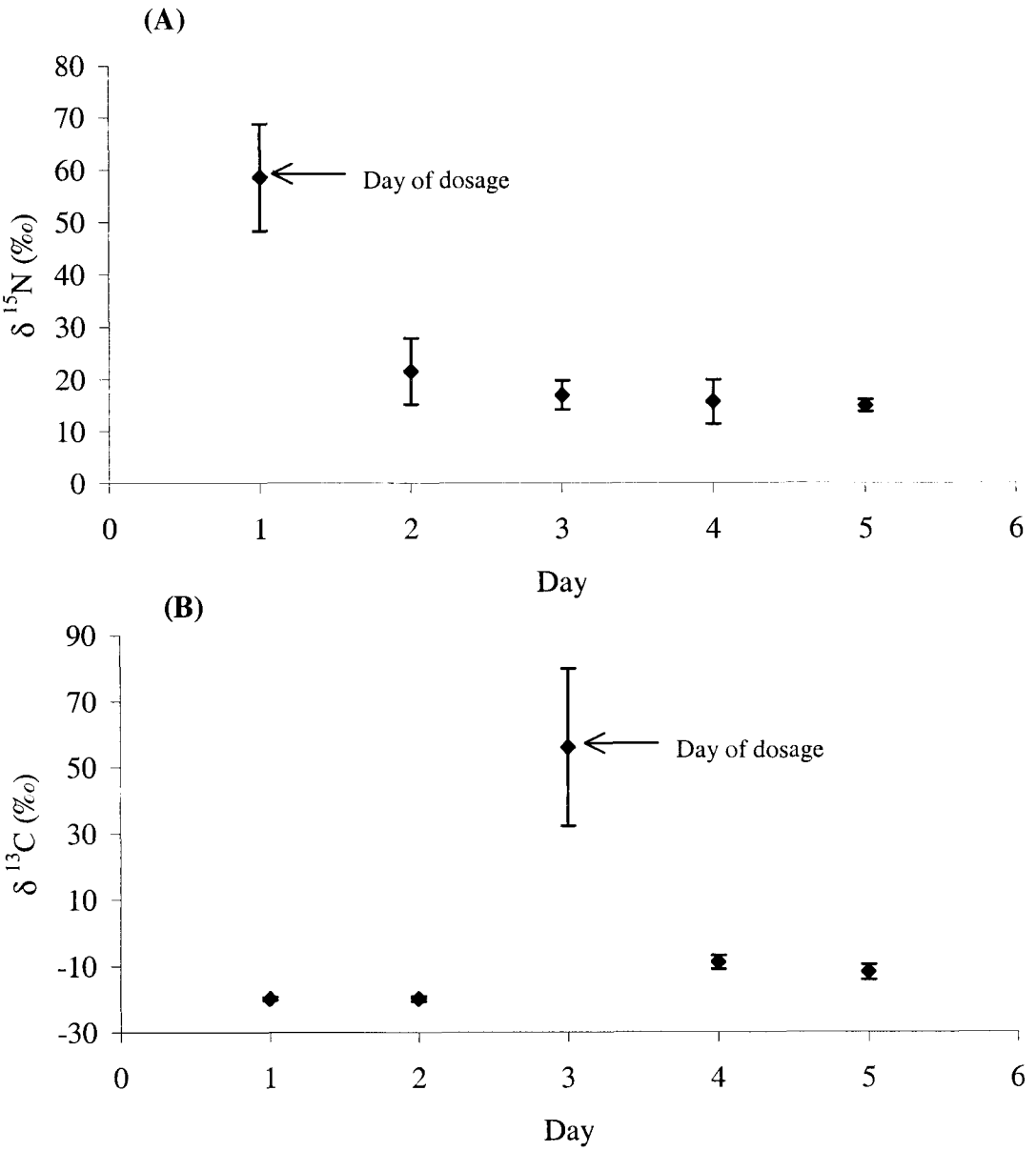

Figure 15. Mean $\delta^{15}N$ **(A)** and $\delta^{13}C$ **(B)** values for Pigeon Guillemot feces collected each day of the experiment. Error bars represent 95% confidence intervals.

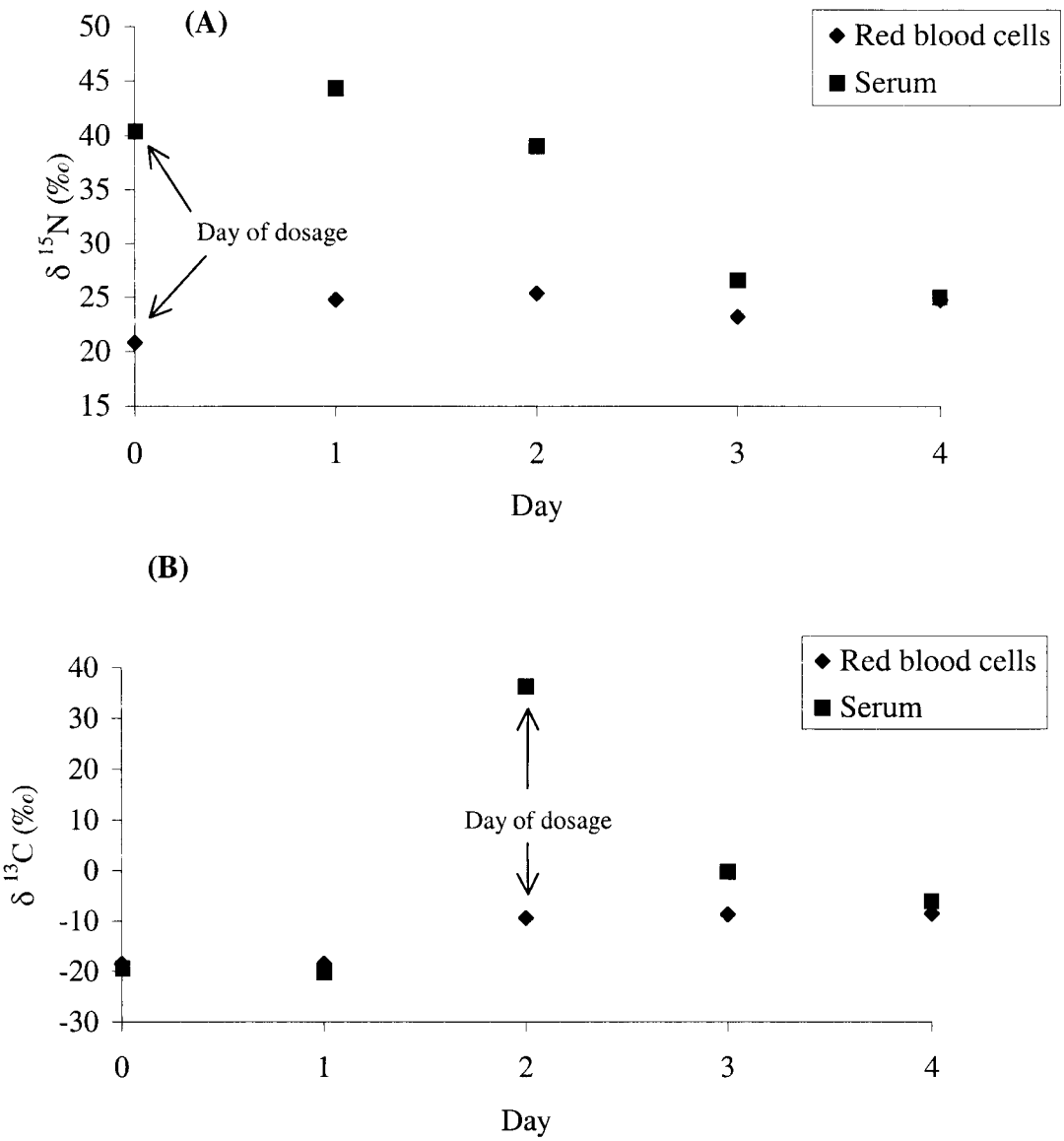

Figure 16. Mean $\delta^{15}N$ **(A)** and $\delta^{13}C$ **(B)** values for Pigeon Guillemot red blood cells and serum collected each day of the experiment.

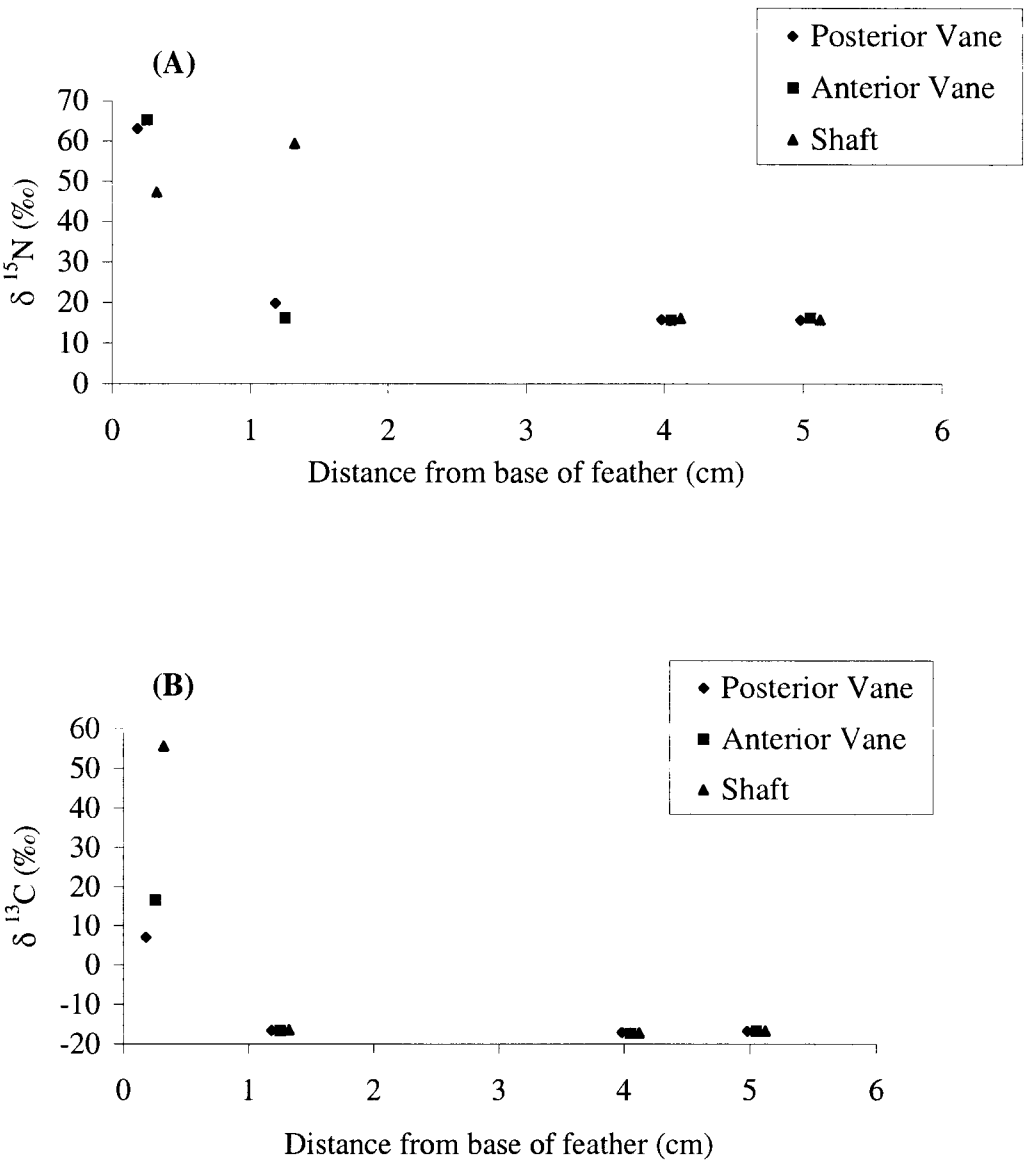

Figure 17. $\delta^{15}N$ **(A)** and $\delta^{13}C$ **(B)** values for a sectioned Pigeon Guillemot secondary feather from Bird 9. The feather was sampled at 4 intervals from base to tip. For each section the posterior vane, anterior vane, and shaft were sampled.

shaft (up to 120‰) compared to the anterior and posterior vanes (Figure 18). On average the secondaries grew 9.6 mm during the five day period.

The $\delta^{15}N$ values in the base of the feather were highly enriched, by 21.10 ± 8.28‰, with respect to the tip (Figure 19). In two cases, the $\delta^{13}C$ values were depleted in the base with respect to the tip.

Tips of feathers collected from the Pigeon Guillemots were compared to their diet in an effort to determine the fractionation coefficient in the formation of keratin. All birds were fed the same diet since hatching so the tips were formed during a constant diet. The mean fractionation between diet and secondary feathers for nitrogen was 3.24 ± 0.46‰ and for carbon was 2.38 ± 0.18‰. The secondary feather value is a mean value of posterior vane, anterior vane, and shaft. Mean values were calculated for the tip of the secondary and the section 1-1.5 cm from the tip. For contour (body feathers) the mean fractionation between diet and feathers for nitrogen was 2.83 ± 0.20‰ and for carbon was 2.70 ± 0.10‰. Birds fed herring had carbon enrichments of 2.30 ± 0.29‰ and 2.63 ± 0.20‰ and nitrogen enrichments of 3.68 ± 0.86‰ and 3.04 ± 0.26‰ for secondary and contour feathers, respectively (Table 6). Secondary and contour feathers of birds fed pollock had carbon enrichments of 2.45 ± 0.27‰ and 2.77 ± 0.11‰, respectively, and nitrogen enrichments of 2.81 ± 0.32‰ and 2.62 ± 0.21‰, respectively (Table 6). Pollock and herring samples were not statistically different in $\delta^{13}C$ or $\delta^{15}N$.

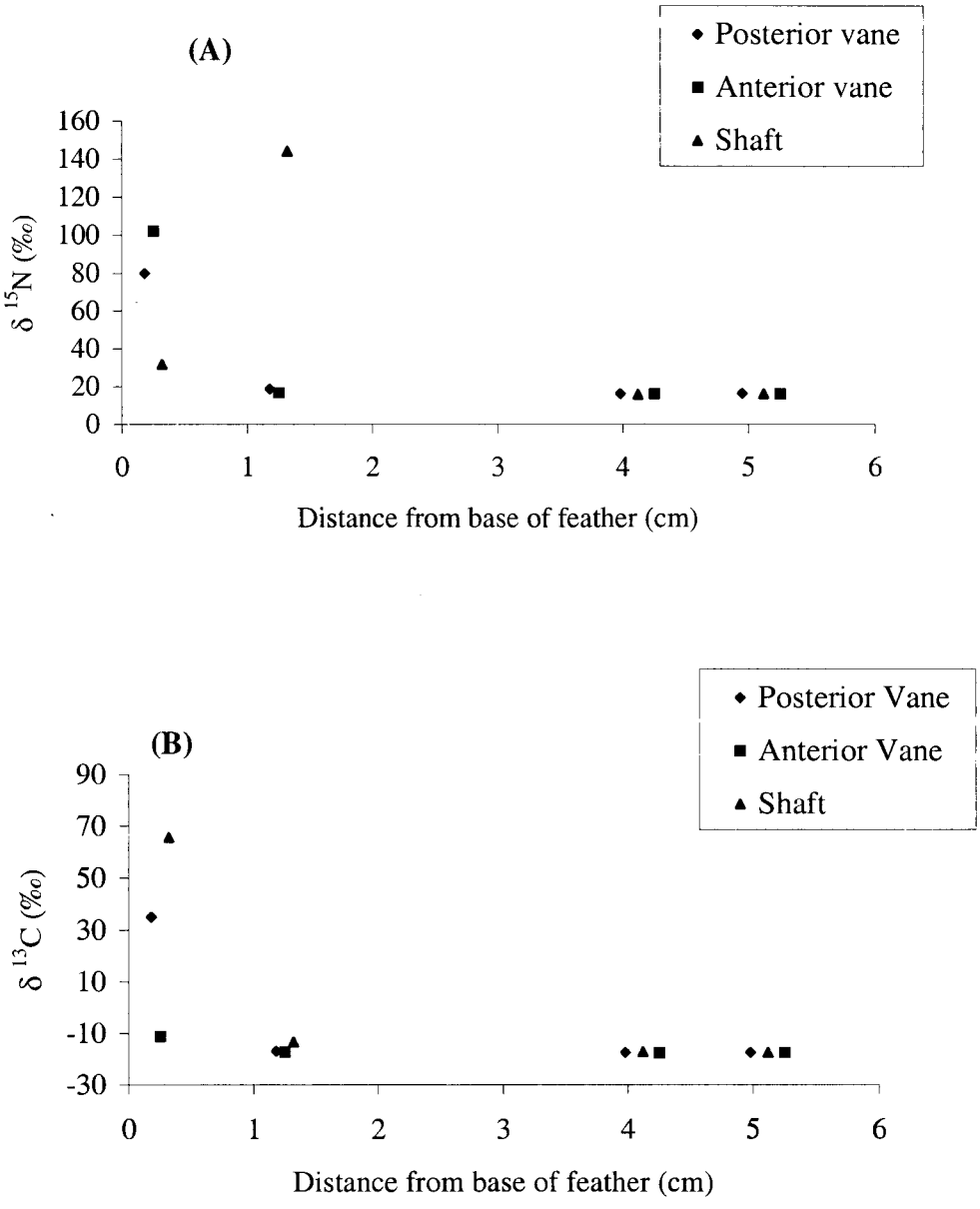

Figure 18. $\delta^{15}N$ (A) and $\delta^{13}C$ (B) values for a sectioned Pigeon Guillemot secondary feather from Bird 7. The feather was sampled at 4 intervals from base to tip. For each section the posterior vane, anterior vane, and shaft were sampled.

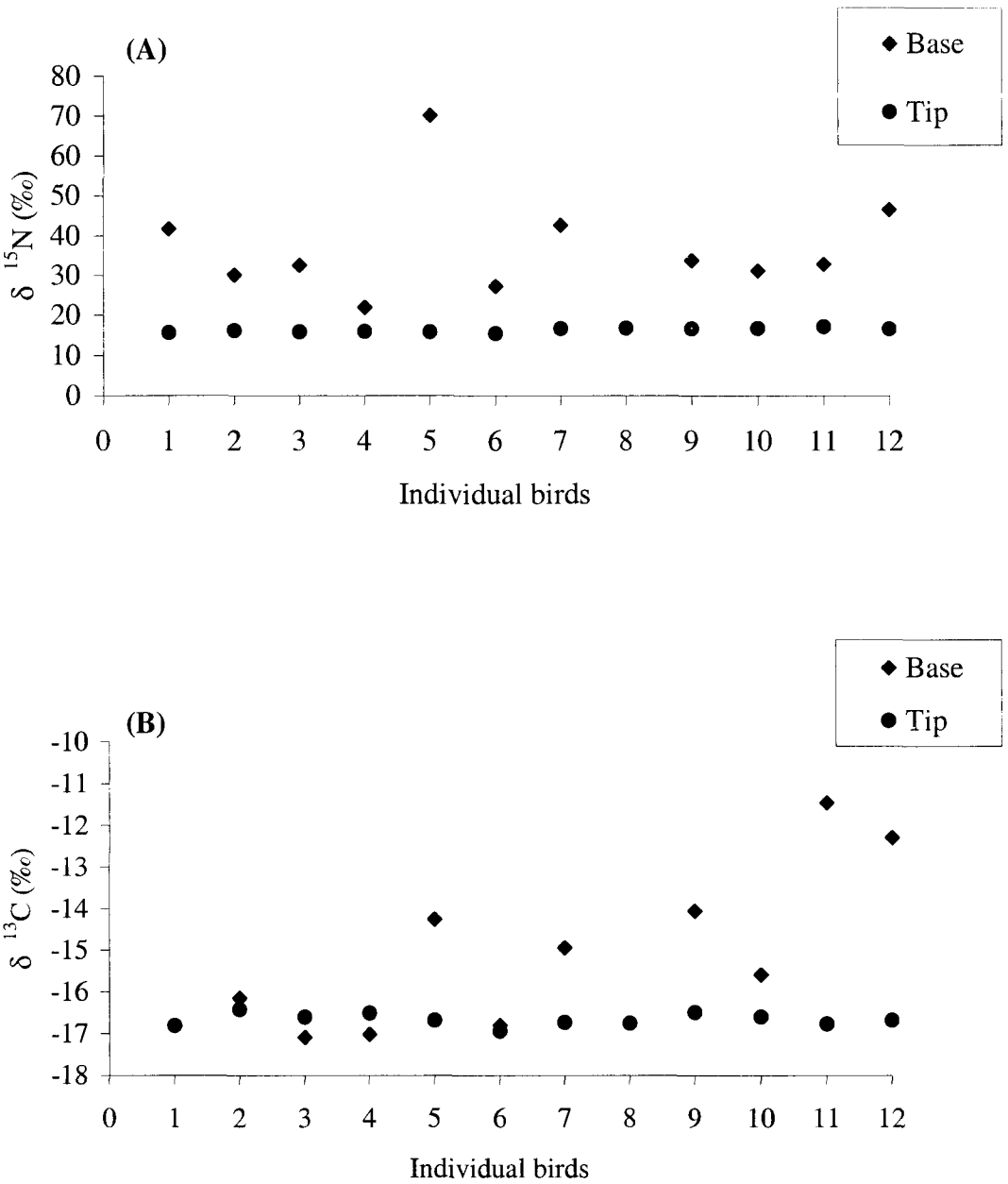

Figure 19. Mean $\delta^{15}N$ (A) and $\delta^{13}C$ (B) values in individual Pigeon Guillemot contour feathers. Base = new feather growth below marker. ^{13}C-glycine was administered two days following ^{15}N-glycine dosage.

Table 6. Average difference in $\delta^{13}C$ and $\delta^{15}N$ between Pigeon Guillemot feathers and their diet (herring or pollock) and 95% confidence intervals. Contour feathers were located on the abdomen of the bird. The posterior vane, anterior vane, and rachis for both the tip and 1-1.5 cm from the tip of each secondary were averaged and compared to diet.

Diet	Secondary		Contour	
	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Herring	2.30 ± 0.29	3.68 ± 0.86	2.63 ± 0.20	3.04 ± 0.26
Pollock	2.45 ± 0.27	2.81 ± 0.32	2.77 ± 0.11	2.62 ± 0.21

Discussion

Thick-billed Murre Tissue Analyses

Interannual Variability

Interannual changes in Thick-billed Murre muscle and feather $\delta^{13}C$ values indicate changes in the isotope abundances of their carbon source(s) (Figures 5, 6). Decreases in food web $\delta^{13}C$ values may indicate a shift to feeding in a lower trophic level, inputs to the ocean of isotopically light carbon from fossil fuel burning, an increase in dissolved CO_2 in seawater, a decrease in phytoplankton growth rate, a decrease in phytoplankton cell size, or a change in cell geometry that increases surface area to volume ratios. There was no indication of murres changing trophic levels between years in either recorded stomach contents or measured $\delta^{15}N$ values (Table 4, Figure 5). $\delta^{15}N$ values would decrease by up to 3.5‰ if murres were eating prey items from a lower trophic level. Fossil fuel burning probably had little influence at the Cape Lisburne latitude (Quay et al. 1992). Surface waters in high latitudes are replaced annually by winter convection of deep water, and in deep water the effect of increased atmospheric CO_2 invasion is diluted to undetectable levels (Takahashi et al. 1999). In addition, dissolved CO_2 has changed very little between the 1970's and 1980's based on evidence from Weather Station P (Takahashi et al. 1997). Therefore, the apparent decline in $\delta^{13}C$ values from 1976-1998 (slope = -0.04‰/year) is most likely linked to decreases in

average phytoplankton growth rates or shifts in phytoplankton species composition in the Chukchi Sea shelf region.

As phytoplankton grow at a faster rate, they discriminate less against the heavy isotope (^{13}C) (Laws et al. 1995). Growth rates may indicate primary productivity when other variables are constant. Lower $\delta^{13}C$ values indicate a lower growth rate, which, in a region of short summers and long days, could indicate lower seasonal primary production. However, species composition is not constant and smaller $\delta^{13}C$ values could also result from phytoplankton populations shifting to species with smaller cell sizes. Smaller cell sizes would increase CO_2 availability by increasing the surface area to volume ratio (Popp et al. 1998). Changes in cell geometry may also result in altered $\delta^{13}C$ values for similar reasons (Popp et al. 1998). Slower seasonal growth rates may decrease the amount and timing of energy readily accessible to the zooplankton and eventually to higher trophic levels.

Bowhead whale baleen collected from animals harvested in the Chukchi Sea showed an even clearer decline in $\delta^{13}C$ (Figure 8). Thick-billed Murre muscle and bowhead whale baleen $\delta^{13}C$ values were positively correlated, suggesting that the change in $\delta^{13}C$ was ecosystem wide. Bowhead whales eat large quantities of zooplankton and feed over a large range including the Beaufort Sea, the northwestern Bering and southern Chukchi shelf region (Schell et al. 1989). Thick-billed Murres are more limited in range when breeding and consume a few fish and invertebrates each day (Tuck 1961; Springer et al. 1984).

The long-term decline in $\delta^{13}C$ may have been a result of climate changes associated with the "regime shift": there was a well described oceanic regime shift in the 1970's that was associated with an intensification of the low pressures associated with the Aleutian Low pressure system (Trenberth and Hurrell 1994). Thick-billed Murre muscle carbon isotope values were negatively correlated to the Pacific Decadal Oscillation or PDO (lag of 1 year) (Figure 7). The PDO changed dramatically with the regime shift and is correlated to sea surface temperature (Mantua et al. 1997). Higher sea surface temperatures or different wind patterns may have set up a stronger thermocline, decreased the mixed layer depth, trapped phytoplankton at the surface, and limited the addition of new nutrients resulting in overall reduced primary productivity. The lag of one year between the changes in the PDO and Thick-billed Murre muscle $\delta^{13}C$ values may have been a result of a delay in ecological changes in response to climate change. This is likely for Thick-billed Murres as their prey is relatively long-lived.

Seasonal and Geographic Variability

Seasonal changes in Thick-billed Murre muscle $\delta^{13}C$ values were not observed. In 1983, neither $\delta^{13}C$ nor $\delta^{15}N$ values varied between samples collected in May, June, and August at Cape Lisburne (Figure 5). However, stomach contents suggested a change of diet in August (Table 4). At that time, sand lance and capelin first appeared in the diet for that year. The diets may have shifted by August, but the turnover rate of muscle (12.4 days in young birds and most likely ~30 days in adults (Hobson and Clark 1992)) may have delayed a shift in $\delta^{13}C$ values. Also, if sand lance and capelin occupied the same

trophic level and were not isotopically different from arctic cod, then there would have been no change in Thick-billed Murre isotope values (Lowry and Frost 1981; Springer et al. 1987).

The geographic location of the colony did have an impact on the isotopic signature of Thick-billed Murre tissue. In 1977, Cape Thompson birds were enriched in $\delta^{13}C$ by 1.6‰ in comparison to the birds from Cape Lisburne (Figure 5). This enrichment did not appear to be a result of dietary differences, because the enrichment was not accompanied by an increase in $\delta^{15}N$ nor by changes in collective stomach contents. Cape Lisburne birds were observed feeding northeast of the Cape Lisburne colony, in Ledyard Bay (Springer et al. 1984). In contrast, the birds from the Cape Thompson colony were observed feeding southwest of their breeding sites (Springer et al. 1984). Ledyard Bay is a shallow, nutrient-limited region where phytoplankton biomass is presumably low (Springer and McRoy 1993). In contrast, the region southwest of Cape Thompson appears to be a region of higher primary productivity, based on chlorophyll and nitrate data (Springer and McRoy 1993). The enrichment found in Cape Thompson birds was probably a result of those birds feeding in an area of higher primary productivity with higher δ^{13} values.

Variability Between Tissues

The $\delta^{13}C$ and $\delta^{15}N$ enrichment of feathers was not consistent between years and ranged between -0.71 to 3.26‰ for carbon and -1.04 to 3.58‰ for nitrogen (Figure 4). Prior studies found feather to muscle enrichments in carbon ranging from -0.1-0.3 ‰ and

0.6-1.6 ‰ for nitrogen (Hobson and Clark 1992). There are several possible causes for this variability in enrichment. The birds may have been molting near the breeding colonies (Chukchi Sea) in some years and molting in the wintering grounds (Bering Sea) in others: molt in murres has been recorded as early as July and as late as October (Thompson et al. 1998). Since feathers incorporated carbon and nitrogen only during growth and were then biologically inert, the $\delta^{13}C$ and $\delta^{15}N$ of feathers reflected the diet during molt. Muscle continually metabolized carbon and nitrogen, and thus the $\delta^{13}C$ and $\delta^{15}N$ values reflected diet close to the time of sampling. If molt location changed between years or environmental isotope ratios changed, the enrichment of feathers over muscle would have been weighted by the carbon and nitrogen sources at the molt location.

An alternative scenario is that the birds shifted their prey base between molt (diet reflected by feather $\delta^{13}C$ and $\delta^{15}N$) and time of collection (diet represented by muscle $\delta^{13}C$ and $\delta^{15}N$). If the birds were feeding at a lower trophic level during molt then the feathers would be less enriched in relation to the muscle. The diet data used in this study was best represented by muscle.

There was no statistical difference between $\delta^{13}C$ and $\delta^{15}N$ values of feathers from 7 body regions on 5 birds, which suggested that those feathers were grown in at the same time or that diet did not vary over the time (Figure 9). The similarity between feathers from different body areas suggested that archived feathers from different body regions could be used to create a timeline.

Variability Within Tissues

In Thick-billed Murre feathers the shaft was more variable, 1.47‰ for carbon and 3.63‰ for nitrogen, than both the posterior vane and anterior vane (Figure 12). However, there was no consistent enrichment or depletion between the vanes and the shaft. In certain segments the shaft was enriched relative to the vanes and in other segments the inverse was true (Figure 11, 12). All the parts of a feather were formed at a given rate at a given time. However, the shaft was a fusion of the barbs and completed formation later than the barbs attached to a given section of shaft (Lucas and Stettenheim 1972). Anterior vane, posterior vane, and shaft were examined in greater detail in Pigeon Guillemot secondary feathers and these results are discussed below.

Pigeon Guillemot Isotope Labeling Experiment

Labeled glycine passed rapidly through the Pigeon Guillemots and was only partially assimilated by the birds (Figure 15). By day 3 or 4, $\delta^{15}N$ values in feces had returned to near background values. Within seven hours after the glycine was fed to the chick, enriched values of both carbon and nitrogen were seen in the serum (Figure 16). The serum was more enriched than the red blood cells and label was found in the serum before the red blood cells. The slight enrichment in the red blood cells was most likely contamination from the serum as the red blood cells were not rinsed.

The labeled glycine was used in feather synthesis, as evident by carbon and nitrogen enrichment in samples taken from the base of growing feathers (Figure 17, 18). After dosage, secondary feather shafts tended to be more enriched in carbon and nitrogen

than were their vanes (Figure 17, 18). Also, some secondary shafts were enriched while vanes did not show any enrichment, indicating blood access to the shaft after the vanes had completed formation (Lucas and Stettenheim 1972). In some cases, enrichment in nitrogen was also found slightly above (~4 mm) the level of measured new elongation. Presumably, nitrogen was incorporated along the feather to the height of the growth tube (~9.8 mm), above the point where the feather exited the skin.

Within individual feathers from birds fed similar diets, differences in $\delta^{13}C$ values between posterior vane, anterior vane, and shaft ranged between 0.43 and 0.98‰ (Figure 13). Differences in $\delta^{15}N$ values between the posterior vane, anterior vane, and shaft ranged between 0.02 and 3.34‰ (Figure 14). The precision of the mass spectrometer could explain some of the variability, as the instrument precision is $\pm$ 0.13‰ for nitrogen and $\pm$ 0.12‰ for carbon. Although there was a range in variability, no portion of the feather was consistently enriched or depleted. Figure 14 shows that in three cases the shaft was depleted relative to the vanes and in seven cases the shaft was enriched relative to one or more of the vanes. In the wild, if diet changed while a bird was molting, then the shaft may be enriched or depleted at that sampling location due to the sequence of feather formation, as mentioned earlier.

Although the bases of all contour feathers showed enrichment in nitrogen, two did not show enrichment in carbon (Figure 19). This suggested that at this point in chick development the emphasis was on secondary growth rather than contour feather growth and more energy was being expended on secondary growth.

When the $\delta^{13}C$ and $\delta^{15}N$ of Pigeon Guillemot unlabeled feathers were compared to their diet, fractionation values within the range found in prior studies of falcons, chickens, quail, gulls, and cormorants (0.2-4‰ in carbon and 1.6-3‰ in nitrogen) were evident (Mizutani et al. 1991; Hobson and Clark 1992).

Conclusions

(1) Thick-billed Murre muscle $\delta^{13}C$ values decreased between 1976-1998 in the feeding area around Cape Lisburne and were correlated with bowhead whale baleen data. This suggested that the decrease in $\delta^{13}C$ values over time was environmental in origin and evident in multiple species.

(2) The apparent correlation of the PDO climate index to isotopic shifts in Thick-billed Murres suggested a bottom-up effect beginning with phytoplankton production and/or species composition.

(3) The variability in isotope ratios between Cape Thompson and Cape Lisburne murres in 1977 suggested that Thick-billed Murres consistently fed in areas of differing isotope ratios.

(4) Isotope ratios in feathers and muscle represented different dietary periods for the bird and were not directly comparable. They should not be used interchangeably due to the differing temporal scales in formation.

(5) Feathers reflected diet with a characteristic enrichment.

Recommendations

For the timeline, feather and muscle samples need to be collected from more years and locations. More controlled experiments need to be conducted using variable diets of high lipid and high protein to explore fractionation of different biochemical components during metabolism. Fewer birds sampled with greater frequency would help to better track a label. A detailed study of a few secondary or primary feathers, where the feather

is sampled at more frequent intervals, would provide information about movements of label in the shaft versus vanes and more temporal information on feather formation. It would be useful to test certain species that can be sacrificed at the end of the experiment to compare more tissue types. Variability in isotope ratios between bird species should be addressed. Finally, seasonality and mobilization of carbon and nitrogen reserves at different times of the year could be investigated with a controlled study. This would allow a description of how physiological processes modify isotopic fractionation during molt and other times of stress.

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Appendix 1. $\delta^{13}C$ and $\delta^{15}N$ values in Thick-billed Murre muscle for individual birds.

Bird ID	Location	Year	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
CL20598	Cape Lisburne	1998	-19.45	16.83
CL20698	Cape Lisburne	1998	-19.01	17.21
CL20798	Cape Lisburne	1998	-19.44	17.49
CL20898	Cape Lisburne	1998	-19.91	17.11
CL20998	Cape Lisburne	1998	-19.87	17.16
CL22998	Cape Lisburne	1998	-19.59	16.62
CL25798	Cape Lisburne	1998	-20.38	17.36
CL25998	Cape Lisburne	1998	-20.28	16.88
CL29298	Cape Lisburne	1998	-20.23	16.98
CL30098	Cape Lisburne	1998	-20.15	17.26
CL-2-97	Cape Lisburne	1997	-18.82	15.71
CL-3-97	Cape Lisburne	1997	-19.04	15.20
CL-5-97	Cape Lisburne	1997	-18.82	14.90
CL-7-97	Cape Lisburne	1997	-18.79	15.20
CL-8-97	Cape Lisburne	1997	-18.56	15.27
CL-9-97	Cape Lisburne	1997	-18.27	15.77
CL-10-97	Cape Lisburne	1997	-18.59	15.32
CL-13-97	Cape Lisburne	1997	-18.56	15.52
CL-27-97	Cape Lisburne	1997	-18.82	15.55
CL-28-97	Cape Lisburne	1997	-18.91	15.34
CL-11-93	Cape Lisburne	1993	-18.88	16.61
CL-13-93	Cape Lisburne	1993	-19.10	16.84
CL-14-93	Cape Lisburne	1993	-18.63	16.93
CL-19-93	Cape Lisburne	1993	-18.31	17.02
CL-20-93	Cape Lisburne	1993	-18.23	15.86
CL-21-93	Cape Lisburne	1993	-18.48	17.44
CL-22-93	Cape Lisburne	1993	-19.05	16.05
CL-23-93	Cape Lisburne	1993	-18.05	16.89
CL-24-93	Cape Lisburne	1993	-18.84	15.91
CL-25-93	Cape Lisburne	1993	-18.96	16.96
CL-2-92	Cape Lisburne	1992	-17.64	16.72
CL-6-92	Cape Lisburne	1992	-16.84	15.84
CL-7-92	Cape Lisburne	1992	-17.07	16.14
CL-8-92	Cape Lisburne	1992	-17.33	16.06
CL-9-92	Cape Lisburne	1992	-16.86	15.88
CL-10-92	Cape Lisburne	1992	-17.89	16.37

Appendix 1 continued.

CL-13-92	Cape Lisburne	1992	-17.26	16.94
CL-20-92	Cape Lisburne	1992	-17.22	15.62
CL-21-92	Cape Lisburne	1992	-16.80	15.90
CL-22-92	Cape Lisburne	1992	-17.20	16.77
CL-50-87	Cape Lisburne	1987	-17.24	18.42
CL-52-87	Cape Lisburne	1987	-18.35	17.80
CL-101-87	Cape Lisburne	1987	-19.67	17.21
CL-102-87	Cape Lisburne	1987	-18.08	17.80
CL-103-87	Cape Lisburne	1987	-18.77	17.84
CL-104-87	Cape Lisburne	1987	-18.64	17.17
CL-105-87	Cape Lisburne	1987	-18.51	17.60
CL-106-87	Cape Lisburne	1987	-18.75	17.39
CL-107-87	Cape Lisburne	1987	-19.47	17.69
CL-2-86	Cape Lisburne	1986	-19.41	17.05
CL-4-86	Cape Lisburne	1986	-18.29	17.02
CL-6-86	Cape Lisburne	1986	-18.36	17.09
CL-9-86	Cape Lisburne	1986	-18.42	17.45
CL-23-86	Cape Lisburne	1986	-17.59	17.30
CL-25-86	Cape Lisburne	1986	-18.82	17.00
CL-26-86	Cape Lisburne	1986	-17.90	16.90
CL-27-86	Cape Lisburne	1986	-17.89	17.39
CL-28-86	Cape Lisburne	1986	-18.24	16.64
CL-29-86	Cape Lisburne	1986	-17.95	17.48
CL-3-85	Cape Lisburne	1985	-19.38	16.60
CL-4-85	Cape Lisburne	1985	-19.30	16.91
CL-6-85	Cape Lisburne	1985	-20.75	16.81
CL-9-85	Cape Lisburne	1985	-18.97	16.66
CL-11-85	Cape Lisburne	1985	-18.78	17.47
CL-14-85	Cape Lisburne	1985	-19.54	16.13
CL-15-85	Cape Lisburne	1985	-18.95	16.16
CL-18-85	Cape Lisburne	1985	-18.65	16.80
CL-23-85	Cape Lisburne	1985	-19.97	16.39
CL-24-85	Cape Lisburne	1985	-18.00	17.14
CL-24-84	Cape Lisburne	1984	-18.58	17.91
CL-38-84	Cape Lisburne	1984	-18.09	16.77
CL-59-84	Cape Lisburne	1984	-18.48	17.18
CL-60-84	Cape Lisburne	1984	-19.22	17.60
CL-61-84	Cape Lisburne	1984	-18.26	17.43
CL-62-84	Cape Lisburne	1984	-18.08	16.84
CL-65-84	Cape Lisburne	1984	-19.02	16.72

Appendix 1 continued.

CL-66-84	Cape Lisburne	1984	-19.18	16.17
CL-67-84	Cape Lisburne	1984	-18.22	16.48
CL-68-84	Cape Lisburne	1984	-18.84	17.28
CL-47-83	Cape Lisburne	1983	-18.60	17.72
CL-48-83	Cape Lisburne	1983	-19.09	17.25
CL-52-83	Cape Lisburne	1983	-18.49	17.21
CL-53-83	Cape Lisburne	1983	-18.60	17.44
CL-54-83	Cape Lisburne	1983	-18.86	17.64
CL-55-83	Cape Lisburne	1983	-18.80	17.02
CL-56-83	Cape Lisburne	1983	-18.53	18.11
CL-57-83	Cape Lisburne	1983	-18.33	17.87
CL-58-83	Cape Lisburne	1983	-18.46	16.97
CL-64-83	Cape Lisburne	1983	-18.43	17.20
CL-186-83	Cape Lisburne	1983	-19.06	17.16
CL-188-83	Cape Lisburne	1983	-18.33	17.94
CL-189-83	Cape Lisburne	1983	-18.30	16.98
CL-191-83	Cape Lisburne	1983	-19.12	17.30
CL-193-83	Cape Lisburne	1983	-18.54	17.23
CL-194-83	Cape Lisburne	1983	-18.62	17.71
CL-195-83	Cape Lisburne	1983	-18.90	17.60
CL-196-83	Cape Lisburne	1983	-18.42	17.42
CL-197-83	Cape Lisburne	1983	-18.64	17.36
CL-198-83	Cape Lisburne	1983	-18.82	18.14
PH-2-83	Point Hope	1983	-18.46	17.48
PH-3-83	Point Hope	1983	-18.33	17.03
PH-4-83	Point Hope	1983	-19.13	16.43
PH-5-83	Point Hope	1983	-17.99	17.38
PH-6-83	Point Hope	1983	-18.10	17.11
PH-7-83	Point Hope	1983	-18.46	17.13
PH-8-83	Point Hope	1983	-18.30	16.30
PH-9-83	Point Hope	1983	-18.63	17.46
PH-10-83	Point Hope	1983	-18.24	16.82
PH-11-83	Point Hope	1983	-18.10	16.81
LAMS-42-80	Cape Lisburne	1980	-17.99	17.23
LAMS-43-80	Cape Lisburne	1980	-17.95	17.94
LAMS-44-80	Cape Lisburne	1980	-18.39	17.10
LAMS-46-80	Cape Lisburne	1980	-18.10	16.61
LAMS-47-80	Cape Lisburne	1980	-17.74	16.05
LAMS-48-80	Cape Lisburne	1980	-17.87	17.04
LAMS-49-80	Cape Lisburne	1980	-18.35	16.69

Appendix 1 continued.

LAMS-50-80	Cape Lisburne	1980	-17.94	16.79
LAMS-51-80	Cape Lisburne	1980	-17.98	17.28
LAMS-52-80	Cape Lisburne	1980	-18.11	17.66
LAMS 59-78	Cape Lisburne	1978	-18.79	16.94
LAMS 63-78	Cape Lisburne	1978	-17.72	17.01
LAMS 57-78	Cape Lisburne	1978	-18.68	17.38
LAMS 58-78	Cape Lisburne	1978	-18.76	17.03
LAMS 67-78	Cape Lisburne	1978	-18.70	16.91
LAMS 62-78	Cape Lisburne	1978	-18.73	17.22
AMS-19-77	Cape Thompson	1977	-18.08	16.18
AMS-20-77	Cape Thompson	1977	-17.44	16.35
AMS-21-77	Cape Thompson	1977	-17.50	16.88
AMS-22-77	Cape Thompson	1977	-17.13	15.99
AMS-23-77	Cape Thompson	1977	-17.74	17.06
AMS-25-77	Cape Thompson	1977	-18.24	16.18
AMS-26-77	Cape Thompson	1977	-18.06	17.34
AMS-28-77	Cape Thompson	1977	-17.58	17.12
AMS-31-77	Cape Thompson	1977	-17.50	16.76
AMS-35-77	Cape Thompson	1977	-17.90	16.33
AMS 174-77	Cape Lisburne	1977	-18.83	16.68
AMS 178-77	Cape Lisburne	1977	-18.98	16.61
AMS 170-77	Cape Lisburne	1977	-19.67	16.99
AMS 177-77	Cape Lisburne	1977	-19.39	16.66
AMS 172-77	Cape Lisburne	1977	-19.60	16.85
AMS 175-77	Cape Lisburne	1977	-19.04	16.87
AMS 171-77	Cape Lisburne	1977	-19.56	17.10
AMS 173-77	Cape Lisburne	1977	-19.28	17.19
AMS 176-77	Cape Lisburne	1977	-19.55	17.18
AMS 13-76	Cape Thompson	1976	-16.54	16.57
AMS 39-76	Cape Thompson	1976	-16.83	16.31
DGR 37-76	Cape Thompson	1976	-17.29	17.35
AMS 10-76	Cape Thompson	1976	-17.07	16.48
AMS 8-76	Cape Thompson	1976	-17.00	16.94
DGR-29-76	Cape Thompson	1976	-17.21	17.05
AM 1-76	Cape Thompson	1976	-16.72	16.72
AM 2-76	Cape Thompson	1976	-17.05	16.87
AMS 11-76	Cape Thompson	1976	-17.10	16.74
AMS 6-76	Cape Thompson	1976	-16.82	17.29

Appendix 2. $\delta^{13}C$ and $\delta^{15}N$ values in Thick-billed Murre chin feathers and feathers located under the wing for individual birds.

Bird ID	Chin feathers		Feathers behind the wing	
	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
CL20598	-18.54	17.96	-18.16	17.36
CL20698	-17.77	18.83	-17.50	16.76
CL20798	-18.36	16.46	-18.39	17.01
CL20898	-18.14	18.17	-18.59	17.21
CL20998	-17.92	18.19	-17.59	16.69
CL22998	-17.92	15.53	-18.56	17.29
CL25798	-17.95	18.00	-18.64	17.71
CL25998	-17.84	18.95	-18.57	17.10
CL29298	-17.76	18.02	-18.15	17.59
CL30098	-17.96	18.71	-18.29	17.12
CL-27-97	-17.83	19.13	-18.30	18.74
CL-28-97	-17.60	18.51	-17.65	17.66
LAMS 59-78	-15.96	19.21	-15.74	16.78
LAMS 63-78	-16.26	17.34	-15.94	17.54
LAMS 57-78	-17.04	15.78	-16.45	16.75
LAMS 58-78	-16.29	19.40	-15.78	17.00
LAMS 67-78	-15.74	19.58	-15.90	17.46
LAMS 62-78	-16.16	19.18	-15.47	18.56
AMS-19-77	-17.42	18.51	-16.78	17.02
AMS-20-77	-17.32	18.56	-16.46	17.22
AMS-21-77	-17.30	19.47	-17.72	18.15
AMS-22-77	-17.00	18.02	-16.70	18.10
AMS-23-77	-17.22	19.73	-16.27	16.98
AMS-25-77	-17.28	19.17	-17.20	17.58
AMS-28-77	-16.75	19.68	-16.76	17.76
AMS-31-77	-17.66	18.85	-16.84	17.34
AMS-35-77	-16.84	18.64	-16.48	18.12
AMS 174-77	-17.06	19.08	-17.16	17.33
AMS 178-77	-17.36	18.54	-16.17	17.05
AMS 170-77	-17.36	18.67	-18.02	17.35
AMS 177-77	-16.94	18.82	-16.56	19.66
AMS 172-77	-17.00	17.95	-16.58	16.46
AMS 175-77	-17.13	18.18	-16.50	17.74
AMS 171-77	-16.73	17.74	-16.42	16.11

Appendix 2 continued.

AMS 173-77	-17.22	19.57	-16.38	19.19
AMS 176-77	-16.82	18.03	-18.16	17.88
AMS 13-76	-17.24	18.72	-16.40	17.75
AMS 39-76	-17.20	18.51	-16.60	18.09
DGR 37-76	-17.44	18.38	-16.98	18.35
AMS 10-76	-17.36	17.98	-16.58	17.26
AMS 8-76	-17.45	18.53	-17.30	16.68
DGR-29-76	-17.10	18.66	-16.46	16.70
AM 1-76	-17.35	17.51	-16.26	16.90
AM 2-76	-17.02	18.34	-16.74	16.50
AMS 11-76	-16.92	18.10	-16.96	18.26
AMS 6-76	-17.14	18.22	-16.36	16.56

Appendix 3. $\delta^{13}C$ and $\delta^{15}N$ values in Thick-billed Murre back feathers from museum study skins.

Bird ID*	Back feathers	
	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
mvz:156834	-16.34	17.61
mvz155991	-16.66	17.09
mvz158312	-16.53	16.31
mvz142053	-16.12	18.03
UAM1941	-20.25	16.27
UAM2401	-16.18	17.73
UAM2402	-16.31	16.73
mvz158313	-17.84	17.30
mvz158314	-16.70	17.13
UAM2398	-16.29	17.07
UAM2400	-16.36	16.78
UAM2399	-17.71	17.69
UAM1676	-16.40	16.48
mvz137407	-16.33	16.82
mvz137408	-16.18	16.42
mvz:60564	-17.10	18.04
mvz:60563	-15.71	17.33
mvz:60569	-16.72	17.29
mvz:60575	-17.18	17.73
mvz:60568	-16.68	17.62
mvz:60558	-17.01	17.48
mvz:60561	-16.84	16.73
mvz:60560	-17.20	18.44
mvz:60559	-16.53	17.58
mvz:60562	-16.18	17.69

*mvz = Museum of Vertebrate Zoology, University of California, Berkeley

UAM = University of Alaska Museum

Appendix 4. $\delta^{13}C$ and $\delta^{15}N$ values in Thick-billed Murre chin feathers, feathers located under the wing, back feathers, secondaries, coverts, primaries and breast feathers for individual birds.

Bird ID	Chin		Under the wing		Back		Secondary		Covert		Primary		Breast	
	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
CL20598	-18.54	17.96	-18.16	17.36	-19.10	17.38	-18.24	17.72	-18.00	17.65	-18.10	17.56	-18.84	17.28
CL20798	-18.36	16.46	-18.39	17.01	-19.46	18.22	-18.97	18.25	-18.54	18.18	-19.06	18.20	-19.11	17.74
CL20898	-18.14	18.17	-18.59	17.21	-18.98	17.59	-18.50	17.81	-18.54	17.80	-19.01	17.50	-18.48	17.76
CL20998	-17.92	18.19	-17.59	16.69	-17.86	16.62	-17.43	16.65	-18.22	17.12	-17.86	16.68	-18.32	16.66
CL25798	-17.95	18.00	-18.64	17.71	-19.06	17.21	-18.24	17.47	-18.88	17.41	-18.81	17.62	-18.62	17.28

Appendix 5. $\delta^{13}C$ and $\delta^{15}N$ values in sectioned primaries of Thick-billed Murres.

Bird ID	Location on feather	Distance base to tip (cm)	$\delta^{13}C$ values (‰)	$\delta^{15}N$ values (‰)
29-76	posterior vane	0-1	-17.16	17.44
29-76	posterior vane	1--2	-17.30	16.94
29-76	posterior vane	2--3	-16.78	16.96
29-76	posterior vane	3--4	-16.80	16.74
29-76	posterior vane	4--5	-16.92	16.82
29-76	posterior vane	5--6	-16.93	16.98
29-76	posterior vane	6--7	-16.92	17.56
29-76	posterior vane	7--8	-16.93	17.74
29-76	posterior vane	8--9.2	-16.97	18.26
29-76	anterior vane	0-1	-17.40	16.95
29-76	anterior vane	1--2	-17.09	16.83
29-76	anterior vane	2--3	-16.79	16.59
29-76	anterior vane	3--4	-16.79	16.52
29-76	anterior vane	4--5	-16.92	16.56
29-76	anterior vane	5--6	-16.96	16.71
29-76	anterior vane	6--7	-17.26	17.11
29-76	anterior vane	7--8	-17.23	17.47
29-76	anterior vane	8--9	-17.23	17.59
29-76	anterior vane	9-9.6	-17.25	17.71
29-76	shaft	0-0.5	-17.22	17.4
29-76	shaft	0.5-1	-17.23	17.43
29-76	shaft	1-1.5	-17.22	17.44
29-76	shaft	1.5-2	-17.08	17.05
29-76	shaft	2-2.5	-17.17	17.07
29-76	shaft	2.5-3	-17.05	16.53
29-76	shaft	3-3.5	-17.14	16.49
29-76	shaft	3.5-4	-16.98	16.26
29-76	shaft	4-4.5	-17.00	16.11
29-76	shaft	4.5-5	-17.09	16.42
29-76	shaft	5-5.5	-16.87	16.40
29-76	shaft	5.5-6	-16.75	16.34
29-76	shaft	6-6.5	-16.63	16.21
29-76	shaft	6.5-7	-16.57	16.32
29-76	shaft	7-7.4	-16.67	16.26
29-76	shaft	7.4-7.75	-16.76	16.33

Appendix 5 continued.

29-76	shaft	7.75-8	lost	lost
29-76	shaft	8-8.6	-16.73	16.5
29-76	shaft	8.6-9	-16.72	16.94
37-76	posterior vane	0-1	-16.63	17.46
37-76	posterior vane	1--2	-16.71	17.54
37-76	posterior vane	2--3	-16.57	17.59
37-76	posterior vane	3--4	-16.67	16.87
37-76	posterior vane	4--5	-16.56	16.58
37-76	posterior vane	5--6	-16.63	16.61
37-76	posterior vane	6--7	-16.98	16.10
37-76	posterior vane	7--8	-16.80	17.13
37-76	posterior vane	8--9.6	-16.75	17.03
37-76	anterior vane	0-1	-19.30	17.24
37-76	anterior vane	1--2	-16.99	17.15
37-76	anterior vane	2--3	-16.94	16.9
37-76	anterior vane	3--4	-16.91	16.36
37-76	anterior vane	4--5	-16.93	16.52
37-76	anterior vane	5--6	-16.98	16.10
37-76	anterior vane	6--7	-16.96	16.38
37-76	anterior vane	7--8	-17.10	16.71
37-76	anterior vane	8--9.5	-17.21	16.74
37-76	shaft	0-0.5	-17.21	15.92
37-76	shaft	.5-1	-17.44	15.49
37-76	shaft	1-1.5	-17.54	14.96
37-76	shaft	1.5-2	-17.66	15.16
37-76	shaft	2-2.5	-17.47	14.80
37-76	shaft	2.5-3	lost	lost
37-76	shaft	3-3.5	-16.81	15.78
37-76	shaft	3.5-4	-16.57	16.08
37-76	shaft	4-4.5	-16.55	15.88
37-76	shaft	4.5-5	-16.66	15.63
37-76	shaft	5-5.5	-16.74	15.45
37-76	shaft	5.5-5.8	-17.13	14.61
37-76	shaft	5.8-6	-17.69	13.17
37-76	shaft	6-6.3	-18.07	13.70
37-76	shaft	6.3-6.5	-17.79	13.99
37-76	shaft	6.5-6.7	-17.61	14.31
37-76	shaft	6.7-7.2	-17.41	14.85
37-76	shaft	7.2-7.5	-17.36	15.07
37-76	shaft	7.5-7.875	-17.18	15.39

Appendix 5 continued.

37-76	shaft	7.875-8.5	-16.86	15.45
37-76	shaft	8.5-10	-16.60	16.17

Appendix 6. Stable carbon and nitrogen isotope ratios in Pigeon Guillemot feces, red blood cells, and serum for individual birds. -- = Not available.

Bird ID	Day Collected	Feces		Red blood cells		Serum	
		$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
6	1	-19.79	83.42	--	--	--	--
6	2	-20.39	19.64	--	--	--	--
6	3	70.81	21.10	-9.62	24.51	40.75	41.40
6	4	-9.55	13.90	--	--	--	--
6	5	-10.99	15.32	--	--	--	--
7	1	-20.54	59.26	--	--	--	--
7	2	-20.85	17.80	--	--	--	--
7	3	61.31	17.95	-9.04	26.27	31.86	36.71
7	4	-8.18	14.22	--	--	--	--
7	5	-13.62	14.82	--	--	--	--
9	1	-19.30	38.00	-18.48	20.55	-19.61	36.97
9	2	-20.31	19.20	--	--	--	--
9	3	5.60	9.84	--	--	--	--
9	4	-7.76	14.20	-9.54	22.42	-1.64	24.85
9	5	-15.56	12.14	--	--	--	--
10	1	-19.45	50.68	-18.44	21.07	-19.10	43.85
10	2	-19.22	20.05	--	--	--	--
10	3	41.03	14.52	--	--	--	--
10	4	-9.36	13.08	-7.80	23.99	1.27	28.40
10	5	-12.23	14.74	--	--	--	--
22	1	-20.72	50.90	--	--	--	--
22	2	-19.47	17.68	-18.48	25.08	-19.75	40.64
22	3	113.4	20.94	--	--	--	--
22	4	-7.41	14.44	--	--	--	--
22	5	-13.41	13.58	-7.80	24.76	-6.02	24.83
23	1	-18.77	68.14	--	--	--	--
23	2	-16.68	15.84	--	--	--	--
23	3	31.74	15.44	--	--	--	--
23	4	-3.41	16.27	--	--	--	--
23	5	-12.53	14.32	--	--	--	--
24	1	-19.90	58.88	--	--	--	--
24	2	-20.22	14.78	--	--	--	--

Appendix 6 continued.

24	4	-13.50	13.07	--	--	--	--
24	5	-10.67	20.05	--	--	--	--
25	1	-19.42	41.79	--	--	--	--
25	2	-21.50	40.92	--	--	--	--
25	5	-12.70	14.74	--	--	--	--
26	1	-19.52	55.24	--	--	--	--
26	2	-19.99	17.27	--	--	--	--
26	3	87.64	23.70	--	--	--	--
26	4	-12.71	11.54	--	--	--	--
26	5	-14.10	14.74	--	--	--	--
32	1	-19.99	85.75	--	--	--	--
32	2	-20.26	44.37	-18.40	24.50	-20.55	48.06
32	3	69.89	17.89	--	--	--	--
32	4	-8.98	14.12	--	--	--	--
32	5	-1.30	15.96	-9.12	24.82	-5.98	25.24
42	1	-20.54	52.23	--	--	--	--
42	2	-18.93	15.00	--	--	--	--
42	3	13.68	11.68	--	--	--	--
42	4	-3.44	36.53	--	--	--	--
42	5	-12.91	13.80	--	--	--	--
43	2	-20.10	15.50	--	--	--	--
43	3	24.20	14.48	--	--	--	--
43	4	-9.11	13.20	--	--	--	--
43	5	-11.82	14.27	--	--	--	--

Appendix 7. $\delta^{13}C$ and $\delta^{15}N$ values in Pigeon Guillemot contour feathers. Base = new growth below marking, tip = pre-enrichment growth

Bird ID	Base		Tip	
	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
6	-16.82	41.70	-16.82	15.67
32	-16.16	30.12	-16.43	16.22
9	-17.10	32.60	-16.61	15.90
22	-17.02	22.03	-16.52	15.99
7	-14.26	70.23	-16.69	15.94
10	-16.81	27.36	-16.95	15.52
42	-14.94	42.71	-16.74	16.71
25	-	-	-16.76	16.85
26	-14.06	33.90	-16.50	16.78
23	-15.59	31.32	-16.61	16.79
43	-11.45	32.99	-16.775	17.27
24	-12.29	46.70	-16.69	16.755

Appendix 8. $\delta^{13}C$ and $\delta^{15}N$ values in Herring and Pollock muscle.

Fish species	Muscle	
	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Herring	-19.41	12.76
Herring	-19.41	13.00
Herring	-19.90	12.73
Herring	-19.30	12.73
Herring	-18.50	12.98
Pollock	-19.59	15.29
Pollock	-20.07	15.23
Pollock	-19.02	13.14
Pollock	-19.08	12.54
Pollock	-19.48	14.99

Appendix 9. The difference in $\delta^{13}C$ and $\delta^{15}N$ between Pigeon Guillemot feathers and their diet (herring or pollock). Contour feathers were located on the abdomen of the bird. Posterior vane, anterior vane, and shaft for both the tip and 1-1.5cm from the tip of each secondary were averaged and compared to diet.

Bird ID	Diet	Secondary tip		Secondary section (1-1.5 cm)		Contour	
		$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
6	Herring	2.44	7.76	1.91	3.55	2.48	2.84
10	Herring	2.23	3.20	2.19	3.20	2.35	2.68
7	Herring	1.86	3.32	1.93	3.17	2.61	3.10
22	Herring	3.60	4.57	2.29	2.98	2.78	3.16
9	Herring	2.62	3.13	2.13	3.09	2.69	3.06
32	Herring	2.25	2.90	2.17	3.26	2.87	3.38
42	Pollock	2.08	3.13	2.32	2.24	2.71	2.47
23	Pollock	2.05	2.74	2.00	2.45	2.84	2.56
24	Pollock	3.12	3.29	2.34	2.55	2.76	2.52
43	Pollock	2.46	2.15	2.27	3.46	2.67	3.03
26	Pollock	3.40	3.65	2.31	2.23	2.95	2.54
25	Pollock	2.69	2.97	2.32	2.82	2.69	2.61