12-15-2017 10:30 AM

Rethinking Holocene Ecological Relationships Among Caribou, Muskoxen, and Human Hunters on Banks Island, NWT, Canada: A Stable Isotope Approach

Jordon S. Munizzi
The University of Western Ontario

Supervisor
Lisa M. Hodgetts
The University of Western Ontario Joint Supervisor
Fred J. Longstaffe
The University of Western Ontario

Graduate Program in Anthropology
A thesis submitted in partial fulfillment of the requirements for the degree in Doctor of Philosophy

Abstract

This dissertation explores the ecology of caribou (*Rangifer tarandus* spp.) and muskoxen (*Ovibos moschatus*), and its relevance to human hunters on Banks Island, NWT, Canada, over the last 4000 years, primarily through the isotopic analysis of modern and archaeological faunal remains.

First, we establish baseline carbon and nitrogen isotope relationships between modern vegetation and caribou and muskox bone collagen using Bayesian mixing models. The models indicate that dwarf shrub (*Salix arctica*) does not contribute significantly to bone collagen isotopic compositions in either species, while sedges and yellow lichen (*Cetraria tilesii*) do. These findings are ecologically significant considering that shrub phytomass is expected to increase across the Circumpolar Arctic, while lichen phytomass is expected to decrease.

Second, we investigate the hypothesis that niche competition caused periodic declines in the caribou and muskox populations over the last 4000 years, using archaeological bone collagen $\delta^{13}C$ and $\delta^{15}N$. After accounting for the possibility of different trophic discrimination factors in both species, the isotopic data suggest that caribou and muskoxen typically occupy the same niche, but tend towards niche expansion during cold or climatically-unstable periods.

Third, we evaluate the potential of reconstructing seasonal movements and migrations in caribou and muskoxen by sequential measurements of tooth enamel $\delta^{18}O$ on the micrometer-scale. We conclude that seasonal variation in precipitation $\delta^{18}O$ obscures geographic variation in $\delta^{18}O$ in these tooth enamel samples. The intra-tooth patterns in $\delta^{18}O$ are useful as paleoenvironmental proxies as they reflect changes in seasonality across time.

Keywords

Caribou, muskox, Banks Island, Canadian Arctic archaeology, isotopic baselines, zooarchaeology, isotopic niche, ecology, arctic herbivore ecology

Dedication

This work is dedicated to the memory of my grandfather, James Neil Kulpan.

Acknowledgments

First and foremost, I thank my two supervisors Lisa Hodgetts and Fred J. Longstaffe for their mentorship and substantial intellectual and financial investments in me over the last four years. Both were fully supportive of this project, encouraged me to pursue whatever interesting questions I could think of related to my research, and never hesitated to provide the tools or funds required for exploratory research or analysis. On many occasions, their confidence in me helped overcome bouts of serious self-doubt and find seemingly impossible solutions to methodological or analytical problems. Both embody the best attributes of academic scientists, and few graduate students are fortunate enough to have such excellent supervisors. I will truly miss our weekly meetings and encounters.

I also thank my dissertation examination committee, Jean-Francois Millaire, Andrew Nelson, Tamara Varney, and Elizabeth Webb for their time, thoughtful comments, and excellent feedback.

I am also indebted to Kim Law, Li Huang, and Grace Yau at the Laboratory for Stable Isotope Science for training me in many sample preparation and analytical techniques, for patiently answering innumerous questions over the last four years, and for sharing so much of their experiential lab wisdom with me (using a screwdriver to listen for the turbo pump wind-down stands out as one example). This project would not be possible without their patience, mentorship, advice, and encouragement.

I thank Trevor Lucas for providing me with modern caribou and muskox bone samples, which enabled me to write Chapter 2, for sharing his knowledge of caribou and muskoxen with me, and for protecting us as Wildlife Monitor during the 2014 field season on Banks Island. I also thank John Lucas Jr. and David Haogak, who were also kind enough to share their knowledge with me, and encouraged me to pursue this project.

Max Friesen graciously allowed me to sample archaeological caribou and muskox remains from the Nelson River collection at the University of Toronto. Ed Eastaugh assisted in sampling from the Nasogaluak/PgPw-3 collection and was always willing to answer questions related to GIS. Caron Olive, Laura Kelvin, and Beth Compton all collected forage plant samples on Banks Island in 2015, which greatly expanded that isotopic dataset. Alexis

Dolphin's expert consultation on embedding and sectioning teeth made Chapter 3 possible. Farnoush Tahmasebi advised me on best practices for preparing and analyzing plant samples, particularly for δ^{15}N-only analysis. I am thankful to Rachel Schwartz-Narbonne for many hours of fruitful discussion on mixing models and herbivore ecology at high latitudes, and tea. Brian Dalrymple at the UWO Physics Machine Shop saved significant amounts of time and money by quickly manufacturing a replacement gear for the micromill on very short notice. Many thanks to Diana Moreiras for her encouragement, help brainstorming in the lab, irrepressible optimism, and friendship over the last four years.

Major funding for this project was provided through Lisa Hodgetts' SSHRC Insight Grant (ID# 435-2012-0367), Polar Continental Shelf Program Awards, and the Northern Scientific Training Program Awards, and through Fred J. Longstaffe's NSERC Discovery Grant, Canada Foundation for Innovation Grant, Ontario Research Fund, and Canada Research Chairs.

I am grateful for additional financial support provided to me by the Arctic Institute of North America's Grant-in-Aid Program, and Western's Faculty of Social Science Graduate Research Award. I am also thankful to Jean-Francois Millaire and Kim Clark for supplementary funding provided through an ancillary summer teaching assistantship, and to Jeannie Taylor for finding work for me around the department in summer 2017.

My parents, Lee and Amy Munizzi, and parents-in law, John and Carmen McCarver, subsidized many of our living costs during the last four years. Without their generosity and encouragement, I would have been forced to abandon this research project. Many thanks as well to the Brozo, Mitchell/Pablo, and Salvador families for their kindness, for making Canada feel like home, and for all the great memories.

Finally, to my "co-author in life" Kelly McCarver Munizzi: thank you for your editing skills, companionship, and especially your patience while I worked through three degrees. And to our son Miles: you're the project of which I'm most proud, and your innate curiosity makes each day an adventure in discovery.

Table of Contents

List of Tables

List of Figures

List of Appendices

Chapter 1

1 Introduction

1.1 Project Overview and Scope

Much of the arctic archaeological research conducted in the late 20th century (Dekin 1972; McGhee 1972; Fitzhugh 1972, 1976; Maxwell 1976; McGhee 1976) attempted to codify the relationship between regional environmental, ecological, and cultural changes in Eastern Arctic[1] prehistory using theory from systems ecology and cultural ecology. These studies argue, for instance, that regional climatic variability over the last 4000 years resulted in human population expansions from, and contractions to, an area of ecological (and therefore demographic) stability around northern Hudson Bay. While these publications represent significant advances in the archaeology of the Eastern Arctic, subsequent work provides stronger evidence for distributed cultural development than for a single "core area" of cultural evolution (Helmer 1991; Fitzhugh 1997; Savelle and Dyke 2014), and suggests that social factors may have been as important as environmental factors in driving cultural change in the Eastern Arctic (Hood 1998; Darwent 2004; Friesen 2007; Hartery 2010; Milne et al. 2012; Savelle et al. 2012; Hodgetts 2013). These studies reiterate earlier calls to understand local social practices and histories before reconstructing regional processes in Eastern Arctic prehistory (McGhee 1982; Helmer 1991). In line with this proposed shift in analytical scale, the Ikaahuk Archaeology Project (IAP), directed by Dr. Lisa Hodgetts, "aims to better understand the historical development of Banks Island's cultural landscape from the earliest human occupation of the area to the present" (Hodgetts et al. 2013:1).

Banks Island, located in the Northwest Territories of Canada (Figure 1.1) is ecologically significant within the Eastern Arctic because it is currently inhabited by major percentages of the world's Peary caribou (*Rangifer tarandus Pearyi*) and muskox (*Ovibos moschatus*)

[1]Following Maxwell (1985), McCartney (1990) and Hood (1998), we use the term "Eastern Arctic" to distinguish the Canadian Arctic and Greenland from Alaska and the Eurasian Arctic.

populations (COSEWIC 2004). Both species also played important roles in the diets, economies, and traditional beliefs of past peoples living on Banks Island, and are today sources of food and revenue for its residents. Inuvialuit traditional knowledge (Nagy 1999, 2004), historical accounts from the last hundred years (Armstrong 1857; Hewitt 1921; Stefansson 1921) and demographic data from the last 50 years (Vincent and Gunn 1981; Gunn et al. 1991, 2000) suggest that caribou and muskoxen experience opposing cycles of growth and decline ("booms and busts") with the muskox population reaching much greater numbers than the caribou population. Whether this demographic cycle is the result of forage competition, environmental variability, or a combination of both is a topic of current debate (Savelle and Dyke 2002; Gunn et al. 2003; Tyler 2010). Along with the overexploitation of muskoxen by prehistoric hunters, faunal population fluctuations may have played a role in periodic human occupational hiatuses on Banks Island and other locations in the Canadian Arctic Archipelago throughout the last 4000 years (Dyke and Savelle 2009; Dyke et al. 2011; Savelle and Dyke 2002, 2009).

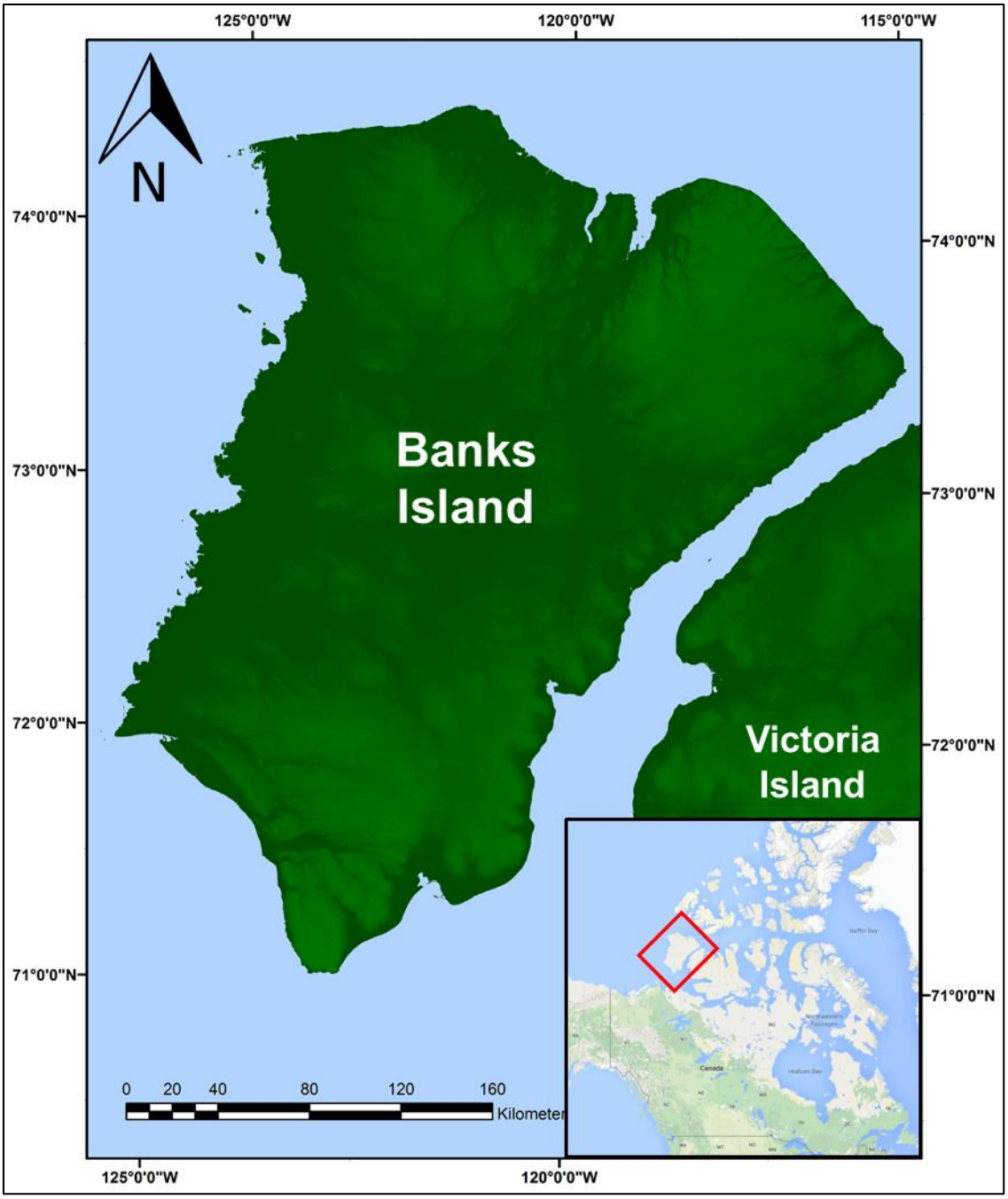


Figure 1.1. Banks Island and its location within North America (inset).

Long-term linkages among caribou and muskox population dynamics, broader ecological and environmental factors, and the activities of human hunters, however, are poorly understood. Knowledge of caribou and muskox ecology does not extend back farther than the mid-1800s – an example of the "pre-1800 dilemma" often faced by conservation biologists (Szabó and Hédl 2011; Rick and Lockwood 2013) – and it is unclear whether booms and busts are a regular part of caribou-muskox population dynamics, are related to intermittent human hunting pressure, or are a recent phenomenon caused by changes in their ecological niches brought about by, for instance, anthropogenic change in the climate regimes and range conditions of the Circumpolar Arctic (Walker et al. 2006; Jia et al. 2009; Forbes et al. 2010; Cohen et al. 2012; Najafi et al. 2015). Likewise, changes in the seasonal movements and migratory routes of caribou and muskoxen are potentially significant – but currently unexplored – factors in the construction of Banks Island's archaeological record. Both Peary caribou (Miller 1990; Miller et al. 2005) and muskoxen (Manning and MacPherson 1958; Nagy 1999) may travel across winter sea ice to the mainland and neighboring islands when local forage conditions are poor, and barren ground caribou (*R. tarandus groenlandicu*s) may also occasionally migrate from the mainland to Banks Island (McGhee 1996).

As a subproject of the Ikaahuk Archaeology Project, this dissertation investigates ecological relationships between caribou and muskoxen, their forage sources, and humans on Banks Island over the last 4000 years utilizing stable isotope analysis as the primary analytical tool. A number of scholars have recognized the potential contribution of traditional zooarchaeological research to archaeological and paleoecological questions like those discussed above (Wolverton and Lyman 2012; Braje and Rick 2013; Rick and Lockwood 2013). Several workers (Ervynck 1999; Lyman 2008; Humphries and Winemiller 2009), however, have raised concerns about the use of zooarchaeological data to make inferences about the relationship between faunal abundance and ecological changes because fauna represented at archaeological sites were first selected from the environment by humans. Consequently, the presence of remains from different taxa at archaeological sites does not *necessarily* reflect their natural abundances, though hunters are obviously limited by the availability of a given species. In this regard, the application

of stable isotope analysis to zooarchaeological remains has a significant advantage over traditional zooarchaeological analysis. The stable isotope compositions of an animal's tissues index information about its relationship to its environment and other sympatric species (e.g. diet, niche competition, migration), and the environment itself (e.g. seasonality, paleoclimate, changes in phytomass diversity and availability) during its lifetime. This information is unaffected by human predation and the structure of the archaeological assemblage in which the animal's remains end up. Within the archaeological context of the Eastern Arctic, it is therefore possible to compare the isotopic compositions of mere bone fragments from ephemeral, limited-use campsites with those from larger, semi-permanent dwellings, and with modern samples to provide otherwise unobtainable context about the deep ecological histories of caribou and muskoxen, and potentially, their relationships with ancient hunters. With this ultimate aim in mind, this dissertation investigates:

1. The relationship between the carbon and nitrogen isotope compositions of modern caribou and muskox bone collagen and forage species on Banks Island;
2. Whether caribou and muskoxen bone collagen carbon and nitrogen isotope compositions, as proxies for diet, have varied across the last 4000 years on Banks Island;
3. Whether dietary variation (if present) correlates with increased niche overlap between caribou and muskoxen; and
4. Whether tooth enamel oxygen isotope compositions can be used to investigate seasonal movements and migrations in caribou and muskoxen over the last 4000 years.

1.2 Stable Isotope Analysis as a Tool in Ecological and Paleoecological Research

1.2.1 Stable Isotope Systematics

Atoms of a given chemical element always contain the same number of protons in their nuclei, but may contain different numbers of neutrons. Atoms with the same number of protons and electrons, but different numbers of neutrons are called isotopes. Stable isotopes

are those that do not undergo radioactive decay, though the half-lives of some radioactive isotopes (e.g. ^{50}V, ^{209}Bi, ^{82}Se, ^{76}Ge, ^{128}Te) are so long that they are essentially stable. Because their electron configurations are the same, the chemical properties of isotopes are nearly identical. However, the atomic masses of different isotopes, determined by the number of neutrons plus protons in their nuclei, will vary. Because of the minute differences in their atomic masses, isotopes of the same element – and *isotopologues* (i.e. compounds or molecules that differ only in their isotopic composition) – will interact differently during physical or chemical reactions, leading to the fractionation of "lighter" and "heavier" isotopes and isotopologues between different geological or biological constituents (Faure and Mensing 2005; Sharp 2007).

A relevant example of this process is the photosynthetic fixation of atmospheric carbon by plants[2]. The nuclei of carbon atoms always contain six protons, but can contain between two and sixteen neutrons. Of these possible isotopic configurations, only carbon atoms with six (^{12}C) or seven (^{13}C) neutrons are stable. Plants that utilize the *ribulose-1, 5-bisphosphate carboxylase oxygenase* (RuBisCo) enzyme to fix atmospheric carbon are referred to as C_3 plants because the first non-intermediate molecule produced from fixation with this enzyme, $C_3H_7O_7P$, contains three carbon atoms (Hayes 2001). The RuBisCo enzyme preferentially fixes $^{12}CO_2$ over $^{13}CO_2$ for the simple reason that "light" isotopologues of CO_2 are more likely than heavy isotopologues to react and pass through the boundary layer of the leaf (Melander and Saunders 1979). This process is also an example of *mass-dependent* isotopic fractionation, though other factors, discussed below, also contribute to the stable isotopic compositions of plants and plant tissues. The variable ratios of heavy-to-light isotopes in primary producers are then passed up the food chain with generally predictable isotopic enrichments at each successive trophic level.

The absolute ratio of heavy-to-light isotopes in most samples is too small to measure directly. Instead, the ratio of two stable isotopes in a sample is measured against that of

[2]Where used, the term "plant" refers to all primary-producers (i.e. photosynthesizing vegetation), and includes lower plants such as mosses, as well as composite organisms such as lichens, which are not, in a phylogenetic sense, plants.

some certified standard (or surrogate standard) material (e.g. Vienna Pee Dee Belemnite (VPDB) for carbon, atmospheric N_2 (AIR) for nitrogen, Vienna Standard Mean Ocean Water (VSMOW) for oxygen and hydrogen) for which the absolute isotopic ratio is known, or defined. To do this, the delta (δ) notation is used (McKinney et al. 1950) (Equation 1.1):

$$\delta = \left[\frac{R_{Sample}}{R_{Standard}} - 1\right]$$

[Equation 1.1]

where R is the ratio of heavy to light isotopes in the analyte. Delta values are reported in per mil (‰).

1.2.2 Basic Skeletal Biology

To investigate the research questions outlined above, we focus mainly on three faunal tissues: bone collagen, dentin collagen, and tooth enamel. The reason is simple: bone and teeth are typically the only faunal remains present at archaeological sites spanning *all* cultural periods on Banks Island. Additionally, each tissue type integrates different isotopic signals at different rates during life.

Bone, dentin, and enamel are all composed of inorganic and organic components. The inorganic component is a biological apatite (i.e. *bioapatite*) with a chemical formula similar to the mineral hydroxylapatite [$Ca_{10}(PO_4)_6(OH)_2$] (Young 1975; LeGeros 1991; Hillson 2000; Elliott 2002; Hughes and Rakovan 2002). Carbonate (CO_3) ions also substitute for structural phosphate (PO_4) and hydroxyl (OH^-) moieties of bioapatite crystals (Penel et al. 1998; Elliott 2002). By weight, bioapatite accounts for ~ 65-70% of bone, 75% of dentin, and 95% of enamel (LeGeros 1991; Wang and Cerling 1994; Hillson 2000).

The organic component in bone and dentin – collagen – is primarily composed of essential and nonessential amino acids (e*AAs* and *nAAs*, respectively), among other components (Abelson and Hoering 1961; Macko et al. 1982; Hare et al. 1991; Ambrose 1993; Schwarcz 2000; Harbeck and Grupe 2009; Wolf et al. 2009). By weight, collagen accounts for 25-30% of bone and dentin (LeGeros 1991; Hillson 2000). The organic portion of full-mineralized enamel is small, only 1-2% by weight, and is composed of various proteins

(e.g. amelogenin, enamelin) and lipids (Lowenstam and Weiner 1989; Fincham and Simmer 1997; Hillson 2000; Veis 2003).

Bone is also continuously remodeled through deposition and resorption (Currey 2002; Ortner 2003; Raggatt and Partridge 2010), and the isotopic compositions of both the inorganic and organic phases may therefore change incrementally during life based on the isotopic compositions of diet and drinking water consumed. Consequently, the isotopic composition of bone reflects average isotopic inputs over approximately the last decade of life (Libby et al. 1965; Tieszen et al. 1983; Ambrose and Norr 1993; Pate 1994).

Conversely, dentin and enamel both develop incrementally, and within the tooth crown, do not remodel after deposition (Longinelli 1984; Luz et al. 1984; Lowenstam and Weiner 1989; Carlson 1990; Hillson 2000). Dentin and enamel therefore record a time series of isotopic inputs during formation, which is useful for investigating seasonal or intra-annual variation in diet (Hobson and Sease 1998; Balasse et al. 2002; Zazzo et al. 2005, 2006; Feranec et al. 2009; Metcalfe et al. 2011), the duration of weaning (Chapter 2; Fricke and O'Neil 1996; Wright and Schwarcz 1998, 1999; Balasse et al. 2001; Dupras et al. 2001; Dupras and Tocheri 2007), and geographic movements (Hoppe et al. 1999; Balasse et al. 2002; Pellegrini et al. 2008; Britton et al. 2009; Julien et al. 2012; Pilaar Birch et al. 2016) during the period the tooth crown developed.

1.2.3 Carbon and Nitrogen Isotope Compositions in Herbivore Bone and Dentin Collagen

We center our investigation of modern and archaeological caribou and muskox dietary ecology on bone collagen for several reasons. First, carbon and nitrogen are both abundant in well-preserved collagen, accounting for ~ 15-47% and ~ 5.5-17% of its weight, respectively (DeNiro 1985; Ambrose 1990; van Klinken 1999). As discussed below, the $\delta^{13}C$ and $\delta^{15}N$ of collagen both reflect different ecological parameters associated with diet. Collagen is also simple to extract from bone samples and relatively inexpensive to analyze. This is an important consideration because many statistical models used to make inferences about diet (Chapter 2) and ecological characteristics (Chapter 3) depend on adequate sample sizes. Finally, due to its gradual turnover, the isotopic compositions of bone

collagen are useful for making inferences about broad trends in ecological variation over long periods.

Experimental studies (Ambrose and Norr 1993; Tieszen and Fagre 1993) demonstrate that the $\delta^{13}C$ of collagen in bone and dentin from a wide range of animals largely reflects the $\delta^{13}C$ of dietary protein sources, though in animals like caribou and muskoxen with very low-protein diets, dietary carbohydrate $\delta^{13}C$ will contribute substantially to collagen $\delta^{13}C$ (Krueger and Sullivan 1984; Ambrose and Norr 1993; Dewhurst et al. 2000; Atasoglu et al. 2004). This topic is considered in greater detail in Chapter 2. Multiple studies (van der Merwe and Vogel 1978; Sullivan and Krueger 1981; Tieszen et al. 1983; van der Merwe 1989; Hare et al. 1991; Hobson and Clark 1992; Ambrose and Norr 1993; Tieszen and Fagre 1993; Bocherens 2000) also demonstrate an enrichment of +1‰ to +6‰ in ^{13}C between diet and bone collagen ($\Delta^{13}C_{collagen\text{-}diet}$) in a range of animals. With these general principles, the $\delta^{13}C$ of bone collagen has been used to reconstruct diet in a wide number of species across space and time.

As autotrophs, plants are able to synthesize both essential and nonessential amino acids *de novo* from basic elements during photosynthesis, but all vertebrates and most other organisms cannot, and must therefore obtain eAAs from dietary sources. Because they cannot be synthesized at higher trophic levels, eAAs are either broken down to be used in the synthesis of nAAs or are routed directly to organic tissues like collagen with little or no isotopic fractionation (Hare et al. 1991). The $\delta^{13}C$ of bulk bone collagen from herbivores therefore represents the averaged $\delta^{13}C$ of its component amino acids, which vary widely (Abelson and Hoering 1961; Benner et al. 1987; Hare et al. 1991) and the $\delta^{13}C$ of herbivore bulk collagen may be biased towards specific amino acids assimilated from forage. Early work (Gannes 1997; Ben-David et al. 2001; Fogel and Tuross 2003) suggested that this bias is not an issue in ruminants like caribou and muskoxen because nutrient recycling during the rumination process itself metabolically homogenizes (i.e. "resets") the $\delta^{13}C$ of both eAAs and nAAs. Copley et al. (2004), however, observed varying contributions of the eAA leucine from C_3 and C_4 plants in the bone collagen of Nubian sheep/goats and cattle. Likewise, Honch et al. (2012) found that the difference in $\delta^{13}C$ between glycine and phenylalanine ($\Delta^{13}C_{Gly\text{-}Phe}$) in several ruminant species resembles that of monogastric

humans from a variety of subsistence backgrounds, implying that an isotopic "reset" may not occur in the rumen. Consequently, although a $\Delta^{13}C_{collagen\text{-}diet}$ of +5‰ is commonly assumed for most large mammals (Sullivan and Krueger 1981; Krueger and Sullivan 1984; van der Merwe 1989; Koch 1998), the ruminant digestive system, along with other factors (see Chapter 2) introduces complexities that can make this assumption fraught.

Likewise, it is often assumed that there is a relatively consistent enrichment in ^{15}N of +2‰ to +5‰ at each trophic level due to fractionation of nitrogen isotopes as they enter the body nitrogen pool (Minagawa and Wada 1984; Ambrose and DeNiro 1986; Macko et al. 1986; Sealy et al. 1987; Fogel et al. 1997; Gannes et al. 1997, 1998), and from the preferential excretion of ^{14}N (Peterson and Fry 1987). Evidence from field studies of herbivores, however, suggests that $\Delta^{15}N_{collagen\text{-}diet}$ increases as dietary protein content increases (DeNiro and Epstein 1981; Sponheimer et al. 2003a, b; Codron et al. 2008; Robbins et al. 2010; Codron et al. 2012), and is related to nitrogen balance in the body and urea recycling (Sponheimer et al. 2003a, b). While early work on trophic enrichment in ^{15}N laid the groundwork for ecological studies using stable isotopes, these studies emphasize the complexities involved in the routing of nitrogen along the foodweb. The role of individual amino acids in determining the $\delta^{13}C$ of bone collagen, and the significance of $\Delta^{13}C_{collagen\text{-}diet}$ and $\Delta^{15}N_{collagen\text{-}diet}$ for reconstructing dietary contributions to bone collagen are discussed further in Chapter 2.

Finally, the gradual depletion of ^{13}C in atmospheric CO_2 (i.e. the "Suess Effect") (Keeling et al. 1979; Tans 1979; Friedli et al. 1986; Keeling et al. 1989; Bacastow et al. 1996) must be taken into account when attempting to reconstruct the $\delta^{13}C$ of plants and organisms at higher trophic levels during the past. Prior to the Industrial Revolution, the global average $\delta^{13}C$ of atmospheric CO_2 was ~ –6.5‰ (Francey et al. 1999; Yakir 2011), which led to an average $\delta^{13}C$ in C_3 plants of –26.5‰. With the increasing emission of CO_2 from fossil hydrocarbon fuel sources, the $\delta^{13}C$ of which ranges from –40 to –25‰, global average atmospheric CO_2 is becoming progressively depleted of ^{13}C. Currently, the $\delta^{13}C$ of atmospheric CO_2 is ~ –8.4‰, and is decreasing by approximately –0.02‰ each year (Hoefs 2009). The average $\delta^{13}C$ of post-industrial C_3 plants is between –27 and –28‰ (Hoefs 2009; Cernusak et al. 2013).

1.2.4 Carbon and Oxygen Isotope Compositions in Mammalian Tooth Enamel

Although structural carbonate (CO_3) and phosphate (PO_4) are commonly extracted from both bone and tooth enamel and analyzed for their carbon and oxygen isotope compositions (Kohn and Cerling 2002), we focus only on tooth enamel in this dissertation for several reasons. First, because tooth enamel develops incrementally and teeth grow sequentially, enamel sampled either serially from individual teeth, or in bulk from multiple teeth in a tooth row provide a level of temporal isotopic resolution more refined than that of bulk bone. Additionally, because fully mineralized enamel is much denser than bone it is much less susceptible to *post-mortem* chemical alteration (Kohn et al. 1999; Kohn and Cerling 2002).

The interpretation of $\delta^{13}C$ from structural carbonate in mammalian bioapatites is perhaps more straightforward than in collagen. Unlike collagen, which is composed of both eAAs routed directly from assimilated food and nAAs produced *de novo* by the body, structural carbonate derives from CO_2 dissolved in blood bicarbonate (HCO_3) through a temperature-dependent ~ +8‰ fractionation from CO_2 to HCO_3 and a +1‰ to +2‰ fractionation from HCO_3 to structural carbonate (Hedges and van Klinken 2000; Koch 2007) (Figure 1.2). Since dietary inputs are the main source of CO_2 incorporated into the blood bicarbonate pool, the $\delta^{13}C$ of structural carbonate should reflect the average $\delta^{13}C$ of all dietary contributions during the time of formation, plus +9 to +10‰. Structural carbonate $\delta^{13}C$ is therefore a useful tool for investigating total diet (as opposed to dietary protein alone).

In large ruminants, however, the enrichment in ^{13}C between diet and structural carbonate ($\Delta^{13}C_{sc\text{-}diet}$) is somewhat greater, between ~ +12 and 14‰ (Hedges and Van Klinken 2000; Balasse 2002; Hedges 2003; Passey et al. 2005). This additional enrichment in ^{13}C occurs because the fermentation of forage by gut microbiota produces ^{13}C-depleted methane (Metges et al. 1990) which is expelled from the body, leaving behind ^{13}C-enriched CO_2 which then exchanges with blood bicarbonate.

The bulk $\delta^{18}O$ of tooth enamel is a composite of oxygen derived from phosphate (PO_4), structural carbonate (CO_3) substitutions, and hydroxyl (OH^-) groups (LeGeros 1991; Penel

et al. 1998; Elliott 2002). The $\delta^{18}O$ of these oxygen-bearing moieties is determined by temperature-dependent fractionations of ^{18}O from the body water pool, the $\delta^{18}O$ of which is determined by the $\delta^{18}O$ of ingested water (Bryant et al. 1996). There is typically no fractionation of ^{18}O during the ingestion and assimilation of water (Luz et al. 1984; White et al. 1985; Ayliffe and Chivas 1990; Bryant and Froelich 1995). In large mammals, catalysis of blood CO_2 by the enzyme *carbonic anhydrase* results in a ~ +26‰ fractionation in ^{18}O between body water and structural carbonate (Silverman 1982; Bryant et al. 1996) (Figure 1.3). Likewise, there is a ~ +17.5‰ fractionation of ^{18}O between body water and bioapatite phosphate in most mammals (Longinelli and Nuti 1973; Kolodny et al. 1983; Bryant et al. 1996; Lécuyer et al. 1996). These fractionation pathways are depicted in Figure 1.3. Since the $\delta^{18}O$ of water ultimately derived from precipitation varies geographically (Epstein and Mayeda 1953; Craig and Gordon 1965; Yurtsever and Gat 1981; Rozanski et al. 2001; Bowen and Wilkinson 2002; Bowen and Revenaugh 2003) and seasonally (Gat 1981a, b; Yurtsever and Gat 1981; Horita and Wesoloski 1994; Gat et al. 2001; Darling et al. 2005), and tooth enamel develops incrementally, the $\delta^{18}O$ of sequentially-sampled enamel structural carbonate and phosphate can provide information about seasonality and migration during the time of formation.

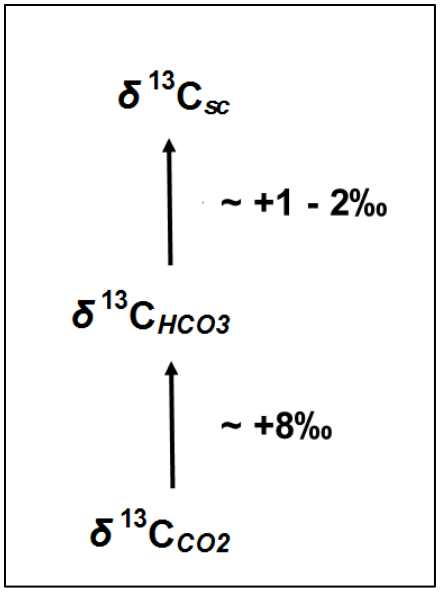


Figure 1.2. Simplified model of fractionation of ^{13}C between CO_2 oxidized from food ($\delta^{13}C_{CO2}$), blood bicarbonate ($\delta^{13}C_{HCO3}$), and structural carbonate ($\delta^{13}C_{sc}$) in mammalian bioapatites. In large ruminants, there is an additional enrichment of ^{13}C between HCO_3 and structural carbonate due to the loss of ^{13}C-depleted methane.

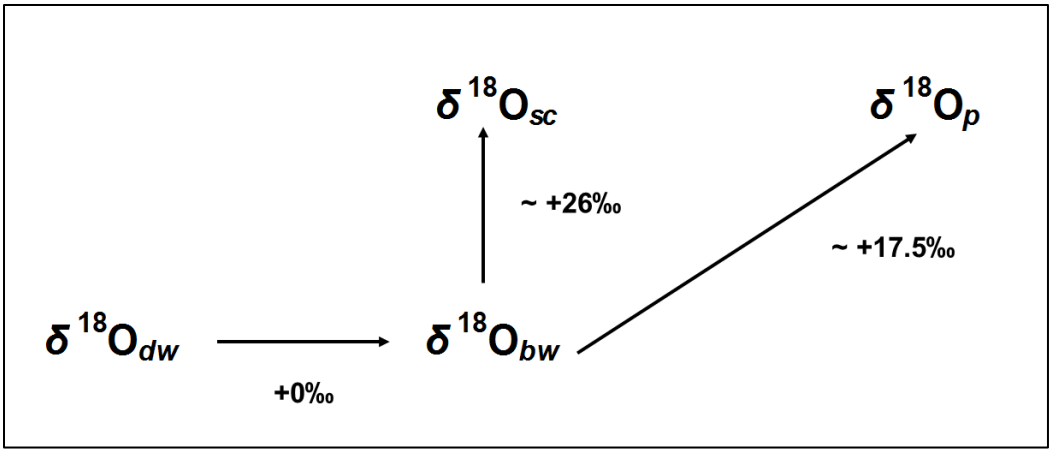


Figure 1.3. Simplified model of fractionation of ^{18}O between drinking water ($\delta^{18}O_{dw}$), body water ($\delta^{18}O_{bw}$), and structural carbonate ($\delta^{18}O_{sc}$) and phosphate ($\delta^{18}O_{p}$) in mammalian bioapatites.

1.3 The Isotopic Ecology of Banks Island

1.3.1 Carbon and Nitrogen Isotope Ecology of Arctic Plants

Aside from the preferential fixation of isotopically "light" isotopologues of CO_2 during photosynthesis (discussed above), several other factors determine the initial $\delta^{13}C$ of C_3 vegetation. Multiple studies demonstrate that the leaves of forbs and shrubs are typically depleted of ^{13}C relative to other plant organs. There are at least seven viable hypotheses for this variation in ^{13}C, which all revolve around differences in one of two basic processes: differences in the way leaves and other tissues fix and respire CO_2, or differences in the way isotopically variable molecules are routed to different plant tissues. These hypotheses are reviewed by Cernusak et al. (2009), Szpak et al. (2013), and Ghashghaie and Badeck (2014). Consequently, the $\delta^{13}C$ of biochemical compounds that compose plant organs varies: lipids, lignin, and cellulose are all depleted of ^{13}C relative to the whole-plant average, while soluble biochemical fractions (sugars, amino acids, hemicellulose, and pectin) are enriched in ^{13}C relative to the plant average (Deines 1980; O'Leary 1981; Monson and Hayes 1982; Benner et al. 1987; Boutton 1996) (Figure 1.4). Variability in the $\delta^{13}C$ of plant parts due to variable proportions of different biochemical compounds has significant implications for the seasonal patterning of $\delta^{13}C$ in herbivore tissues. Caribou and muskoxen provide a relevant example: early in the growing season, both species take advantage of highly nutritious buds, shoots, and leaves enriched in ^{13}C relative to other plant parts. As the summer continues, production and maintenance of aboveground phytomass ceases, and many forage species go dormant. Shoots and leaves become increasingly scarce due to continuous foraging, and woody stems therefore compose a greater proportion of ingested foods over winter (Larter and Nagy 1997, 2004). Thus, an overall shift towards lower tissue $\delta^{13}C$ may occur in caribou and muskoxen during winter.

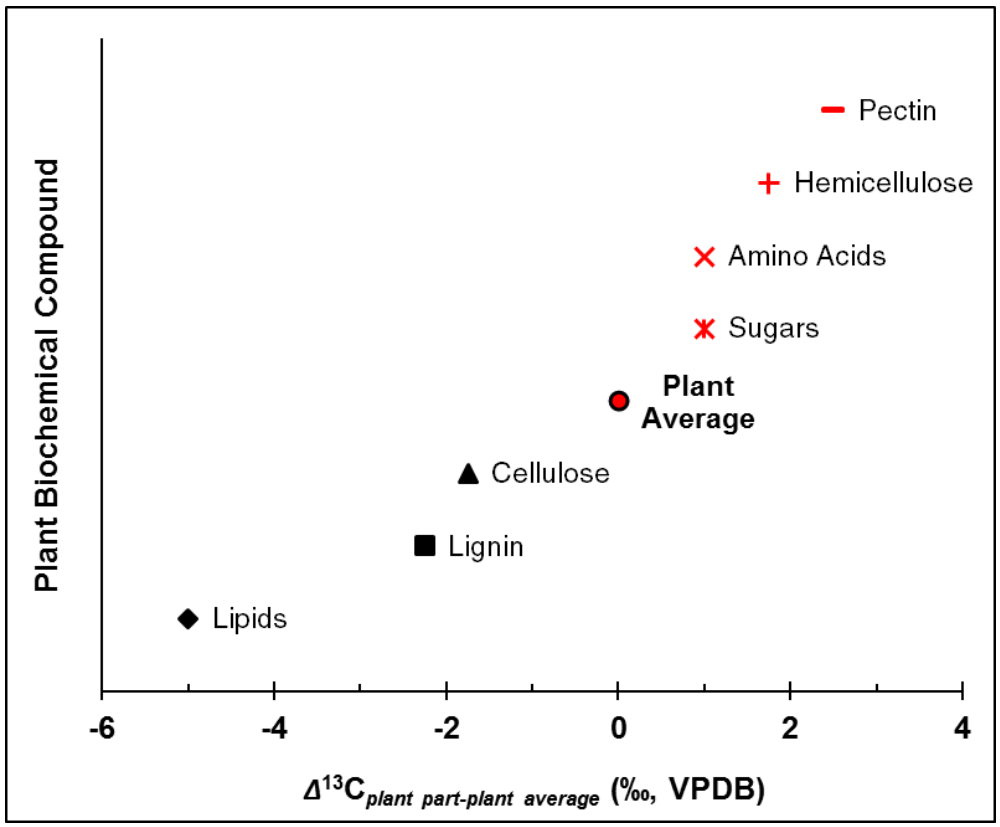


Figure 1.4. *Relative* difference in the $\delta^{13}C$ of different plant biochemical compounds compared to the whole-plant average $\delta^{13}C$ (here, set to 0‰). Figure is adapted from Deines (1980) and Boutton (1996).

Many of the environmental factors that further contribute to variation in the $\delta^{13}C$ of plants in temperate areas (reviewed in Farquhar et al. 1989, and Szpak et al. 2013) are absent on Banks Island. All vegetation currently growing north of the treeline utilizes the C_3 photosynthetic pathway for carbon fixation (Teeri and Stowe 1976; Osborne and Beerling 2006). There is no "canopy effect" (Vogel 1978; Ehleringer et al. 1986, 1987; van der Merwe 1989; van der Merwe and Medina 1989) because there are no trees and little layering of vegetation. Elevational gradients in plant $\delta^{13}C$ (Körner and Diemer 1987; Körner et al. 1988; Vitousek et al. 1990; Körner et al. 1991; Sparks and Ehleringer 1997; Zhu et al. 2010) are possible on Banks Island, although most of the forage species utilized by caribou and muskoxen tend to grow in lower, wet sedge meadows, hummock tundra, graminoid/dwarf shrub tundra, and barren uplands, as opposed to the high, sparsely-vegetated stony barrens (Ferguson 1991; Larter and Nagy 2001a), and the total change in elevation on Banks Island is less than 1000 meters (Usher 1965). Changes in soil moisture and humidity that cause *seasonal* variation in vegetation $\delta^{13}C$ are limited because plants in the High Arctic only grow during the short summer (June to August) when soil moisture is abundant and relative humidity is high. The absence of these environmental factors, and the exclusive use of the C_3 photosynthetic pathway in arctic vegetation should subsequently limit the amount of intra- and inter-species variation in $\delta^{13}C$.

Factors that affect the nitrogen isotope compositions of plants in temperate regions are also absent or limited in boreal and tundra ecosystems. Low soil temperatures inhibit microbial decomposition, mineralization, and N_2-fixation by cyanobacteria (van Cleve and Alexander 1981; van Cleve et al. 1991; Kielland 1994; Vitousek et al. 2002). The availability of soil-bound ammonium (NH_4^+), nitrate (NO_3^-), and N_2 is therefore limited (Shaver and Chapin 1980; Chapin and Bledsoe 1992; Schulze et al. 1994; Shaver and Chapin 1995). Competition for scarce soil nitrogen is circumvented by arctic plants in several ways. Leguminous species like alpine milk vetch (*Astragalus alpinus*) and arctic oxytropes (*Oxytropis* spp.) utilize atmospheric nitrogen (N_2) via associations with root-borne bacterial (rhizobial) symbionts (Alexander et al. 1978; Zahran 1999; Vitousek et al. 2002). Many non-leguminous plants must rely on associations with fungal (mycorrhizal) symbionts to acquire nitrogen from soil-bound proteins and amino acids (Abuzinadah and

Read 1986; Hodge et al. 1995; Kielland 1995; Michelsen et al. 1998; Lipson and Näsholm 2001), though certain plant species can also directly assimilate soil-bound amino acids without any symbiotic associations (Chapin et al. 1988, 1993; Kielland 1994; Schimel and Chapin 1996).

Different nitrogen sources also result in variable intraplant $\delta^{15}N$. In non-symbiotic species that rely on inorganic nitrogen, Evans et al. (1996) report significant intraplant $\delta^{15}N$ variation when NO_3^- is the primary nitrogen source (because it is assimilated via roots and shoots), and little intraplant $\delta^{15}N$ variation when NH_4^+ is the primary nitrogen source (because it is absorbed via the roots alone). Similarly, Michelsen et al. (1998) demonstrate depletion of ^{15}N in the tissues of primary producers with mycorrhizal associations, relative to those with rhizobial or no symbiotic associations, presumably due to fractionations during fungal breakdown of soil-bound amino acids. The $\delta^{15}N$ of soil-bound amino acids, however, varies widely depending on earlier soil conditions and biosynthetic reactions that occurred in the plant from which they originate (Ostle et al. 1999; Werner and Schmidt 2002). These variations are passed on to different plant parts upon assimilation by living plants (Hofmann et al. 1997; Werner and Schmidt 2002).

Variations in plant $\delta^{15}N$ across the landscape are also complex. In their analysis of muskox forage in Greenland, Kristensen et al. (2011) observed lower $\delta^{15}N$ in the leaves of leguminous forbs (~ –2.5 to –3‰) than graminoids (~ +1.5‰), and this relationship was the same across their collection area. The $\delta^{15}N$ of catkins from dwarf willows (*Salix arctica*) collected from *Salix*-dominated areas, however, was significantly lower (~ –5.5‰) than catkins of *S. arctica* collected from graminoid-dominated areas (~ –3‰). Together, these findings emphasize the role of microenvironment in nitrogen uptake, and ultimately plant $\delta^{15}N$. Indeed, several researchers (Schulze et al. 1994; Nadelhoffer et al. 1996; McKane et al. 2002; Clemmensen et al. 2008) demonstrate that arctic plant communities reduce competition for the limited inorganic and organic nitrogen pools through chemical, temporal, and stratigraphic partitioning of nitrogen and other nutrients. For instance, McKane et al. (2002) found that on the Alaskan tundra, sedges of the genus *Carex* utilized NO_3^- nearly exclusively, and did so early in the growing season, while cotton sedges (*Eriophorum* spp.) and dwarf cranberry (*Vaccinium* spp.) utilized both soil-bound glycine

and ammonium. Dwarf cranberry utilized these resources earlier in the season, and from a shallower depth than cotton sedge. Likewise, Labrador tea (*Ledum* spp.) and dwarf birch (*Betula* spp.) both utilized ammonium, but Labrador tea started earlier in the season, and avoided competition with dwarf cranberry by utilizing ammonium at deeper soil levels. The use of nitrogen resources from different soil depths can impart variation in plant $\delta^{15}N$. Soil $\delta^{15}N$ typically increases with depth because ^{15}N-enriched plant matter dominates the top of the soil profile whereas plant matter at depth has been exposed to mineralization and microbial degradation for longer periods (Högberg 1997; Martinelli et al. 1999).

1.3.2 Surface Hydrology and $\delta^{18}O$ and $\delta^{2}H$ in Surface and Plant Water

The hydrology of Banks Island is typical of islands in the Canadian Arctic Archipelago. Precipitation is minimal, averaging ~ 150 mm yearly (Usher 1965; Gray 1997). Approximately two thirds of this precipitation comes in the early winter and late spring in the form of fine snow (Usher 1965), which strong winds tend to sweep off ridges and hills and into valleys where it accumulates and mixes (Edlund 1986; Lechler and Niemi 2012). Although no such data exist for Banks Island, precipitation isotope data collected by the Global Network of Isotopes in Precipitation (GNIP) at Mould Bay (Northwest Territories, Canada)[3] (IAEA/WMO 2017) confirm that variations of $\delta^{18}O$ and $\delta^{2}H$ in fall and spring snow relative to winter snow occur as air temperature oscillates, and as expected, the variations are much greater for $\delta^{2}H$ than $\delta^{18}O$ due to the mass-dependent nature of fractionation. Sublimation of snow occurs throughout the winter, leading to enrichment of ^{18}O and ^{2}H in the remaining snowpack. As air temperatures begin rising in late spring, increasing evaporation causes further enrichment of ^{18}O and ^{2}H in the snowpack, and the $\delta^{18}O$ and $\delta^{2}H$ of melting snowpack is locally homogenized (MacPherson and Krause 1967; Judy et al. 1970). Consequently, snowmelt percolating into soil during the spring thaw

[3]For several decades, the Global Network of Isotopes in Precipitation (GNIP) program, run jointly by the IAEA and WMO, has provided data on the $\delta^{18}O$ and $\delta^{2}H$ compositions of water from a worldwide network of precipitation monitoring and collection stations. The now-defunct Mould Bay station, located on Prince Patrick Island, was the collection station farthest west in the Canadian Arctic, and the closest to Banks Island in terms of longitude.

should represent the locally-homogenized isotopic compositions of fall, winter, and spring snows, as modified by any evaporative enrichment in ^{18}O and ^{2}H (Halevy 1970; Arnason 1981; Gat 1981c).

Lakes and ponds on Banks Island originated through glacial scouring or ice calving and kettle formation that occurred during the several Pleistocene glaciations experienced by the island (Mackay and Løken 1974; England et al. 2009; Lakeman and England 2012). They are therefore relatively shallow and are typically well-mixed biogeochemically (Vincent and Hobbie 2000). Because there is no groundwater system on Banks Island, all watercourses are predominantly recharged by meltwater and precipitation during the summer. Major rivers on Banks Island mainly drain the high southeastern and northern uplands (Usher 1965). In temperate zones, the $\delta^{18}O$ and $\delta^{2}H$ of runoff-dominated rivers should vary throughout the year, given that the $\delta^{18}O$ and $\delta^{2}H$ of summer precipitation, and subsequently, river water, are more enriched in ^{18}O and ^{2}H than winter precipitation (Dansgaard 1964; Fritz 1981; Yurtsever and Gat 1981; Gonfiatini 1986; Rozanski et al. 2001; Darling et al. 2005). This is not the case on Banks Island or in other arctic locations lacking groundwater systems. By late summer, most small rivers have drained all of the meltwater from their watershed and have run or are close to running dry. In winter, the larger rivers freeze solid (Trevor Lucas 2014, personal communication) and precipitation is "locked" on land in the form of snow and ice. When the air temperature rises above freezing again, the rivers are rapidly recharged with meltwater from their watersheds.

Snowmelt percolating into the soil from snowpack, lateral runoff, or flooding of the rivers comprises most of water absorbed by the roots of growing plants on Banks Island (Usher 1965). Typically, no isotopic exchange occurs between water and soil during percolation (Gat 1981c, Dawson et al. 2002) or during uptake of soil water by plants (Wershaw et al. 1966; Ehleringer et al. 2000; Yakir and da Silveira Lobo Sternberg 2000). The $\delta^{18}O$ and $\delta^{2}H$ of water in the root and stem tissues of plants early in the growing season should therefore directly reflect those of meltwater. Leaf water, however, is further enriched in ^{18}O and ^{2}H because isotopologues of H_2O that include ^{16}O and ^{1}H are preferentially transpired from the stomata (Gonfiatini et al. 1965; Epstein et al. 1977; Yakir and da Silveira Lobo Sternberg 2000). Experiments designed to measure the amount of

fractionation in leaf water during transpiration (Allison et al. 1985; Yakir et al. 1990) demonstrate that observed $\delta^{18}O$ and $\delta^{2}H$ are more positive than expected based on modified steady-state evaporation models from inorganic systems (Ferhi and Letolle 1977; Leaney et al. 1985). Yakir et al. (1990) propose that this discrepancy between expected and observed $\delta^{18}O$ and $\delta^{2}H$ is explained by the fact that leaf water is not composed of a single homogenized pool, but is made up of at least three different fractions. These leaf water pools include: (1) water in cells surrounding the stomata that exchange with the atmosphere (the transpiration pool); (2) water in the inner membrane of the cell wall (the symplast) that does not exchange with the atmosphere but may exchange with the transpiration pool; and (3) water in the veins of leaves, which does not exchange at all, and like the roots and stems of the plant, directly reflects the isotopic compositions of soil water (which directly reflects those of precipitation). The $\delta^{18}O$ and $\delta^{2}H$ of this mixed water pool will therefore be passed to caribou and muskoxen feeding on the aerial portions of plant matter during peak phytomass productivity.

1.4 The Archaeology of Banks Island

The earliest human inhabitants of the Eastern Arctic migrated from the Bering Strait region, and began moving east around 4500 cal. BP (Arundale 1981; McGhee 1982; Helmer 1994) (Figure 1.5). These people are often referred to as *Sivullirmiut* or *Paleo-Inuit* (formerly *Paleoeskimo*[4]) to distinguish them from the second major dispersal of humans into the Eastern Arctic by Thule Inuit (formerly called the *Neoeskimo*) that migrated from Alaska between 1100 and 800 cal. BP (Friesen and Arnold 2008; Raghavan et al. 2014) (Figure 1.5). The *Sivullirmiut* brought with them to the Eastern Arctic lithic technology referred to as the *Arctic Small Tool tradition* (*ASTt*) (Irving 1962), which likely developed from the Denbigh Flint Complex of Northwestern Alaska (Collins 1953; Giddings 1964; Bielawski 1988). This lithic technology centers on an array of small, finely-knapped stone tools, but also included bows and composite arrows, small antler harpoon heads, and bone needles and awls.

[4]The *-eskimo* suffix, like the word *Eskimo* itself, was imposed by outsiders and is often considered derogatory (see Steckley (2008) for a general discussion of its etymology).

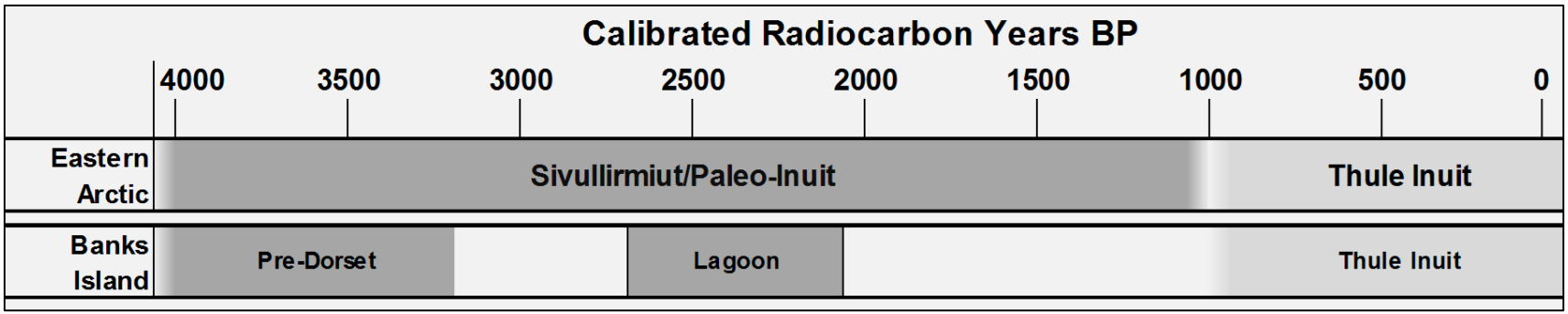


Figure 1.5. Timeline of archaeological human occupations in the Eastern Arctic overall (top), and on Banks Island (bottom) in calibrated radiocarbon years BP.

While there are several documented Pre-Dorset period sites on Banks Island, and likely many more that are undocumented (Müller-Beck 1977a, b; Stevenson 1993; Hodgetts et al. 2009), this archaeological period is perhaps best represented by the Shoran Lake (PjRa-1) and Umingmak (PjRa-2) sites (Taylor 1967; Müller-Beck 1977a, b; Münzel 1987). Although both sites are presumed to date to ~ 3500 cal. BP (Wilmeth 1978; Arnold 1983), recent radiocarbon dates (Hodgetts, unpublished data; see also Chapter 3) suggest that Shoran Lake may be several hundred years older than Umingmak. The faunal assemblage at Umingmak indicates heavy reliance on muskoxen (Figure 1.6) and, to a smaller extent, caribou, snow goose, small mammals, and fish. The site was used during the summer months to process meat from muskox, bird, and fox hunts (Muller-Beck 1977b; Münzel 1987) and in the fall and winter possibly as a basecamp from which to hunt muskoxen and caribou (Münzel 1987). Based on radiocarbon dates (Hodgetts, unpublished data), it is likely that the site represents several years, decades, or even centuries of use (Hahn 1977), and was reoccupied once again during the later Classic Thule and Inuit periods (Muller-Beck 1977b; Münzel 1987).

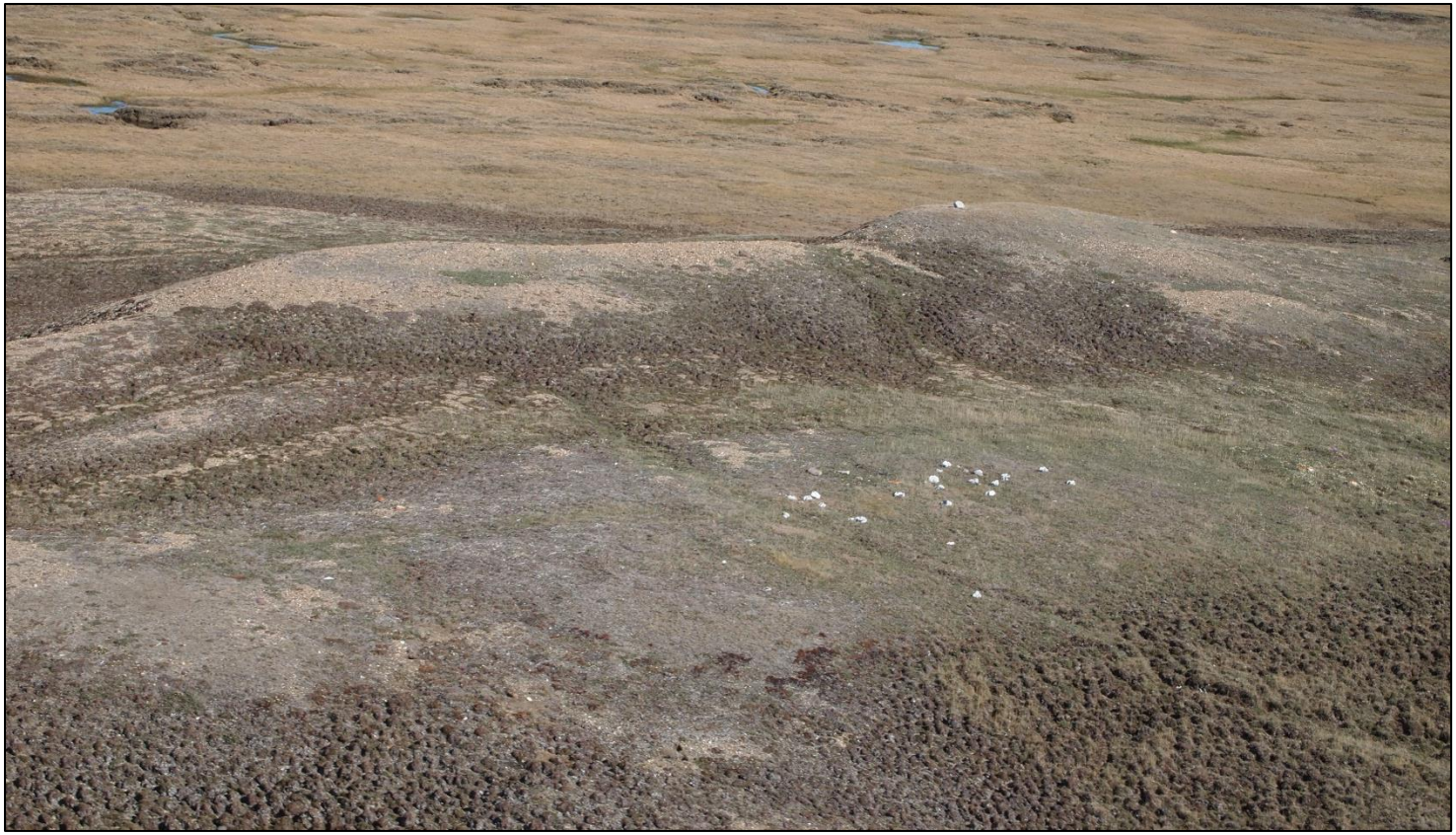


Figure 1.6. Muskox skeletal remains (white objects) scattered across the surface of the Umingmak (PjRa-2) site. Photo by author.

The ASTt toolkit was used across large parts of the Eastern Arctic with minimal modification until around 2500 cal. BP. At this point, several changes appeared in the material cultures of ASTt groups that signify the emergence of the Dorset period: less emphasis on microblade tools, abandonment of bows and arrows, and a shift in harpoon morphology from open socket to closed socket forms (Maxwell 1984, 1985). During the Dorset period, items associated with an increased focus on winter hunting and dwellings, such as snowshoes and snow knives appear, and the remains of seals, walruses, and less frequently, whales also comprise larger parts of faunal record at sites.

There are no known Dorset sites on Banks Island, but a transitional Paleo-Inuit cultural phase is represented at several sites. This phase, which has local expressions in a number of Arctic Regions, including Newfoundland where it is termed "Groswater" (Fitzhugh 1972; Hodgetts et al. 2003; Renouf 2011; Wells 2011) falls temporally between Pre-Dorset and Dorset in a particular region and displays characteristics of both. In the Western Arctic, it is known as the Lagoon Phase, after the type site. The Lagoon (OjRl-3) site (Figure 1.7) is located on the south coast of Banks Island and dates to between ~ 2700 and 2100 cal. BP (Figure 1.5). Arnold (1980) suggests that it represents the in-situ development of Pre-Dorset material culture influenced both by Dorset groups from the east, probably on Victoria Island, and by Alaskan groups known as Norton.

The faunal material at the Lagoon site indicates an occupation in the early summer, possibly extending to fall, with a heavy reliance on geese, juvenile seals, and muskoxen (Arnold 1980). The Crane site (ObRv-1), located on the Bathurst Peninsula, displays many technological parallels with the Lagoon site (Le Blanc 1994), suggesting that the Lagoon Phase was a regional phenomenon encompassing Banks Island and the immediately-adjacent mainland. Recent radiocarbon dates from the Arviq site (QaPv-5) (Figure 1.8) on the north coast of Banks Island and another site in Aulavik National Park (PkPx-18) indicate that they fall within the range of dates from the Lagoon site (Hodgetts and Eastaugh 2010; Hodgetts et al. 2013), extending the geographical range of the Lagoon Phase further north. Both sites display stone tools and raw materials similar to the Lagoon site.

Figure 1.7. The Lagoon (OjRl-3) site (image courtesy of Lisa Hodgetts).

Figure 1.8. The boulder-strewn surface of the Arviq (QaPv-5) site, with Mercy Bay visible in the background. Photo by author.

Like the ASTt before it, the Dorset material culture endured for around 1500 years. Around 1000 cal. BP however, the Dorset culture appears to have ended abruptly across most of the Eastern Arctic, around the same time that traces of Thule Inuit material culture begin to appear (Maxwell 1985; McGhee 1990; Friesen and Arnold 2008). Genetic evidence (Park 2014; Raghavan et al. 2014) indicates that this transition in material culture was the result of a new dispersal of humans rather than *in-situ* technological evolution. McGhee (1984) suggests that the Thule Inuit culture developed from the Birnirk culture in northern Alaska between ~ 1500 and 1100 cal. BP, but the motive for its subsequent expansion into the Eastern Arctic is poorly understood. Early work (McGhee 1972; McCartney 1977) explored the hypothesis that the Thule followed growing bowhead whale populations as they moved into the northern reaches of the Arctic Ocean during the Medieval Warm Period. Early archaeological work also supported the idea that the incoming Thule groups replaced Dorset groups, possibly by force, though reinterpretations of radiocarbon dates by Park (1993) and Friesen and Arnold (2008) reveal an interlude of several hundred years between the decline of the Dorset and the appearance of the Thule. Recent work (Harritt 2004; Mason 2009; Friesen 2010) has also shifted from trying to identify environmental factors that may have brought about the Thule expansion into the Eastern Arctic towards identifying and characterizing its social context.

The success of the Thule Inuit is reflected in the fact that they are the direct genetic ancestors of modern Inuit groups (Raghavan et al. 2014). Emphasizing an increasing reliance on maritime resources, mainly bowhead whales and ringed seals, Thule hunting technology centered on harpoons tipped with bone or antler harpoon heads. Lithics during this period also shifted from knapped to sharper ground forms more effective in hide and blubber processing (Maxwell 1985). The Nelson River (OhRh-1) site, located on the southwestern coast of Banks Island is currently the earliest-known Thule site in the Eastern Arctic, dating to ~ 950 cal. BP (Arnold 1986; Friesen and Arnold 2008). Excavation by Arnold (1986) at the site revealed a large, two-room house framed partially with driftwood poles, floored with small logs and wooden planks, and insulated by turf—construction methods similar to those employed by Birnirk people in Alaska around the same time (McGhee 1984). Artifacts from the site demonstrate the use of harpoons to hunt seals on

the open water and at breathing holes in the sea ice, bows and arrows to hunt muskoxen, caribou, and small birds, bola slings and gorges to hunt waterfowl, and leisters (multi-pronged spears) to catch fish. The faunal remains at OhRh-1 also demonstrate that, of these resources, ringed seals and likely also bowhead whales were most important, followed by arctic fox and other small mammals, birds, caribou, and finally muskoxen which were only minimally utilized.

Following their initial proliferation in the Eastern Arctic, the geographic range of the Thule appears to have contracted around 500 cal. BP. During this period, subsistence patterns also shifted away from bowhead whales towards seals, fish, and terrestrial resources (Schledermann 1979; Dumond 1984), potentially as a response to the end of the Medieval Warm Period, the onset of the Little Ice Age, and a subsequent reduction in bowhead availability (Maxwell 1985; Fitzhugh 1997). On Banks Island, Thule sites also begin to appear further inland during this period, and these sites contain greater frequencies of caribou and muskox remains. Although this period is sometimes referred to as the "Copper Inuit" (Jenness 1917, 1923; Hickey 1982; Will 1985) or "Inuinnait" (Collignon and Weber Müller-Wille 2006) period, we refer to it simply as the Inuit period, as these people are direct ancestors of Inuvialuit (i.e. Inuit Peoples of the Northwest Territories and the Northern Yukon) living on Banks Island today. During this time, family-based groups exploited both marine and terrestrial resources in an annual round (Hickey 1982; Hodgetts 2013). Generally, throughout the summer, muskoxen, caribou, and other inland fauna were hunted in the northern interior of the island, often at existing Pre-Dorset sites (Hickey 1982; Hodgetts et al. 2009), while during the winter seals and polar bears were hunted on the sea ice.

The intensive focus on terrestrial resources by the Inuit during summers is exemplified by the Head Hill site (PlPx-1) (Figure 1.9), where the crania and other skeletal elements of over 500 muskoxen, have accumulated from summer hunts (Wilkinson and Shank 1975; Hickey 1982). In many ways, the Head Hill site is at the core of academic hypotheses concerning faunal use (or overuse) by the people on Banks Island and the ecological relationships between caribou and muskoxen.

Figure 1.9. The skeletal remains of muskoxen – many still partially-articulated – at the Head Hill (PlPx-1) site (image courtesy of Lisa Hodgetts).

Originally, Head Hill was thought to date to ~ 1855-1890 AD, when Kangiryuarmiut from Victoria Island visited Banks Island to salvage wood from the British ship HMS *Investigator* (Stefansson 1921). The *Investigator*, on its search for Sir John Franklin's lost expedition to the Northwest Passage, was the first European ship to visit Banks Island, but became trapped in ice at Mercy Bay in 1851 (Figure 1.10). Ranging expeditions by the crew in the interior of Banks Island suggested that very few muskoxen – but many caribou – inhabited the island during this period (Skead 1849-1854; Armstrong 1857; Barr 1991). The *Investigator* was finally abandoned in 1853, but not before her crew offloaded several tons of coal, and a large cache of provisions and equipment on the western shore of Mercy Bay (Figure 1.11). To the Kangiryuarmiut and any other groups that visited, the cache provided a valuable supply of metal and wood useful for fashioning tools and sled-runners (Stefansson 1913, 1921; Hickey 1979, 1981; Barr 1991; Shank et al. 1994).

Figure 1.10. Portrait of the HMS *Investigator* trapped in pack ice at Mercy Bay, by Samuel Gurney Cresswell and William Simpson (image courtesy of Library and Archives Canada, C-016105). The *Investigator* now lies at the bottom of Mercy Bay, partially buried in silt but largely intact.

Figure 1.11. The remains of the HMS *Investigator's* cache in 2014, with the pile of offloaded coal and many barrel staves visible (image courtesy of Lisa Hodgetts).

When arctic explorer Vilhjalmur Stefansson visited the Head Hill site in 1915, he observed wood and metal scraps of clear European origin and theorized that, because muskoxen are easy to approach and kill, the Kangiryuarmiut had hunted them to the point of extirpation while traveling back and forth from the *Investigator* (Stefansson 1913; 1921), explaining why he, and the crew of the *Investigator* before him saw few muskoxen during their stays on Banks Island. However, radiocarbon dating by Shank et al. (1994) and Hodgetts (unpublished data) demonstrates that much of the Head Hill faunal assemblage accumulated prior to the arrival of the *Investigator*, sometime between 1650 and the early 1800s cal. AD, and that the site was simply reused by Inuit groups during the *Investigator* period.

Nevertheless, the Canadian government, motivated by Stefansson's reports, instituted a ban on muskox hunting from 1917 to 1971 (Barr 1991). Sachs Harbour Elder Susie Tiktalik warned that this would lead to an explosion in the muskox population and the concomitant decline of the Peary caribou population, both of which later occurred (Nagy 1999). Oral history also records that at some point after the *Investigator* was abandoned, most of the muskoxen on Banks Island died of starvation after freezing spring rains. After this, there were few caribou or muskoxen on the island and during this time, fox trapping and fur trading became an important economic focus for "Bankslanders", leading to the establishment of Sachs Harbour (Nagy 1999; Kelvin 2016). Management programs enacted with the input of the Inuvialuit during the 1970's returned the dwindling muskox population from ~ 4000 non-calf individuals in 1972 to ~ 47,000 non-calf individuals in 2005 (Barr 1991; Gunn et al. 1991; Reynolds 1998; Nagy et al. 2009). Recent reports however, suggest that the muskox population is again declining (Kelvin 2016).

1.5 Caribou and Muskox Diet on Banks Island and Physiological Considerations

Because of the nutritional challenges imposed by the arctic winter, both muskoxen and caribou must achieve most of their dietary intake, and fat and protein accumulation, during the short summer. As a species, caribou are classified as selective intermediate (i.e. between browse and forage) feeders that nevertheless require feed with high nutritional

content and limited fiber (Hofmann 1989). In summer, when the aerial organs of plants (green stems, shoots, flowers, and catkins) are still growing, they feed as concentrate selectors. In winter, when plants have entered dormancy, they feed as near-grazers (Hofmann 1989, 2000).

Studies of dietary variation by age and sex in caribou are limited, and no published studies exist for Peary caribou on Banks Island, probably because they move fast and frequently, and startle more easily than muskoxen. Several studies of monthly fecal compositions in caribou by Larter and Nagy (1997, 2004), however, found that dwarf willow comprised approximately sixty percent of summer diet, with sedges, legumes, and saxifrages making up the remaining forty percent of fecal content. In winter, dwarf willow content declined, and concentrations of legumes and rose/saxifrage increased, and throughout the year, sedge consumption accounted for ~ 25% of fecal content. Larter and Nagy (1997, 2004) suggest that lichen intake by caribou is minimal due to its limited availability. Personal observation in the 2014 field season, however, suggested that yellow lichen (*Cetraria tilesii*) and reindeer lichen (*Cladina* spp.) are abundant in both the northern and southern parts of the island. Further, community members from Sachs Harbour have remarked that lichen must be very healthy, because the caribou consume it in abundance throughout the year (Trevor Lucas 2014, personal communication). Given that lichens are fungi with cell walls composed of chitin, it may be that they are digested in such a way that their presence in diet is not reflected in the feces of ruminants.

An experimental feeding trial with reindeer (Dearden et al. 1975) suggests that lichen is prone to underestimation in fecal samples, and El Seed et al. (2002) found that chitin is significantly more digestible than the fibrous biochemical fractions of plants. Determining whether Banks Island caribou ingest lichen is important for the interpretation of their $\delta^{13}C$ and $\delta^{15}N$. Like all arctic plants, the green algae (*Trebouxia* spp.) that symbiotically associate with *Cetraria* and *Cladina* utilize the C_3 (or Calvin) photosynthetic pathway (Teeri and Stowe 1976; Osborne and Beerling 2006). The absence of vascular systems in lichens, however, inhibits the diffusion of dissolved CO_2 once it reaches their thalli, resulting in smaller isotopic fractionations and more positive $\delta^{13}C$ (–21 to –18‰) relative to C_3 plants ($\delta^{13}C$ average: –26.5‰) (Park and Epstein 1960; Maguas and Brugnoli 1996;

Evans et al. 2009). Lichens are also depleted of ^{15}N relative to many other terrestrial plants because they do not possess the ability to fix atmospheric N_2 (Virginia and Delwiche 1982; France et al. 2007). We consider the potential role of lichens in the diets of caribou and muskoxen on Banks Island in Chapter 2.

Forchhammer et al. (2002) classify muskoxen as generalist browsers, and Hofmann (2000:72, 78) argues that the digestive systems of muskoxen are "developed in accordance with that of a typical grazer or roughage feeder" and are "equipped with a very robust [grazer] digestive system." Like most grazers, muskoxen have large, complex gastrointestinal tracts that allow them to extract energy from large volumes of high fiber, high protein forage. By observing muskoxen on Banks Island, Oakes et al. (1992) matched feces to individual muskoxen, and therefore differentiated fecal samples by age and sex. Contrary to the findings of Larter and Nagy (1997, 2004) discussed below, Oakes et al. (1992) found that shrub (*S. arctica, Dryas integrifolia*) consumption was relatively low across all categories of muskoxen, suggesting that non-woody vegetation is preferred when it is available during the summer. Adult female muskoxen had significantly greater proportions of forbs in their feces than adult males, who had a significantly greater proportion of sedges and rushes in their feces than adult females (Oakes et al. 1992). The feces of yearlings contained significantly greater proportions of shrubs than yearlings and adults of either sex (Oakes et al. 1992). When all non-adults were pooled, they had significantly greater proportions of shrub leaves (as opposed to other parts) in their feces than adults of both sexes (Oakes et al. 1992).

In their analysis of monthly muskox fecal content, Larter and Nagy (1997) found that in both the summer and winter, muskoxen on Banks Island, pooled across age and sex categories, relied on a seasonally stable combination of sedge, representing 30-50% of their diet, and dwarf willow, representing the remaining 40% of their diet. In agreement with the findings of Oakes et al. (1992), Larter and Nagy (1997) also found that sedges and grasses composed the majority of the adult male diet, while sedges and forbs composed the majority of diet in nonlactating adult females, subadults, and calves. Contrary to nutritional expectations, the diets of lactating adult females were similar to adult males, with sedges

and grasses making up the majority of their diets. Yearlings primarily consumed forbs and grasses, though they also consumed the most shrubs of any of the groups.

Despite the ability of the ruminant digestive system to extract nutrients from plant matter, the different biochemical fractions composing plant tissues are not all equally digestible. Several physiological studies demonstrate that ruminants are unable to digest the lignin fraction of plant matter effectively, if at all (Elsden and Phillipson 1948; Larter and Nagy 2001b). Several studies (Gill et al. 1983; Holechek and Valdez 1985; Bartolomé et al. 1995; Hwang et al. 2007) have also established that fecal content analysis may overestimate indigestible forage types while also underestimating highly digestible forage. Isotopic analysis may therefore provide a more accurate portrayal of diet: as Hedges and van Klinken (2000:224) note, "[isotopic fractionation] during metabolism will only apply to food that has been digested," not merely food that has been eaten. Still, if some plant tissues are more readily digested than others, and their carbon isotope compositions all vary based on the proportions of different biochemical compounds (Deines et al. 1980; Benner et al. 1987), then the δ^{13}C of bone collagen from herbivores may not reflect all forage sources, or their biochemical fractions, equally. The presence of lignin in the diets of ruminants may also affect the δ^{15}N of body tissues in a complex system of digestive feedbacks. Work by McAnally and Phillipson (1944) and Van Soest (1963) determined that the presence of lignin in the rumen reduces cellulose digestibility and subsequent protein assimilation. Therefore, the ingestion of plants with high lignin content should result in ^{15}N-depleted body tissues. Additionally, the proportion of lignin to cellulose in plants increases throughout the growing season and remains high during dormancy (Larter and Nagy 2001b). Larter and Nagy (2001b) found that dicots, especially shrubs (*S. arctica, D. integrifolia, and Cassiope tetragona*), have the highest lignin content of all plants eaten by caribou and muskoxen. Therefore, consumption of these plants during the summer feeding period, and consumption of old plant material during the winter should both be associated with decreased body protein and subsequently decreased δ^{15}N in body tissues. The amount of crude protein in the diet also affects the digestibility of cellulose in ruminants. Mitchell et al. (1940) found that cellulose was digested more effectively when the protein percentage of the ingested plant material was low rather than high, though Harris and Mitchell (1941) demonstrate that some protein is necessary to contribute nitrogen to cellulose-digesting

microflora. These issues, and their implications for biases in mixing models, are considered at length in Chapter 2.

1.6 Organization of the Dissertation

The body of this dissertation is divided into three chapters. In Chapter 2, we use a mixing model to infer the relative contributions of different forage sources to the bone collagen $\delta^{13}C$ and $\delta^{15}N$ of modern caribou and muskoxen from Banks Island. These data provide insight into the relationship among bone collagen isotopic compositions and diet in caribou and muskoxen, which is essential for interpreting archaeological isotope data. We also investigate differences in weaning, and seasonal variation in diet using $\delta^{13}C$ and $\delta^{15}N$ of sequentially sampled dentin collagen from modern caribou and muskox teeth. Overall, these data suggest that muskoxen have a reproductive advantage over caribou in periods of poor forage availability, but that recent changes in phytomass composition on Banks Island may favor caribou in the future.

In Chapter 3, we apply multivariate and Bayesian ellipse metrics to caribou and muskox bone collagen $\delta^{13}C$ and $\delta^{15}N$ spanning the last 4000 years to investigate potential changes in diet and niche relationships between caribou and muskoxen. This chapter represents a considerable advancement in our understanding of caribou and muskox ecology during the Holocene, and demonstrates that caribou and muskoxen are flexible intermediate feeders that mitigate niche competition during periods of reduced forage availability by using different resources. The shift from forb- to graminoid-dominated tundra around 3000 years ago, however, may have imparted muskoxen with a dietary advantage over caribou until recently, when dwarf willow phytomass started to increase in the Arctic (Walker et al. 2006; Forbes et al. 2009; Jia et al. 2009). In any case, interspecific forage competition, and overexploitation by humans are probably not significant factors in the periodic abandonment of Banks Island during the last 4000 years.

In Chapter 4, we use laser ablation-GC-IRMS to evaluate the potential of sequential tooth enamel $\delta^{18}O$ for reconstructing seasonal movement patterns in caribou and muskoxen. Our results suggest that enamel $\delta^{18}O$ captures seasonal variability in precipitation, rather than geographical variation in surface waters taken up by vegetation. At greater sample sizes

however, these data would be useful for investigating broad scale changes in seasonality on Banks Island over the last 4000 years.

In Chapter 5, we discuss the potential implications of this project for understanding tissue-diet isotope relationships and differences between two statistical models used to evaluate stable isotope data. We also consider its contribution to research regarding archaeological relationships between human hunters and caribou and muskoxen on Banks Island, and the use of isotopic data presented here in future ecological research at high latitudes. Finally, we suggest several avenues of research which could be explored based on findings presented here.

1.7 References

Abelson PH, Hoering TC. 1961. Carbon Isotope Fractionation in Formation of Amino Acids by Photosynthetic Organisms. Proceedings of the National Academy of Sciences 47(5): 623-632.

Abuzinadah RA, Read DJ. 1986. The Role of Proteins in the Nitrogen Nutrition of Ectomycorrhizal Plants: III. Protein Utilization by *Betula*, *Picea* and *Pinus* in Mycorrhizal Association with *Hebeloma crustuliniforme*. New Phytologist 103: 507-514.

Alexander VM, Billington M, Schell DM. 1978. Nitrogen Fixation in Arctic and Alpine Tundra. In: Tieszen LL, editor. Vegetation and Production Ecology of an Alaskan Arctic Tundra. Ecological Studies Series 29. New York: Springer-Verlag. Pp. 539-558.

Allison GB, Gat JR, Leaney FWJ. 1985. The Relationship Between Deuterium and Oxygen-18 Delta Values in Leaf Water. Chemical Geology (Isotope Geoscience Section) 58: 145-156.

Ambrose SH, DeNiro MJ. 1986. The Isotopic Ecology of East African Mammals. Oecologia 69: 395-406.

Ambrose SH. 1990. Preparation and Characterization of Bone and Tooth Collagen for Isotopic Analysis. Journal of Archaeological Science 17: 431-451.

Ambrose SH. 1993. Isotopic Analysis of Paleodiets: Methodological and Interpretive Considerations. In: Sandford MK, editor. Investigations of Ancient Human Tissue. Langhorne: Gordon and Breach. Pp. 59-130.

Ambrose SH, Norr L. 1993. Experimental Evidence for the Relationship of the Carbon Isotope Ratios of Whole Diet and Dietary Protein to Those of Bone Collagen and Carbonate. In: Lambert JB, Grupe G, editors. Prehistoric Human Bone: Archaeology at the Molecular Level. Berlin: Springer-Verlag. Pp. 1-38.

Armstrong A. 1857. A Personal Narrative of the Discovery of the North-West Passage: While in Search of the Expedition Under Sir John Franklin. London: Hurst and Blackett.

Arnason B. 1981. Ice and Snow Hydrology. In: Gat JR, Gonfiatini R, editors. Stable Isotope Hydrology, Deuterium and Oxygen-18 in the Water Cycle. IAEA Technical Reports Series 210. Vienna: IAEA. Pp. 143-176.

Arnold CD. 1980. A Paleoeskimo Occupation on Southern Banks Island, N.W.T. Arctic 33(3): 400-426.

Arnold 1983. A Summary of the Prehistory of the Western Canadian Arctic. Arctic Archaeology 33: 10-20.

Arnold CD. 1986. In Search of the Thule Pioneers. In: Bielawski E, Kobelka C, Janes RR, editors. Thule Pioneers: Occasional Papers of the Prince of Whales Northern Heritage Centre Number 2. Pp. 1-93.

Arundale WH. 1981. Radiocarbon Dating in Eastern Arctic Archaeology: A Flexible Approach. American Antiquity 46(2): 244-271.

Atasoglu C, Guliye AY, Wallace RJ. 2004. Use of Stable Isotopes to Measure *de novo* Synthesis and Turnover of Amino Acid-C and -N in Mixed Micro-Organisms from the Sheep rumen *in vitro*. British Journal of Nutrition 91: 253-261.

Ayliffe LK, Chivas AR. 1990. Oxygen Isotope Composition of the Bone Phosphate of Australian Kangaroos: Potential as a Palaeoenvironmental Recorder. Geochimica et Cosmochimica Acta 54: 2603-2609.

Bacastow RB, Keeling CD, Lueker TJ, Wahlen M, Mook WG. 1996. The $\delta^{13}C$ Suess Effect in the World Surface Oceans and Its Implications for Oceanic Uptake of CO_2: Analysis of Observations at Bermuda. Global Biogeochemical Cycles 10: 335-346.

Balasse M, Bocherens H, Mariotti A, Ambrose SH. 2001. Detection of Dietary Changes by Intra-tooth Carbon and Nitrogen Isotopic Analysis: An Experimental Study of Dentine Collagen of Cattle (*Bos taurus*). Journal of Archaeological Science 28: 235-245.

Balasse M. 2002. Reconstructing Dietary and Environmental History from Enamel Isotopic Analysis: Time Resolution of Intra-tooth Sequential Sampling. International Journal of Osteoarchaeology 12: 155-165.

Balasse M, Ambrose SH, Smith AB, Price TD. 2002. The Seasonal Mobility Model for Prehistoric Herders in the South-western Cape of South Africa Assessed by Isotopic Analysis of Sheep Tooth Enamel. Journal of Archaeological Science 29: 917-932.

Barr W. 1991. Back from the Brink: The Road to Muskox Conservation in the Northwest Territories. Komatik Series 3. Calgary: The Arctic Institute of North America.

Bartolomé J, Franch J, Gutman M, Seligman NAG. 1995. Technical Note: Physical Factors That Influence Fecal Analysis Estimates of Herbivore Diets. Journal of Range Management 48: 267-270.

Benner R, Fogel ML, Sprague EK, Hodson RE. 1987. Depletion of 13C in Lignin and its Implications for Stable Carbon Isotope Studies. Nature 329: 708-710.

Ben-David M, Shochat E, Adams LG. 2001. Utility of Stable Isotope Analysis in Studying Foraging Ecology of Herbivores: Examples from Moose and Caribou. Alces 37(2): 421-434.

Bielawski E. 1988. Paleoeskimo Variability: The Early Arctic Small-Tool Tradition in the Central Canadian Arctic. American Antiquity 53(1): 52-74.

Bocherens H. 2000. Preservation of Isotopic Signals (^{13}C, ^{15}N) in Pleistocene Mammals. In: Ambrose SH, Katzenberg MA, editors. Biogeochemical Approaches to Paleodietary Analysis. New York: Kluwer Academic/Plenum Publishers. Pp. 65-88.

Boutton TW. 1996. Stable Carbon Isotope Ratios of Soil Organic Matter and Their Use as Indicators of Vegetation and Climate Change. In: Boutton TW, Yamasaki SI, editors. Mass Spectrometry of Soils. New York: Marcel Dekker Inc. Pp. 47-82.

Bowen GJ, Wilkinson B. 2002. Spatial Distribution of $\delta^{18}O$ in Meteoric Precipitation. Geology 30(4): 315-318.

Bowen GJ, Revenaugh J. 2003. Interpolating the Isotopic Composition of Modern Meteoric Precipitation. Water Resources Research 39(10): 1299.

Braje TJ, Rick TC. 2013. From Forest Fires to Fisheries Management: Anthropology, Conservation Biology, and Historical Ecology. Evolutionary Anthropology 22: 303-311.

Britton K, Grimes V, Dau J, Richards MP. 2009. Reconstructing Faunal Migrations Using Intra-tooth Sampling and Strontium and Oxygen Isotope Analyses: a Case Study of Modern Caribou (*Rangifer tarandus granti).* Journal of Archaeological Science 36: 1163-1172.

Bryant JD, Froelich PN. 1995. A Model of Oxygen Isotope Fractionation in Body Water of Large Mammals. Geochimica et Cosmochimica Acta 59(21): 4523-4537.

Bryant JD, Koch PL, Froelich PN, Showers WJ, Genna BJ. 1996. Oxygen Isotope Partitioning Between Phosphate and Carbonate in Mammalian Apatite. Geochimica et Cosmochimica Acta 60(24): 5145-5148.

Carlson SJ. 1990. Vertebrate Dental Structures. In: Carter JG, editor. Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends, Volume 1. New York: Van Nostrand Reinhold.

Cernusak LA, Tcherkez G, Keitel C, Cornwell WK, Santiago LS, Knohl A, Barbour MM, Williams DG, Reich PB, Ellsworth DS, Dawson TE, Griffiths HG, Farquhar GD, Wright IJ. 2009. Why are Non-photosynthetic Tissues Generally ^{13}C Enriched Compared with Leaves in C_3 Plants? Review and Synthesis of Current Hypotheses. Functional Plant Biology 36: 199-213.

Cernusak LA, Ubierna N, Winter K, Holtum JAM, Marshall JD, Farquhar GD. 2013. Environmental and Physiological Determinants of Carbon Isotope Discrimination in Terrestrial Plants. New Phytologist 200: 950-965.

Chapin FS, III, Fetcher N, Kielland K, Everett KR, Linkins AE. 1988. Productivity and Nutrient Cycling of Alaskan Tundra: Enhancement by Flowing Soil Water. Ecology 69(3): 693-702.

Chapin DM, Bledsoe C. 1992. Nitrogen Fixation in Arctic Plant Communities. In: Chapin FS, III, Jeffries RL, Reynolds JF, Shaver GR, Svoboda J, editors. Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective. San Diego: Academic Press. Pp. 301-319.

Chapin FS, III, Moilanen L, Kielland K. 1993. Preferential Use of Organic Nitrogen for Growth by a Non-mycorrhizal Arctic Sedge. Nature 361: 150-153.

Clemmensen KE, Sorensen PL, Michelsen A, Jonasson S, Ström L. 2008. Site-dependent N Uptake from N-form Mixtures by Arctic Plants, Soil Microbes and Ectomycorrhizal Fungi. Oecologia 155: 771-783.

Codron D, Brink JS, Rossouw L, Clauss M, Codron J, Lee-Thorp JA, Sponheimer M. 2008. Functional Differentiation of African Grazing Ruminants: An Example of Specialized Adaptations to Very Small Changes in Diet. Biological Journal of the Linnean Society 94: 755-764.

Codron D, Sponheimer M, Codron J, Newton I, Lanham JL, Clauss M. 2012. The Confounding Effects of Source Isotopic Heterogeneity on Consumer-diet and Tissue-tissue Stable Isotope Relationships. Oecologia 169: 939-953.

Cohen JL, Furtado JC, Barlow MA, Alexeev VA, Cherry JE. 2012. Arctic Warming, Increasing Snow Cover and Widespread Boreal Winter Cooling. Environmental Research Letters 7: 1-8.

Collignon B, Weber Müller-Wille L. 2006. Knowing Place: the Inuinnait, Landscapes, and the Environment. Edmonton: Canadian Circumpolar Institute Press.

Collins HB. 1953. Radiocarbon Dating in the Arctic. American Antiquity 18(3): 197-203.

Copley MS, Jim S, Jones V, Rose P, Clapham A, Edwards DN, Horton M, Rowley-Conwy P, Evershed RP. 2004. Short- and Long-term Foraging and Foddering Strategies of Domesticated Animals from Qasr Ibrim, Egypt. Journal of Archaeological Science 31: 1273-1286.

COSEWIC. 2004. COSEWIC Assessment and Update Status Report in the Peary caribou *Rangifer tarandus Pearyi* and the barren-ground caribou *Rangifer tarandus groenlandicus* (Dolphin and Union Population) in Canada. Ottawa: Committee on the Status of Endangered Wildlife in Canada.

Craig H, Gordon LI. 1965. Deuterium and Oxygen 18 Variations in the Ocean and the Marine Atmosphere. In: Tongiorgi E, editor. Stable Isotopes in Oceanographic Studies and Paleotemperatures. Pisa: Consiglio Nazionale delle Richerche Laboratorio di Geologia Nucleare. Pp. 9-130.

Currey J. 2002. Bones: Structure and Mechanics. Princeton: Princeton University Press.

Dansgaard W. 1964. Stable Isotopes in Precipitation. Tellus 16(4): 436-468.

Darling WG, Bath AH, Gibson JJ, Rozanski K. 2005. Isotopes in Water. In: Leng MJ, editor. Isotopes in Palaeoenvironmental Research. New York: Springer. Pp. 1-66.

Darwent CM. 2004. The Highs and Lows of High Arctic Mammals: Temporal Change and Regional Variability in Paleoeskimo Subsistence. In: Mondini M, Muñoz S, Wickler S, editors. Colonisation, Migration, and Marginal Areas: A Zooarchaeological Approach. Oxford: Oxbow Books. Pp. 62-73.

Dawson TE, Mambelli S, Plamboeck AH, Templer PH, Tu KP. 2002. Stable Isotopes in Plant Ecology. Annual Review of Ecological Systematics 33: 507-559.

Dearden BL, Pegau RE, Hansen RM. 1975. Precision of Microhistological Estimates of Ruminant Food Habits. The Journal of Wildlife Management 39(2): 402-407.

Dekin, AA Jr. 1972. Climatic Change and Cultural Change: A Correlative Study from Eastern Arctic Prehistory. Polar Notes 12: 11-31.

Deines P. 1980. The Isotopic Composition of Reduced Organic Carbon. In: Fritz P, Fontes JC, editors. Handbook of Environmental Isotope Geochemistry. New York: Elsevier Scientific. Pp. 329-406.

DeNiro MJ, Epstein S. 1981. Influence of Diet on the Distribution of Nitrogen Isotopes in Animals. Geochimica et Cosmochimica Acta 45: 341-351.

DeNiro MJ. 1985. Postmortem Preservation and Alteration of *In Vivo* Bone Collagen Isotope Ratios in Relation to Palaeodietary Reconstruction. Nature 317: 806-809.

Dewhurst RJ, Davies DR, Merry RJ. 2000. Microbial Protein Supply from the Rumen. Animal Feed Science and Technology 85: 1-21.

Dumond DE. 1984. Prehistory: Summary. In: Handbook of North American Indians, Volume 5: Arctic. Damas D, editor. Washington: Smithsonian Institution. Pp. 72-79.

Dupras TL, Schwarcz HP, Fairgrieve SI. 2001. Infant Feeding and Weaning Practices in Roman Egypt. American Journal of Physical Anthropology 115: 204-212.

Dupras TL, Tocheri MW. 2007. Reconstructing Infant Weaning Histories at Roman Period Kellis, Egypt Using Stable Isotope Analysis of Dentition. American Journal of Physical Anthropology 134: 63-74.

Dyke AS, Savelle JM. 2009. Paleoeskimo Demography and Sea-level History, Kent Peninsula and King William Island, Central Northwest Passage, Arctic Canada. Arctic 62: 371-392.

Dyke AS, Savelle JM, Johnson DS. 2011. Paleoeskimo Demography and Holocene Sea-level History, Gulf of Boothia, Arctic Canada. Arctic 64: 151-168.

Edlund SA. 1986. Modern Arctic Vegetation Distribution and Its Congruence with Summer Climate Patterns. In: French HM, editor. Climate Change Impacts in the Canadian Arctic, Proceedings of a Canadian Climate Program Workshop, March 3-5, 1986, Geneva Park, Ontario.

Ehleringer JR, Field CB, Lin ZF, Kuo CY. 1986. Leaf Carbon Isotope Ratio and Mineral Composition in Subtropical Plants Along an Irradiance Cline. Oecologia 70: 520-526.

Ehleringer JR, Lin ZF, Field CB, Kuo CY. 1987. Leaf Carbon Isotope Ratios of Plants from a Subtropical Monsoon Forest. Oecologia 72: 109-114.

Ehleringer JR, Roden J, Dawson TE. 2000. Assessing Ecosystem-level Water Relations Through Stable Isotope Ratio Analyses. In: Sala OE, Jackson RB, Mooney HA, Howarth RW, editors. Methods in Ecosystem Science. New York: Springer. Pp. 181-198.

Elliott JC. 2002. Calcium Phosphate Biominerals. In: Kohn MJ, Rakovan J, Hughes JM, editors. Phosphates – Geochemical, Geobiological, and Materials Importance. Reviews in Mineralogy and Geochemistry 48. Chantilly: Mineralogical Society of America. Pp. 427-453.

Elsden SR, Phillipson AT. 1948. Ruminant Digestion. Annual Review of Biochemistry 17(1): 705-726.

El-Seed ANMA, Kamel HEM, Sekine J, Hishinuma M, Hamana K. 2002. Chitin and Chitosan as Possible Novel Nitrogen Sources for Ruminants. Canadian Journal of Animal Science 83: 161-163.

England JH, Furze MFA, Doupe JP. 2009. Revision of the NW Laurentide Ice Sheet: Implications for Paleoclimate, the Northeast Extremity of Beringia, and Arctic Ocean Sedimentation. Quaternary Science Reviews 28: 1573-1596.

Epstein S, Mayeda T. 1953. Variation in O^{18} Content of Waters from Natural Sources. Geochimica et Cosmochimica Acta 4: 213-224.

Epstein S, Thompson P, Yapp CJ. 1977. Oxygen and Hydrogen Isotopic Ratios in Plant Cellulose. Science, New Series 198(4323): 1209-1215.

Ervynck A. 1999. Possibilities and Limitations of the Use of Archaeozoological Data in Biogeographical Analysis: A Review with Examples from the Benelux Region. Belgian Journal of Zoology 129: 125-138.

Evans RD, Blooms AJ, Sukrapanna SS, Ehleringer JR. 1996. Nitrogen Isotope Composition of Tomato (Lycopersicon esculentim Mill. cv. T-5) Grown Under Ammonium or Nitrate Nutrition. Plant, Cell, and Environment 19: 1317-1323.

Evans JR, Kaldenhoff R, Genty B, Terashima I. 2009. Resistances Along the CO_2 Diffusion Pathway Inside Leaves. Journal of Experimental Botany 60(8): 2235-2248.

Farquhar GD, Ehleringer JR, Hubick KT. 1989. Carbon Isotope Discrimination and Photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology 40: 503-537.

Faure G, Mensing TM. 2005. Isotopes: Principles and Applications. Hoboken: John Wiley & Sons.

Feranec RS, Hadly EA, Paytan A. 2009. Stable Isotopes Reveal Seasonal Competition for Resources Between Late Pleistocene Bison (Bison) and Horse (Equus) from Rancho La Brea, Southern California. Palaeogeography, Palaeoclimatology, Palaeoecology 271: 153-160.

Ferguson RS. 1991. Detection and Classification of Muskox Habitat on Banks Island, Northwest Territories, Canada, Using Landsat Thematic Mapper Data. Arctic 44(S1): 66-74.

Ferhi A, Letolle R. 1977. Transpiration and Evaporation as the Principal Factors in Oxygen Isotope Variation of Organic Matter in Land Plants. Physiologic Vegetale 15: 363-370.

Fincham AG, Simmer JP. 1997. Amelogenin Proteins of Developing Dental Enamel. Ciba Foundation Symposium 205: 118-130.

Fitzhugh WW. 1972. Environmental Archeology and Cultural Systems in Hamilton Inlet, Labrador. A Survey of the Central Labrador Coast from 3000 B.C. to the Present. Smithsonian Contributions to Anthropology 16.

Fitzhugh WW. 1976. Environmental Factors in the Evolution of Dorset Culture: A Marginal Proposal for Hudson Bay. Memoirs of the Society for American Archaeology, No. 31, Eastern Arctic Prehistory: Paleoeskimo Problems: 139-149.

Fitzhugh WW. 1997. Biogeographical Archaeology in the Eastern North American Arctic. Human Ecology 25(3): 385-418.

Fogel ML, Tuross N, Johnson BJ, Miller GH. 1997. Biogeochemical Record of Ancient Humans. Organic Chemistry 26(5-6): 275-287.

Fogel ML, Tuross N. 2003. Extending the Limits of Paleodietary Studies of Humans with Compound Specific Carbon Isotope Analysis of Amino Acids. Journal of Archaeological Science 30: 535-545.

Forbes BC, Fauria MM, Zetterbergs P. 2010. Russian Arctic Warming and 'Greening' are Closely Tracked by Tundra Shrub Willows. Global Change Biology 16: 1542-1554.

Forchhammer MC, Post E, Stenseth NC, Boertmann DM. 2002. Long-term Responses in Arctic Ungulate Dynamics to Changes in Climatic and Trophic Processes. Population Ecology 44: 113-120.

France CAM, Zelanko PM, Kaufman AJ, Holtz TR. 2007. Carbon and Nitrogen Isotopic Analysis of Pleistocene Mammals from the Saltville Quarry (Virginia, USA): Implications for Trophic Relationships. Palaeogeography, Palaeoclimatology, Palaeoecology 249: 271-282.

Francey RJ, Allison CE, Etheridge DM, Trudinger CM, Enting IG, Leuenberger M, Langenfelds RL, Michel E, Steele LP. 1999. A 1000-year High Precision Record of $\delta^{13}C$ in Atmospheric CO_2. Tellus 51B: 170-193.

Fricke HC, O'Neil JR. 1996. Inter- and Intra-tooth Variation in the Oxygen Isotope Composition of Mammalian Tooth Enamel Phosphate: Implications for Palaeoclimatological and Palaeobiological Research. Palaeogeography, Palaeoclimatology, Palaeoecology 126: 91-99.

Friedli H, Lötscher H, Oeschger H, Siegenthaler U, Stauffer B. 1986. Ice Core Record of the $^{13}C/^{12}C$ Ratio of Atmospheric CO_2 of the Past Two Centuries. Nature 324: 237-238.

Friesen TM. 2007. Hearth Rows, Hierarchies and Arctic Hunter-Gatherers: The Construction of Equality in the Late Dorset Period. World Archaeology 39(2): 194-214.

Friesen TM, Arnold CD. 2008. The Timing of the Thule Migration: New Dates from the Western Canadian Arctic. American Antiquity 73(3): 527-538.

Friesen TM. 2010. Dynamic Inuit Social Strategies in Changing Environments: A Long-term Perspective. Geografisk Tidsskrift – Danish Journal of Geography 110(2): 215-225.

Fritz P. 1981. River Waters. In: Gat JR, Gonfiatini R, editors. Stable Isotope Hydrology, Deuterium and Oxygen-18 in the Water Cycle. IAEA Technical Reports Series 210. Vienna: IAEA. Pp. 177-201.

Gannes LZ, O'Brien DM, Martinez del Rio C. 1997. Stable Isotopes in Animal Ecology: Assumptions, Caveats, and a Call for More Laboratory Experiments. Ecology 78(4): 1271-1276.

Gannes LZ, Martinez del Rio C, Koch P. 1998. Natural Abundance Variations in Stable Isotopes and Their Potential Uses in Animal Physiological Ecology. Comparative Biochemistry and Physiology 119A(3): 725-737.

Gat JR. 1981a. Properties of the Isotopic Species of Water: the 'Isotope Effect'. In: Gat JR, Gonfiatini R, editors. Stable Isotope Hydrology, Deuterium and Oxygen-18 in the Water Cycle. IAEA Technical Reports Series 210. Vienna: IAEA. Pp. 7-19.

Gat JR. 1981b. Isotopic Fractionation. In: Gat JR, Gonfiatini R, editors. Stable Isotope Hydrology, Deuterium and Oxygen-18 in the Water Cycle. IAEA Technical Reports Series 210. Vienna: IAEA. Pp. 21-33.

Gat JR. 1981c. Groundwater. In: Gat JR, Gonfiatini R, editors. Stable Isotope Hydrology, Deuterium and Oxygen-18 in the Water Cycle. IAEA Technical Reports Series 210. Vienna: IAEA. Pp. 223-240.

Gat JR, Mook WG, Meijer AJ. 2001. Atmospheric Water. In: Mook WG, editor. Environmental Isotopes in the Hydrological Cycle: Principles and Applications. IHP-V Technical Documents in Hydrology 39(2). Paris: International Hydrological Programme.

Ghashghaie J, Badeck FW. 2014. Opposite Carbon Isotope Discrimination During Dark Respiration in Leaves Versus Roots—a Review. New Phytologist 201: 751-769.

Giddings JL. 1964. The Archaeology of Cape Denbigh. Rhode Island: Brown University Press.

Gill RB, Carpenter LH, Bartmann RM, Baker DL, Schoonveld GG. 1983. Fecal Analysis to Estimate Mule Deer Diets. Journal of Wildlife Management 47: 902-915.

Gonfiatini R, Gratziu S, Tongiorgi E. 1965. Oxygen Isotopic Composition of Water in Leaves. In: Isotopes and Radiation in Soil-Plant Nutrition Studies: Proceedings of the Symposium on the Use of Isotopes and Radiation in Soil-Plant Nutrition Studies Jointly Organized by the International Atomic Energy Agency and the Food and Agricultural Organization of the United Nations and Held in Ankara, 28 June-2 July 1965. Pp. 405-412.

Gonfiatini R. 1986. Environmental Isotopes in Lake Studies. In: Fritz P, Fontes JC, editors. Handbook of Environmental Isotope Geochemistry: The Terrestrial Environment B, Volume 2. Amsterdam: Elsevier. Pp. 113-168.

Gray DR. 1997. Climate. In: The Natural and Cultural Resources of Aulavik National Park. Report on file at Parks Canada Western Service Centre, Winnipeg, Manitoba.

Gunn A, Shank C, McLean B. 1991. The History and Management of Muskoxen on Banks Island. Arctic 44(3): 188-195.

Gunn A, Miller FL, Nishi J. 2000. Status of Endangered and Threatened Caribou on Canada's Arctic Islands. Rangifer 12: 39-50.

Gunn A. Miller FL, Barry SJ. 2003. Conservation of Erupting Ungulate Populations on Islands – a Comment. Rangifer 23: 57-65.

Hahn J. 1977. Excavation at Umingmak, Area I D. In: Müller-Beck H, editor. Excavations at Umingmak on Banks Island, N.W.T., 1970 and 1973: Preliminary Report. Urgeschichtliche Materialhefte 1. Pp. 23-46.

Halevy E. 1970. The Relationship Between Isotopic Composition of Precipitation and Lysimeter Percolates. In: Interpretation of Environmental Isotope Data in Hydrology: Report of a Panel Sponsored by the International Atomic Energy Agency and Held in Vienna, 24-28 June 1968. Pp. 10-13.

Harbeck M, Grupe G. 2009. Experimental Chemical Degradation Compared to Natural Diagenetic Alteration of Collagen: Implications for Collagen Quality Indicators for Stable Isotope Analysis. Archaeological and Anthropological Sciences 1: 43-57.

Hare PE, Fogel ML, Stafford TW Jr., Mitchell AD, Hoering TC. 1991. The Isotopic Composition of Carbon and Nitrogen in Individual Amino Acids Isolated from Modern and Fossil Proteins. Journal of Archaeological Science 18: 277-292.

Harris LE, Mitchell AG. 1941. The Value of Urea in the Synthesis of Protein in the Paunch of the Ruminant. I. In Maintenance. Journal of Nutrition 22: 167-175.

Harritt RK. 2004. A Preliminary Reevaluation of the Punuk-Thule Interface at Wales, Alaska. Arctic Anthropology 41(2): 163-176.

Hartery L. 2010. Dorset Paleoeskimo Warm Season Adaptations in Newfoundland and Labrador. [Dissertation]. [Calgary (AB)]: University of Calgary.

Hayes JM. 2001. Fractionation of Carbon and Hydrogen Isotopes in Biosynthetic Processes. Reviews in Mineralogy & Geochemistry 43(1): 225-277.

Hedges REM, van Klinken GJ. 2000. “Consider a Spherical Cow…”—on Modeling and Diet. In: Ambrose SH, Katzenberg MA, editors. Biogeochemical Approaches to Paleodietary Analysis. New York: Kluwer Academic Publishers. Pp. 211-242.

Hedges REM. 2003. On Bone Collagen – Apatite-Carbonate Isotopic Relationships. International Journal of Osteoarchaeology 13: 66-79.

Helmer JW. 1991. The Palaeo-Eskimo Prehistory of the North Devon Lowlands. Arctic 44(4): 301-317.

Helmer JW. 1994. Resurrecting the Spirit(s) of Taylor's "Carlsberg Culture": Cultural Traditions and Cultural Horizons in Eastern Arctic Prehistory. In: Morrison D, Pilon J-L, editors. Threads of Arctic Prehistory: Papers in Honour of William E. Taylor, Jr. Mercury Series, Archaeological Survey of Canada Paper 149. Quebec: Canadian Museum of Civilization. Pp. 15-34.

Hewitt CG. 1921. The Conservation of the Wild Life of Canada. New York: Charles Scribner & Sons.

Hickey CG. 1979. Archaeological and Ethnohistorical Research on Banks Island. Ètudes/Inuit/Studies 3(2): 132-133.

Hickey CG. 1981. Preliminary Report: 1980 Field Season, Banks Island, N.W.T.: Investigation of the 19th Century Occupation of Banks Island by Copper Inuit. Report on file at the Canadian Museum of Civilization, Ottawa, Ontario.

Hickey CG. 1982. Archaeological and Historical Investigations of Nineteenth Century Copper Inuit Culture. Report on file at the Canadian Museum of Civilization, Ottawa, Ontario.

Hillson S. 2000. Teeth. Cambridge: Cambridge University Press.

Hobson KA, Clark RG. 1992. Assessing Avian Diets Using Stable Isotopes II: Factors Influencing the Diet-tissue Fractionation. Condor 94: 189-197.

Hobson KA, Sease J. 1998. Stable Isotope Analyses of Tooth Annuli Reveal Temporal Dietary Records: An Example Using Steller Sea Lions. Marine Mammal Science 14(1): 116-129.

Hodge A, Alexander IJ, Gooday GW. 1995. Chitinolytic Enzymes of Pathogenic and Ectomycorrhizal Fungi. Mycological Research 99: 935-941.

Hodgetts LM, Renouf MAP, Murray MS, McCuaig-Balkwill D, Howse L. 2003. Changing Subsistence Practices at the Dorset Paleoeskimo Site of Phillip's Garden, Newfoundland. Arctic Anthropology 40(1): 106-120.

Hodgetts L, Eastaugh E, Moody J. 2009. The Aulavik Archaeology Project Report on the 2008 Field Season. Report on file, Parks Canada Western and Northern Service Centre, Winnipeg, Manitoba.

Hodgetts LM, Eastaugh E. 2010. The Aulavik Archaeology Project. Report on the 2009 Field Season. Report on file, Parks Canada Western and Northern Service Centre, Winnipeg, Manitoba.

Hodgetts LM. 2013. Gendered Inuinnait (Copper Inuit) Landscapes of Banks Island's Northern Interior, Arctic Canada, 17^{th}-20^{th} Centuries A.D. Journal of Field Archaeology 38(1): 54-67.

Hodgetts L, Eastaugh E, Haukaas C, Kelvin L. 2013. The Ikaahuk Archaeology Project: Report On the 2013 Field Season. Report on file, Parks Canada Western and Northern Service Centre, Winnipeg, Manitoba.

Hoefs J. 2009. Stable Isotope Geochemistry, Sixth Edition. Berlin: Springer-Verlag.

Hofmann RR. 1989. Steps of Ecophysiological Adaptation and Diversification of Ruminants: A Comparative Overview of Their Digestive System. Oecologia 78(4): 443-457.

Hofmann D, Jung K, Bender J, Gehre M, Schüürmann G. 1997. Using Natural Isotope Variations of Nitrogen in Plants as an Early Indicator of Air Pollution Stress. Journal of Mass Spectrometry 32: 855-863.

Hofmann RR. 2000. Functional and Comparative Digestive System Anatomy of Arctic Ungulates. Rangifer 20(2-3): 71-81.

Högberg P. 1997. ^{15}N Natural Abundance in Soil-plant Systems. New Phytologist 137: 179-203.

Holechek JL, Valdez R. 1985. Magnification and Shrub Stemmy Material Influences on Fecal Analysis Accuracy. Journal of Range Management 38(4): 350-352.

Honch NV, McCullagh JSO, Hedges REM. 2012. Variation of Bone Collagen Amino Acid δ^{13}C Values in Archaeological Humans and Fauna with Different Dietary Regimes: Developing Frameworks of Dietary Discrimination. American Journal of Physical Anthropology 148: 495-511.

Hood BC. 1998. Theory on Ice: The Discourse of Eastern Canadian Arctic Paleo-Eskimo Archaeology. Acta Borealia: A Nordic Journal of Circumpolar Societies 15(2): 3-58.

Hoppe KA, Koch PL, Carlson RW, Webb SD. 1999. Tracking Mammoths and Mastodons: Reconstruction of Migratory Behavior Using Strontium Isotope Ratios. Geology 27(5): 439-442.

Horita J, Wesoloski DJ. 1994. Liquid-vapor Fractionation of Oxygen and Hydrogen Isotopes of Water from the Freezing to the Critical Temperature. Geochimica et Cosmochimica Acta 58(16): 3425-3437.

Hughes JM, Rakovan J. 2002. The Crystal Structure of Apatite, $Ca_5(PO_4)_3(F,OH,Cl)$. In: Kohn MJ, Rakovan J, Hughes JM, editors. Phosphates – Geochemical, Geobiological, and Materials Importance. Reviews in Mineralogy and Geochemistry 48. Chantilly: Mineralogical Society of America. Pp. 1-12.

Humphries P, Winemiller KO. 2009. Historical Impacts on River Fauna, Shifting Baselines, and Challenges for Restoration. BioScience 59(8): 673-684.

Hwang YT, Millar JS, Longstaffe FJ. 2007. Do δ^{15}N and δ^{13}C Values of Feces Reflect the Isotopic Composition of Diets in Small Mammals? Canadian Journal of Zoology 85: 388-396.

IAEA/WMO. 2017. Global Network of Isotopes in Precipitation. The GNIP Database. Available from: https://nucleus.iaea.org/wiser.

Irving WN. 1962. Field Work in the Western Brooks Range, Alaska: Preliminary Report. Arctic Anthropology 1(1): 76-83.

Jenness D. 1917. The Copper Eskimos. Geographical Review 4(2): 81-91.

Jenness D. 1923. Origin of the Copper Eskimos and Their Copper Culture. Geographical Review 13(4): 540-551.

Jia GJ, Epstein HE, Walker DA. 2009. Vegetation Greening in the Canadian Arctic Related to Decadal Warming. Journal of Environmental Monitoring 11: 2231-2238.

Judy C, Meiman JR, Friedman I. 1970. Deuterium Variations in an Annual Snowpack. Water Resources Research 6: 125-129.

Julien M-A, Bocherens H, Burke A, Drucker DG, Patou-Mathis M, Krotova O, Péan S. 2012. Were European Steppe Bison Migratory? ^{18}O, ^{13}C and Sr Intra-tooth Isotopic Variations Applied to a Palaeoethological Reconstruction. Quaternary International 271: 106-119.

Keeling CD, Mook WG, Tans PP. 1979. Recent Trends in the $^{13}C/^{12}C$ Ratio of Atmospheric Carbon Dioxide. Nature 277: 121-123.

Keeling CD, Bacastow RB, Carter AF, Piper SC, Whorf TP, Heimann M, Mook WG, Roeloffzer H. 1989. A Three-dimensional Model of Atmospheric CO_2 Transport Based on Observed Winds: 1. In: Peterson DH, editor. Analysis of Observational Data. American Geophysical Monograph 55: Washington, DC: American Geophysical Union. Pp. 165-236.

Kelvin LE. 2016. There Is More Than One Way to Do Something Right: Applying Community-Based Approaches to an Archaeology of Banks Island, NWT. [Dissertation]. [London (ON)]: University of Western Ontario.

Kielland K. 1994. Amino Acid Absorption by Arctic Plants: Implications for Plant Nutrition and Nitrogen Cycling. Ecology 75: 2373-2383.

Kielland K. 1995. Landscape Patterns of Free Amino Acids in Arctic Tundra Soils. Biogeochemistry 31: 85-98.

Koch PL. 1998. Isotopic Reconstruction of Past Continental Environments. Annual Review of Earth and Planetary Sciences 26: 573-613.

Koch PL. 2007. Isotopic Study of the Biology of Modern and Fossil Vertebrates. In: Michener R, Lajtha K, editors. Stable Isotopes in Ecology and Environmental Science. Malden: Blackwell. Pp. 99-154.

Kolodny Y, Luz B, Navon O. 1983. Oxygen Isotope Variations in Phosphate of Biogenic Apatites: I. Fish Bone Apatite-Rechecking the Rules of the Game. Earth and Planetary Science Letters 64: 398-404.

Kohn MJ, Schoeninger MJ, Barker WW. 1999. Altered States: Effects of Diagenesis on Fossil Tooth Chemistry. Geochimica et Cosmochimica Acta 63(18): 2737-2747.

Kohn MJ, Cerling TE. 2002. Stable Isotope Compositions of Biological Apatites. In: Kohn MJ, Rakovan J, Hughes JM, editors. Reviews in Mineralogy and Geochemistry 48: Phosphates. Geochemical, Geobiological, and Materials Importance. Washington, DC: Mineralogical Society of America. Pp. 455-488.

Körner C, Diemer M. 1987. In Situ Photosynthetic Responses to Light, Temperature and Carbon Dioxide in Herbaceous Plants from Low and High Altitude. Functional Ecology 1: 179-194.

Körner C, Farquhar GD, Roksandic Z. 1988. A Global Survey of Carbon Isotope Discrimination in Plants from High Altitude. Oecologia 74: 623-632.

Körner C, Farquhar GD, Wong SC. 1991. Carbon Isotope Discrimination by Plants Follows Latitudinal and Altitudinal Trends. Oecologia 88: 30-40.

Kristensen DK, Kristensen E, Forchhammer MC, Michelsen A, Schmidt NM. 2011. Arctic Herbivore Diet Can Be Inferred from Stable Carbon and Nitrogen Isotopes in C_3 Plants, Faeces, and Wool. Canadian Journal of Zoology 89: 892-899.

Krueger HW, Sullivan CH. 1984. Models for Carbon Isotope Fractionation Between Diet and Bone. In: Turnlund JR, Johnson PE, editors. ACS Symposium Series Number 258 Stable Isotopes in Nutrition. Pp. 205-220.

Lakeman TR, England JH. 2012. Paleoglaciological Insights from the Age and Morphology of the Jesse Moraine Belt, Western Canadian Arctic. Quaternary Science Reviews 47: 82-100.

Larter NC, Nagy JA. 1997. Peary Caribou and Banks Island Forage: Assessing Seasonal Diet Similarities. Rangifer 17(1): 9-16.

Larter NC, Nagy JA. 2001a. The Distribution of Forage Types Among Four Terrestrial Habitats on Southern Banks Island. Department of Resources, Wildlife & Economic Development, Government of the Northwest Territories, Manuscript Report Number 142. Northwest Territories: Inuvik.

Larter NC, Nagy JA. 2001b. Seasonal and Annual Variability in the Quality of Important Forage Plants on Banks Island, Canadian High Arctic. Applied Vegetation Science 4: 115-128.

Larter NC, Nagy JA. 2004. Seasonal Changes in the Composition of the Diets of Peary Caribou and Muskoxen on Banks Island. Polar Research 23(2): 131-140.

Leaney FW, Osmond CB, Allison GB, Ziegler H. 1985. Hydrogen-isotope Composition of Leaf Water in C_3 and C_4 Plants: its Relationship to the Hydrogen-isotope Composition of Dry Matter. Planta 164: 215-220.

Le Blanc RJ. 1994. The Crane Site and the Lagoon Complex in the Western Canadian Arctic. In: Morrison D, Pilon J-L, editors. Threads of Arctic Prehistory: Papers in Honour of William E. Taylor, Jr. Mercury Series, Archaeological Survey of Canada Paper 149. Quebec: Canadian Museum of Civilization. Pp. 87-101.

Lechler AR, Niemi NA. 2012. The Influence of Snow Sublimation on the Isotopic Composition of Spring and Surface Waters in the Southwestern United States: Implications for Stable Isotope-Based Paleoaltimetry and Hydrologic Studies. Geological Society of America Bulletin 124(3/4): 318-334.

Lécuyer C, Grandjean P, Emig CC. 1996. Determination of Oxygen Isotope Fractionation Between Water and Phosphate from Living Lingulids: Potential Application to Palaeoenvironmental Studies. Palaeogeography, Palaeoclimatology, Palaeoecology 126: 101-108.

LeGeros RZ. 1991. Calcium Phosphates in Oral Biology and Medicine, Volume 15. Paris: Karger Press.

Libby WF, Berger R, Mead J, Alexander G, Ross J. 1964. Replacement Rates for Human Tissue from Atmospheric Radiocarbon. Science 146: 1170-1172.

Lipson D, Näsholm T. 2001. The Unexpected Versatility of Plants: Organic Nitrogen Use and Availability in Terrestrial Ecosystems. Oecologia 128: 305-316.

Longinelli A, Nuti S. 1973. Revised Phosphate-water Isotopic Temperature Scale. Earth and Planetary Science Letters 19: 373-376.

Longinelli A. 1984. Oxygen Isotopes in Mammal Bone Phosphate: A New Tool for Paleohydrological and Paleoclimatological Research? Geochimica et Cosmochimica Acta 48: 385-390.

Lowenstam HA, Weiner S. 1989. On Biomineralization. New York: Oxford University Press.

Luz B, Kolodny Y, Horowitz M. 1984. Fractionation of Oxygen Isotopes Between Mammalian Bone-phosphate and Environmental Drinking Water. Geochimica et Cosmochimica Acta 48: 1689-1693.

Lyman RL. 2008. Estimating the Magnitude of Data Asymmetry in Palaeozoological Biogeography. International Journal of Osteoarchaeology 18: 85-94.

Mackay DK, Løken OH. 1974. Arctic Hydrology. In: Ives JD, Barry RG, editors. Arctic and Alpine Environments. London: Methuen. pp. 111-158.

Macko SA, Estep MLF, Hare PE, Hoering TC. 1982. Stable Nitrogen and Carbon Isotopic Composition of Individual Amino Acids Isolated from Cultured Microorganisms. Annual Report of the Director, Geophysical Laboratory, Carnegie Institution, Washington, 1981-1982. Pp. 404-410.

Macko SA, Fogel Estep ML, Engel MH, Hare PE. 1986. Kinetic Fractionation of Stable Nitrogen Isotopes During Amino Acid Transamination. Geochimica et Cosmochimica Acta 50: 2143-2146.

Macpherson D, Krause H. 1967. O^{18}/O^{16} Ratios in Snow and Ice of the Hubbard and Kaskawulsh Glaciers. In: Geophysical Monographs 11: Isotope Techniques in the Hydrologic Cycle. Washington D.C.: American Geophysical Union. pp. 180-194.

Maguas C, Brugnoli E. 1996. Spatial Variation in Carbon Isotope Discrimination Across the Thalli of Several Lichen Species. Plant, Cell and Environment 19: 437-446.

Manning TH, MacPherson AH. 1958. The Mammals of Banks Island. Arctic Institute of North America Technical Papers 2: 5-74.

Mason OK. 2009. "The Multiplication of Forms:" Bering Strait Harpoon Heads as a Demic and Macroevolutionary Proxy. In: Prentiss A, Kujit I, Chatters JC, editors. Macroevolution in Human Prehistory. New York: Springer. Pp. 73-107.

Maxwell MS. 1976. Pre-Dorset and Dorset Artifacts: The View from Lake Harbour. Memoirs of the Society for American Archaeology 31, Eastern Arctic Prehistory: Paleoeskimo Problems: 58-78.

Maxwell MS. 1984. Pre-Dorset and Dorset Prehistory of Canada. In: Handbook of North American Indians, Volume 5: Arctic. Damas D, editor. Washington: Smithsonian Institution. Pp. 359-368.

Maxwell MS. 1985. Prehistory of the Eastern Arctic. New York: Academic Press.

McAnally RA, Phillipson AT. 1944. Digestion in the Ruminant. Biological Reviews 19(2): 41-54.

McCartney AP. 1977. Thule Eskimo Prehistory Along North-western Hudson Bay. Mercury Series, Archaeological Survey of Canada Paper 70. Ottawa: Canadian Museum of Civilization.

McCartney PH. 1990. Palaeoeskimo Subsistence and Settlement in the High Arctic. [Dissertation]. [Calgary (AB)]: University of Calgary.

McGhee R. 1972. Climatic Change and the Development of Canadian Arctic Cultural Traditions. In: Vasari Y, Hyvärinen H, Hicks S, editors. Climatic Changes in Arctic Areas During the Last Ten-Thousand Years, A Symposium Held at Oulanka and Kevo, 4-10 October, 1971. Oulu: University of Oulu Press. Pp. 39-60.

McGhee R. 1976. Paleoeskimo Occupations of Central and High Arctic Canada. Memoirs of the Society for American Archaeology, No. 31, Eastern Arctic Prehistory: Paleoeskimo Problems: 15-39.

McGhee R. 1982. The Past Ten Years in Canadian Arctic Prehistory. Canadian Journal of Archaeology 6: 65-77.

McGhee R. 1984. Thule Prehistory of Canada. In: Damas D, editor. Handbook of North American Indians, Volume 5 Arctic. Washington, Smithsonian Institution Press. Pp. 369-376.

McGhee R. 1990. Canadian Arctic Prehistory. Gatineau: Canadian Museum of Civilization.

McGhee R. 1996. Ancient People of the Arctic. Gatineau: Canadian Museum of Civilization.

McKane RB, Johnson LC, Shaer GR, Nadelhoffer KJ, Rastetter EB, Fry B, Giblin AE, Kielland K, Kwiatkowski BL, Laundre JA, Murray G. 2002. Resource-based Niches Provide a basis for Plant Species Diversity and Dominance in Arctic Tundra. Nature 415: 68-71.

McKinney CR, McCrea JM, Epstein S, Allen HA, Urey HC. 1950. Improvements in Mass Spectrometers for the Measurement of Small Differences in Isotope Abundance Ratios. Review of Scientific Instruments 21: 724-730.

Melander L, Saunders WH. 1979. Reaction Rates of Isotopic Molecules. New York: John Wiley and Sons.

Metcalfe JZ, Longstaffe FJ, Ballenger JAM, Haynes Jr., CV. 2011. Isotopic Paleoecology of Clovis Mammoths from Arizona. Proceedings of the National Academy of Sciences 108(44): 17916-17920.

Metges C, Kempe K, Schmidt H-L. 1990. Dependence of the Carbon-isotope Contents of Breath Carbon Dioxide, Milk, Serum, and Rumen Fermentation Products on the δ^{13}C Value of Food in Dairy Cows. British Journal of Nutrition 63: 187-196.

Michelsen A, Quarmby C, Sleep D, Jonasson S. 1998. Vascular Plant ^{15}N Natural Abundance in Heath and Forest Tundra Ecosystems is Closely Correlated with Presence and Type of Mycorrhizal Fungi in Roots. Oecologia 115: 406-418.

Miller FL. 1990. Inter-island Movements of Peary Caribou: A Review and Appraisement of Their Ecological Importance. In: Harington CR, editor. Canada's Missing Dimension: Science and History in the Canadian Arctic Islands. Ottawa: Canadian Museum of Nature. Pp. 608-632.

Miller FL, Barry SJ, Calvert WA. 2005. Sea-ice Crossings by Caribou in the South-central Canadian Arctic Archipelago and their Ecological Importance. Rangifer 16: 77-88.

Milne SB, Park RW, Stenton DR. 2012. Dorset Culture Land Use Strategies and the Case of Inland Southern Baffin Island. Canadian Journal of Archaeology 36: 267-288.

Minagawa M, Wada E. 1984. Stepwise Enrichment of ^{15}N Along Food Chains: Further Evidence and the Relation Between $\delta^{15}N$ and Animal Age. Geochimica et Cosmochimica Acta 48: 1135-1140.

Mitchell HH, Hamilton TS, Haines WT. 1940. The Utilization by Calves of Energy in Rations Containing Different Percentages of Protein and Glucose Supplements. Journal of Agricultural Research 61: 847-861.

Monson KD, Hayes JM. 1982. Carbon Isotopic Fractionation in the Biosynthesis of Bacterial Fatty Acids. Ozonolysis of Unsaturated Fatty Acids as a Means of Determining the Intramolecular Distribution of Carbon Isotopes. Geochimica et Cosmochimica Acta 46: 139-149.

Müller-Beck H. 1977a. Excavations at Umingmak on Banks Island, N.W.T., 1970 and 1973: Preliminary Report. Urgeschichtliche Materialhefte 1: 174 pages.

Müller-Beck H. 1977b. The Excavation at Umingmak, Banks Island 1970 & 1973. In: Müller-Beck H, editor. Excavations at Umingmak on Banks Island, N.W.T., 1970 and 1973: Preliminary Report. Urgeschichtliche Materialhefte 1. Pp. 1-6.

Münzel S. 1987. Umingmak: ein Muschusochsenjagdplatz auf Banks Island, N.W.T., Canada. Archäozoologische Auswertung des Areals ID. Urgeschichtliche Materialhefte 5(2): 188 pages.

Nadelhoffer G, Shaver G, Fry B, Giblin A, Johnson L, McKane R. 1996. ^{15}N Natural Abundances and N Use by Tundra Plants. Oecologia 107(3): 386-394.

Nagy M. 1999. Aulavik Oral History Project on Banks Island, NWT: Final Report. Prepared for Inuvialuit Social Development Program.

Nagy M. 2004. 'We Did Not Want the Muskox to Increase': Inuvialuit Knowledge About Muskox and Caribou Populations on Banks Island, Canada. In: In: Anderson DG, Nuttall M, editors. Cultivating Arctic Landscapes: Knowing and Managing Animals in the Circumpolar North. New York: Berghahn Books. Pp. 93-109.

Nagy JA, Gunn A, Wright WH. 2009. Population Estimates for Peary Caribou and Muskox on Banks Island, NT, July 2005. Report on file at Canadian Wildlife Service, Yellowknife, Northwest Territories.

Najafi MR, Zweirs FW, Gillett NP. 2015. Attribution of Arctic Temperature Change to Greenhouse-gas and Aerosol Influences. Nature Climate Change 5: 246-249.

Oakes EJ, Harmsen R. 1992. Sex, Age, and Seasonal Differences in the Diets and Activity Budgets of Muskoxen (*Ovibos moschatus*). Canadian Journal of Zoology 70: 605-616.

O'Leary MH. 1981. Carbon Isotope Fractionation in Plants. Phytochemistry 20(4): 553-567.

Ortner DJ. 2003. Identification of Pathological Conditions in Human Skeletal Remains. Cambridge: Academic Press.

Osborne CP, Beerling DJ. 2006. Nature's Green Revolution: The Remarkable Evolutionary Rise of C_4 Plants. Philosophical Transactions of the Royal Society B: The Biological Sciences 361(1465): 173-194.

Ostle NJ, Bol R, Petzke KJ, Jarvis SC. 1999. Compound Specific δ^{15}N‰ Values: Amino Acids in Grassland and Arable Soils. Soil Biology and Biochemistry 31: 1751-1755.

Park R, Epstein S. 1960. Carbon Isotope Fractionation During Photosynthesis. Geochimica et Cosmochimica Acta 21: 110-126.

Park RW. 1993. The Dorset-Thule Succession in Arctic North America: Assessing Claims for Cultural Contact. American Antiquity 58(2): 203-234.

Park RW. 2014. Stories of Arctic Colonization. Science 345(6200): 1004-1005.

Passey BH, Cerling TE, Schuster GT, Robinson TF, Roeder BL, Krueger SK. 2005. Inverse Methods for Estimating Primary Input Signals from Time-averaged Isotope Profiles. Geochimica et Cosmochimica Acta 69(16): 4101-4116.

Pate FD. 1994. Bone Chemistry and Paleodiet. Journal of Archaeological Method and Theory 1(2): 161-209.

Pellegrini M, Donahue RE, Chenery C, Evans J, Lee-Thorp J, Montgomery J, Mussi M. 2008. Faunal Migration in Late-glacial Central Italy: Implications for Human Resource Exploitation. Rapid Communications in Mass Spectrometry 22: 1714-1726.

Penel G, Leroy G, Rey C, Bres E. 1998. MicroRaman Spectral Study of the PO4 and CO3 Vibrational Modes in Synthetic and Biological Apatites. Calcified Tissue International 63: 475-481.

Peterson BJ, Fry B. 1987. Stable Isotopes in Ecosystem Studies. Annual Review of Ecology and Systematics 18: 293-320.

Pilaar Birch SE, Miracle PT, Stevens RE, O'Connell TC. 2016. Late Pleistocene/Early Holocene Migratory Behavior of Ungulates Using Isotopic Analysis of Tooth Enamel and Its Effects on Forager Mobility. PLoS ONE 11(6): e0155714.

Raggatt LJ, Partridge NC. 2010. Cellular and Molecular Mechanisms of Bone Remodeling. Journal of Biological Chemistry 285(33): 25103-25108.

Raghavan M, DeGiorgio M, Albrectsen A, Moltke I, Skoglund P, Korneliussen TS, Gronnow B, Appelt M, Gullov HC, Friesen TM, Fitzhugh W, Malmstrom H, Rasmussen S, Olsen J, Melchior L, and 41 others. The Genetic Prehistory of the New World Arctic. Science 345(6200): 1020-1031.

Renouf MAP. 2011. Introduction: Archaeology at Port au Choix. In: Renouf MAP, editor. The Cultural Landscapes of Port au Choix: Precontact Hunter-Gatherers of Northwestern Newfoundland. New York: Springer. Pp. 1-20.

Reynolds PE. 1998. Dynamics and Range Expansion of a Reestablished Muskox Population. The Journal of Wildlife Management 62(2): 734-744.

Rick TC, Lockwood R. 2013. Integrating Paleobiology, Archeology, and History to Inform Biological Conservation. Conservation Biology 27(1): 45-54.

Robbins CT, Felicetti LA, Florin ST. 2010. The Impact of Protein Quality on Stable Nitrogen Isotope Ratio Discrimination and Assimilated Diet Estimation. Oecologia 162: 571-579.

Rozanski K, Froehlich K, Mook WG. 2001. Surface Water. In: Mook WG, editor. Environmental Isotopes in the Hydrological Cycle: Principles and Applications. International Hydrological Programme Technical Documents in Hydrology 39, Volume 3.

Savelle JM, Dyke AS. 2002. Variability in Paleoeskimo Occupation on South-western Victoria Island, Arctic Canada: Causes and Consequences. World Archaeology 33(3): 508-522.

Savelle JM, Dyke AS. 2009. Paleoeskimo Demography on Western Boothia Peninsula, Arctic Canada. Journal of Field Archaeology 34: 267-283.

Savelle JM, Dyke AS, Whitridge PJ, Poupart M. 2012. Paleoeskimo Demography on Western Victoria Island, Arctic Canada: Implications for Social Organization and Longhouse Development. Arctic 65(2): 167-181.

Savelle JM, Dyke AS. 2014. Paleoeskimo Occupation History of Foxe Basin, Arctic Canada: Implications for the Core Area Model and Dorset Origins. American Antiquity 79(2): 249-276.

Schimel JP, Chapin FS, III. 1996. Tundra Plant Uptake of Amino Acid and NH_4^+ Nitrogen in Situ: Plants Compete Well for Amino Acid N. Ecology 77(7): 2142-2147.

Schledermann P. 1979. The “Baleen Period” of the Arctic Whale Hunting Tradition. In: McCartney AP, editor. Thule Eskimo Culture: An Anthropological Retrospective. Mercury Series, Archaeological Survey of Canada Paper 88. Quebec: Canadian Museum of Civilization. Pp. 134-148.

Schulze E-D, Chapin FS III, Gebauer G. 1994. Nitrogen Nutrition and Isotope Differences Among Life Forms at the Northern Treeline of Alaska. Oecologia 100(4): 406-412.

Schwarcz HP. 2000. Some Biochemical Aspects of Carbon Isotopic Paleodiet Studies. In: In: Ambrose SH, Katzenberg MA, editors. Biogeochemical Approaches to Paleodietary Analysis. New York: Kluwer Academic/Plenum Publishers. Pp. 189-209.

Sealy JC, van der Merwe NJ, Lee Thorp JA, Lanham JL. 1987. Nitrogen Isotopic Ecology in Southern Africa: Implications for Environmental and Dietary Tracing. Geochimica et Cosmochimica Acta 51: 2707-2717.

Shank CC, Barr W, Arnold CD. 1994. Muskox Hunting Sites on Northern Banks Island – Resolving the Contradictions. Unpublished manuscript on file at Prince of Wales Northern Heritage Centre, Yellowknife, Northwest Territories.

Sharp Z. 2007. Principles of Stable Isotope Geochemistry. New Jersey: Pearson Prentice Hall.

Shaver GR, Chapin, FS III. 1980. Response to Fertilization by Various Plant Growth Forms in an Alaskan Tundra: Nutrient Accumulation and Growth. Ecology 61: 662-675.

Shaver GR, Chapin, FS III. 1995. Long-term Responses to Factorial, NPK Fertilizer Treatment by Alaskan Wet and Moist Tundra Sedge Species. Ecography 18(3): 259-275.

Silverman DN. 1982. Carbonic Anhydrase: Oxygen-18 Exchange Catalyzed by an Enzyme with Rate-contributing Proton-transfer Steps. Methods in Enzymology 87: 732-752.

Skead F. 1849-1854. Private Journal, H.M. Ship Enterprise. SPRI MS. 1161 D.

Sparks JP, Ehleringer JR. 1997. Leaf Carbon Isotope Discrimination and Nitrogen Content for Riparian Trees Along Elevational Transects. Oecologia 109: 362-367.

Sponheimer M, Robinson T, Ayliffe L, Roeder B, Hammer J, Passey B, West A, Cerling T, Dearing D, Ehleringer J. 2003a. Nitrogen Isotopes in Mammalian Herbivores: Hair δ^{15}N Values from a Controlled Feeding Study. International Journal of Osteoarchaeology 13: 80-87.

Sponheimer M, Robinson TF, Roeder BL, Passey BH, Ayliffe LK, Cerling TE, Dearing MD, Ehleringer JR. 2003b. An Experimental Study of Nitrogen Flux in Llamas: is ^{14}N Preferentially Excreted? Journal of Archaeological Science 30(12): 1649-1655.

Steckley JL. 2008. White Lies About the Inuit. Ontario: Broadview Press.

Stefansson V. 1913. My Life with the Eskimo. New York: Collier Books.

Stefansson V. 1921. The Friendly Arctic: The Story of Five Years in Polar Regions. New York: The MacMillan Company.

Stevenson M. 1993. Supplement to Man and Muskox: Human-Land Relationships on Banks Island, Northwest Territories, Archaeological Sites on Banks Island with Reference to Aulavik National Park. Report on file at the Parks Canada Western Service Centre, Winnipeg, Manitoba.

Sullivan CH, Krueger HW. 1981. Carbon Isotope Analysis of Separate Chemical Phases in Modern and Fossil Bone. Nature 292: 333-335.

Szabó P, Hédl R. 2011. Advancing the Integration of History and Ecology for Conservation. Environmental Conservation 37: 380-387.

Szpak P, White CD, Longstaffe FJ, Milliare J-F, Vásquez Sánchez VF. 2013. Carbon and Nitrogen Isotopic Survey of Northern Peruvian Plants: Baselines for Paleodietary and Paleoecological Studies. PLoS One 8(1): 1-28.

Tans PP, DeJong AFM, Mook WG. 1979. Natural Atmospheric ^{14}C Variation and the Suess Effect. Nature 280: 826-828.

Taylor WE. 1967. Summary of Archaeological Field Work on Banks and Victoria Islands, Arctic Canada, 1965. Arctic Anthropology 4(1): 221-243.

Teeri JA, Stowe LG. 1976. Climatic Patterns and the Distribution of C_4 Grasses in North America. Oecologia 23: 1-12.

Tieszen LL, Boutton TW, Tesdahl KG, Slade NA. 1983. Fractionation and Turnover of Stable Carbon Isotopes in Animal Tissues: Implications for $\delta^{13}C$ Analysis of Diet. Oecologia 57: 32-37.

Tieszen LL, Fagre T. 1993. Effect of Diet Quality and Composition on the Isotopic of Respiratory CO_2, Bone Collagen, Bioapatite, and Soft Tissues. In: Lambert JB, Grupe G, editors. Prehistoric Human Bone: Archaeology at the Molecular Level. Berlin: Springer-Verlag. Pp. 121-156.

Tyler NJC. 2010. Climate, Snow, Ice, Crashes, and Declines in Populations of Reindeer and Caribou (*Rangifer tarandus L.*). Ecological Monographs 80(2): 197-219.

Usher PJ. 1965. Banks Island: An Area Economic Survey. Report on file at Industrial Division, Department of Northern Affairs and National Resources, Ottawa, Ontario.

van Cleve K, Alexander V. 1981. Nitrogen Cycling in Tundra and Boreal Ecosystems. In: Clark FE, Rosswall T, editors. Terrestrial Nitrogen Cycles. Ecological Bulletins 33: Stockholm: Swedish Natural Science Research Council. Pp. 375-404.

van Cleve K, Chapin FS III, Dyrness CT, Viereck LA. 1991. Element Cycling in Taiga Forests: State-factor Control. BioScience 41(2): 78-88.

van der Merwe NJ, Vogel JC. 1978. ^{13}C Content of Human Collagen as a Measure of Prehistoric Diet in Woodland North America. Nature 276: 815-816.

van der Merwe NJ. 1989. Natural Variation in ^{13}C Concentration and Its Effect on Environmental Reconstruction Using $^{13}C/^{12}C$ Ratios in Animal Bones. In: Price TD, editor. The Chemistry of Prehistoric Human Bone. Cambridge: Cambridge University Press. Pp. 105-125.

van der Merwe NJ, Medina E. 1989. Photosynthesis and $^{13}C/^{12}C$ Ratios in Amazonian Rain Forests. Geochimica et Cosmochimica Acta 53: 1091-1094.

van Klinken GJ. 1999. Bone Collagen Quality Indicators for Palaeodietary and Radiocarbon Measurements. Journal of Archaeological Science 26: 687-695.

Van Soest PJ. 1963. Use of Detergents in the Analysis of Fibrous Feeds. II. A Rapid Method for the Determination of Fiber and Lignin. Journal of the Association of Official Agricultural Chemists 46(5): 829-835.

Veis A. 2003. Mineralization in Organic Matrix Frameworks. In: Dove PM, De Yoreo JJ, Weiner S, editors. Reviews in Mineralogy and Geochemistry 54: Biomineralization. Washington, DC: Mineralogical Society of America. Pp. 249-289.

Vincent D, Gunn A. 1981. Population Increase of Muskoxen on Banks Island and Implications for Competition with Peary Caribou. Arctic 34(2): 175-179.

Vincent WF, Hobbie JE. 2000. Ecology of Arctic Lakes and Rivers. In: Nuttall M, Callaghan TV, editors. The Arctic: Environment, People, Policy. Amsterdam: Harwood Academic Publishers. Pp. 197-232.

Virginia RA, Delwiche CC. 1982. Natural 15N Abundance of Presumed N_2-Fixing and Non-N_2-Fixing Plants from Selected Ecosystems. Oecologia 54(3): 317-325.

Vitousek PM, Field CB, Matson PA. 1990. Variation in Foliar $\delta^{13}C$ in Hawaiian *Metrosideros polymorpha*: A Case of Internal Resistance? Oecologia 84: 362-370.

Vitousek PM, Cassman K, Cleveland C, Crews T, Field CB, Grimm NB, Howarth RW, Marino R, Martinelli L, Rastetter EB, Sprent JI. 2002. Towards an Ecological Understanding of Biological Nitrogen Fixation. Biogeochemistry 57/58: 1-45.

Vogel JC. 1978. Recycling of CO_2 in a Forest Environment. Oecologia Plantarum 13: 89-94.

Walker MD, Wahren CH, Hollister RD, Henry GHR, Ahlquist LE, Alatalo JM, Bret-Harte MS, Calef MP, Callaghan TV, Carroll AB, Epstein HE, Jónsdóttir IS, Klein JA, Magnússon B, Molau U, and 12 others. 2006. Plant Community Responses to Experimental Warming Across the Tundra Biome. Proceedings of the National Academy of Sciences 103(5): 1342-1346.

Wang Y, Cerling TE. 1994. A Model of Fossil Tooth and Bone Diagenesis: Implications for Paleodiet Reconstruction from Stable Isotopes. Palaeogeography, Palaeoclimatology, Palaeoecology 107: 281-289.

Wells PJ. 2011. Ritual Activity and the Formation of Faunal Assemblages at Two Groswater Palaeoeskimo Sites at Port au Choix. In: Renouf MAP, editor. The Cultural Landscapes of Port au Choix: Precontact Hunter-Gatherers of Northwestern Newfoundland. New York: Springer. Pp. 65-90.

Werner RA, Schmidt H-L. 2002. The In Vivo Nitrogen Isotope Discrimination Among Organic Plant Compounds. Phytochemistry 61: 465-484.

Wershaw RL, Friedman I, Heller SJ. 1966. Hydrogen Isotope Fractionation of Water Passing Through Trees. In: Hobson F, Speers M, editors. Advances in Organic Geochemistry. New York: Pergamon. Pp. 55-67.

White JWC, Cook ER, Lawrence JR, Broecker WS. 1985. The D/H Ratios of Sap in Trees: Implications for Water Sources and Tree Ring D/H Ratios. Geochimica et Cosmochimica Acta 49: 237-246.

Wilkinson PF, Shank CC. 1975. Archaeological Observations in North Central Banks Island. Arctic Anthropology 12(1): 104-112.

Will RT. 1985. Nineteenth Century Copper Inuit Subsistence Practices on Banks Island, N.W.T. [Dissertation]. [Edmonton (AB)]: University of Alberta.

Wilmeth R. 1978. Canadian Archaeological Radiocarbon Dates (Revised Edition). Mercury Series, Archaeological Survey of Canada Paper 77. Quebec: Canadian Museum of Civilization.

Wolf N, Carleton SA, Martinez del Rio C. 2009. Ten Years of Experimental Animal Isotopic Ecology. Functional Ecology 23: 17-26.

Wolverton S, Lyman RL. 2012. Introduction to Applied Zooarchaeology. In: Wolverton S, Lyman RL, editors. Conservation Biology and Applied Zooarchaeology. Tucson: University of Arizona Press. Pp. 1-22.

Wright LE, Schwarcz HP. 1998. Stable Carbon and Oxygen Isotopes in Human Tooth Enamel: Identifying Breastfeeding and Weaning in Prehistory. American Journal of Physical Anthropology 106: 1-18.

Wright LE, Schwarcz HP. 1999. Correspondence Between Stable Carbon, Oxygen and Nitrogen Isotopes in Human Tooth Enamel and Dentine: Infant Diets at Kaminaljuyú. Journal of Archaeological Science 26: 1159-1170.

Yakir D, DeNiro MJ, Gat JR. 1990. Natural Deuterium and Oxygen-18 Enrichment in Leaf Water of Cotton Plants Grown Under Wet and Dry Conditions: Evidence for Water Compartmentation and Its Dynamics. Plant, Cell, and Environment 13: 49-56.

Yakir D, da Silveira Lobo Sternberg L. 2000. The Use of Stable Isotopes to Study Ecosystem Gas Exchange. Oecologia 123(3): 297-311.

Yakir D. 2011. The Paper Trail of the ^{13}C of Atmospheric CO_2 Since the Industrial Revolution Period. Environmental Research Letters 6: 1-4.

Young RA. 1975. Biological Apatite vs. Hydroxyapatite at the Atomic Level. Clinical Orthopaedics and Related Research 113: 249-262.

Yurtsever Y, Gat JR. 1981. Atmospheric Waters. In: Stable Isotope Hydrology, Deuterium and Oxygen-18 in the Water Cycle. IAEA Technical Reports Series 210. Vienna: IAEA. Pp. 103-142.

Zahran HH. 1999. *Rhizobium*-legume Symbiosis and Nitrogen Fixation Under Severe Conditions and in an Arid Climate. Microbiology and Molecular Biology Reviews 63(4): 968-989.

Zazzo A, Balasse M, Patterson WP. 2005. High-resolution δ^{13}C Intratooth Profiles in Bovine Enamel: Implications for Mineralization Pattern and Isotopic Attenuation. Geochimica et Cosmochimica Acta 69(14): 3631-3642.

Zazzo A, Balasse M, Patterson WP. 2006. The Reconstruction of Mammal Individual History: Refining High-resolution Isotope Record in Bovine Tooth Dentine. Journal of Archaeological Science 33: 1177-1187.

Zhu Y, Siegwolf RTW, Durka W, Körner C. 2010. Phylogenetically Balanced Evidence for Structural and Carbon Isotope Responses in Plants Along Elevational Gradients. Oecologia 162: 853-863.

Chapter 2

2 Do Caribou (*Rangifer tarandus* spp.) and Muskoxen (*Ovibos moschatus*) Utilize the Same Forage Sources? An Isotopic Approach to an Ecological Question on Banks Island, NWT, Canada

In this chapter, we investigate average and seasonal dietary compositions of modern caribou (*Rangifer tarandus* spp.) and muskoxen (*Ovibos moschatus*) on Banks Island, NWT, Canada. We use Bayesian mixing models to evaluate the contribution of different forage items to the $\delta^{13}C$ and $\delta^{15}N$ of bulk bone collagen. Then, we investigate seasonal dietary variation using sequentially-sampled crown dentin collagen $\delta^{13}C$ and $\delta^{15}N$. Contrary to previous ideas, the dietary mixing models suggest that yellow lichen (*Cetraria tilesii*), sedges (*Cyperaceae* spp.), and forbs (*Astragalus alpinus, Oxytropis* spp., *Saxifraga* spp.) are dominant forage items for both caribou and muskoxen. Shrubs like dwarf willow (*Salix arctica*) do not appear to contribute significantly to bone collagen isotopic compositions. Dentin collagen $\delta^{13}C$ ($\delta^{13}C_{dc}$) in both species suggests that dietary overlap does occur in winter, probably in the consumption of yellow lichen and sedge. Conversely, dentin collagen $\delta^{15}N$ ($\delta^{15}N_{dc}$) in both species reflects differences in the duration of nursing. Caribou $\delta^{15}N_{dc}$ indicates that the individuals whose teeth we sampled weaned within the first year of life, in line with existing research on caribou weaning times. Muskox $\delta^{15}N_{dc}$, however, suggests that the individuals whose teeth we sampled continued to nurse into at least the second year of life, which is longer than expected. This may reflect recent reductions in the fecundity of the Banks Island muskox population. Overall, the high degree of apparent lichen consumption by both caribou and muskoxen may negatively affect the winter survivability of both species in the future, which could have significant impacts on the health and economy of people living on Banks Island.

2.1 Introduction

Analysis of rumen and fecal content indicates dietary overlap and the potential for forage competition between caribou (*Rangifer tarandus* spp.) and muskoxen (*Ovibos moschatus*) on Banks Island, NWT, Canada. Our primary purpose in this paper is to further investigate

dietary similarities between caribou and muskoxen on Banks Island using the stable carbon and nitrogen isotope compositions of bone and crown dentin collagen. Because hard tissue isotopic compositions reflect assimilated dietary items, this research complements fecal and rumen content data, which may be biased towards undigested forage. As a secondary benefit, the creation of modern isotopic baselines for caribou and muskoxen allows us to make more nuanced interpretations about archaeological caribou and muskox ecology and its potential impact on the past inhabitants of Banks Island (discussed in Chapter 3).

Banks Island, located in the Northwest Territories of Canada (Figure 2.1) is unique within the Canadian Arctic Archipelago in that it is inhabited by substantial portions of the global muskox and Peary caribou populations. Additionally, barren-ground and Dolphin-Union caribou (*R. tarandus groenlandicus*) occasionally migrate to Banks Island (Manning and MacPherson 1958; Manning 1960; McGhee 1996)[5]. Because of their significance to Indigenous heritage and identity, northern economies, and Arctic biodiversity, both species are of considerable interest to the Inuvialuit (the Inuit Peoples of the Northwest Territories and the Northern Yukon) and wildlife biologists. Arctic archaeologists also recognize long-standing relationships among caribou, muskoxen, and humans and are interested in how their interactions shaped the archaeological record of the North American Arctic.

[5]To account for possible admixture of caribou subspecies on Banks Island, we use the generalized taxonomic identifiers "*Rangifer tarandus* spp." and "caribou" in this paper, unless referring to studies specific to Peary caribou.

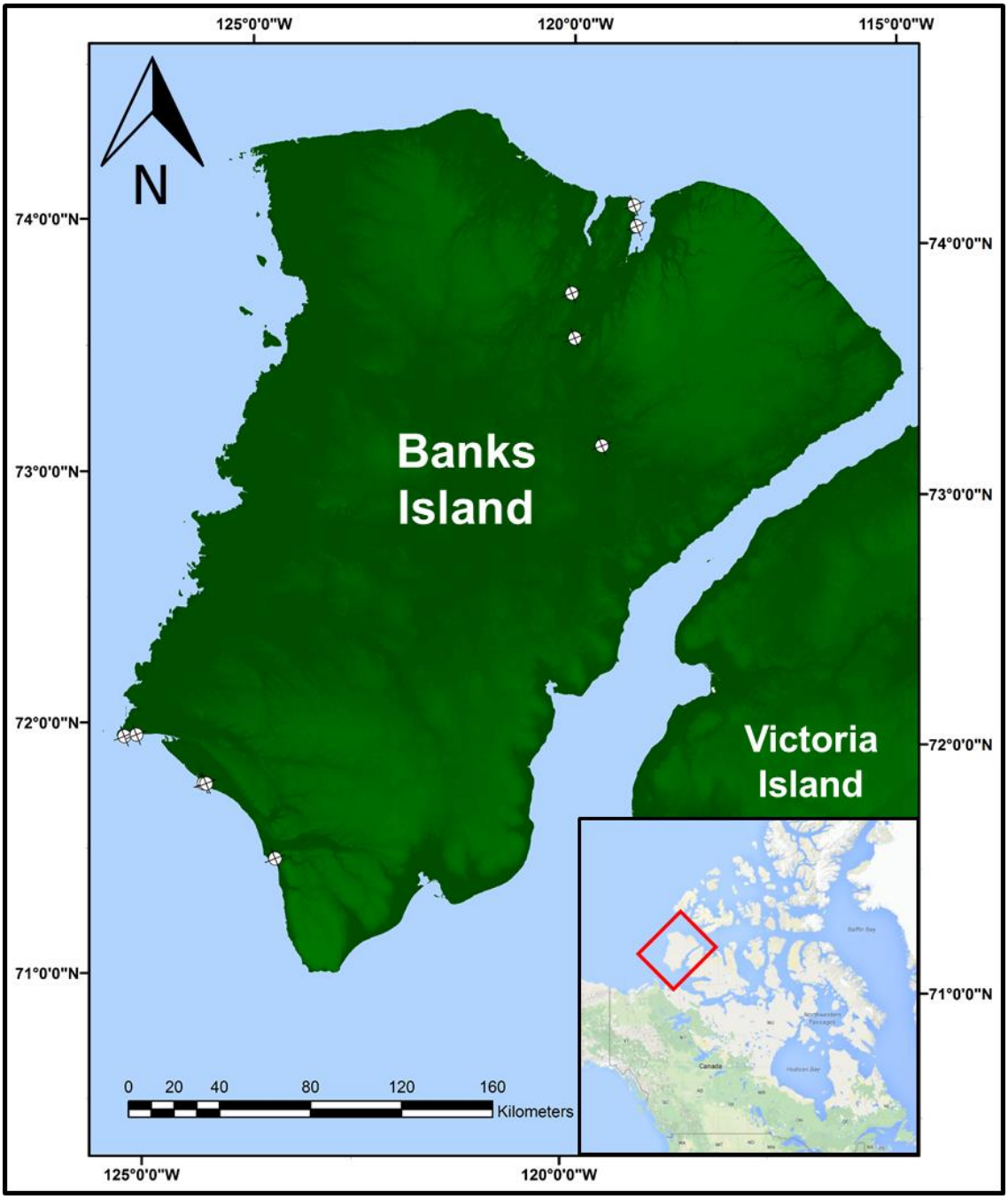


Figure 2.1. Locations of forage sample collection sites on Banks Island (white circles) and the location of Banks Island within North America (inset). Exact coordinates and elevations of each sampling site are listed in Table 2.5.

Traditional ecological knowledge (Nagy 1999; Kelvin 2016) and demographic studies (Latour 1987; Gunn et al. 1991; Jenkins et al. 2011) indicate that the caribou and muskox populations of Banks Island undergo opposing cycles of growth and decline, where the muskox population experiences an explosive increase (i.e. "booms") followed by a rapid decline in size (i.e. "busts"). During muskox population "booms", the caribou population size is depressed, but appears to increase simultaneously with muskox "busts". In some cases, catastrophic "busts" in the muskox population are clearly the result of mass starvations due to heavy snow or ice crusts that make forage[6] inaccessible (Gunn 1991; Larter and Nagy 1997; Grayhound Information Services 1997). However, there are also longstanding questions about the role of forage competition in caribou and muskox demographic cycles on Banks Island. Some people in Sachs Harbour believe that muskoxen outcompete caribou for forage either directly, or by driving them away with their scent (Nagy 1999), and these ideas are also shared by some members of Tetlit Gwich'in First Nation in Fort McPherson (Wishart 2004). Field observations (Gray 1973; Wilkinson et al. 1976; Hickey 1982) also suggest that caribou generally avoid muskoxen on Banks Island, potentially because of antagonistic behaviors (i.e. gland rubbing, stamping) directed towards the caribou (Gray 1973). It is conceivable then, that during winter when forage availability is limited and travel is metabolically costly, large numbers of muskoxen occupying feeding areas impart nutritional disadvantages on caribou simply by their presence.

2.1.1 Caribou and Muskox Dietary Ecology

Though caribou and muskoxen are adapted to distinct forage types (Hofmann 2000), both species are relatively flexible in their nutritional requirements, and their diets depend largely on forage available at individual locations. However, research offers conflicting evidence for forage competition between caribou and muskoxen. Gunn et al. (1991)

[6]We use the term "forage" to refer to all photosynthetic vegetation potentially consumed by caribou and muskoxen on Banks Island, including vascular plants, mosses (non-vascular plants), and lichens (organisms composed of symbiotic fungi and algae or cyanobacteria).

suggest that the different physiological adaptations of muskoxen and caribou probably prevent the two species from utilizing the same forage types. Conversely, fecal and rumen content analyses (see below) suggests considerable seasonal overlap in the diets of both species on Banks Island (Larter and Nagy 1997, 2004). Here, we review current research on caribou and muskox diet on Banks Island in greater detail.

Ruminant species are commonly differentiated by their stomach anatomies and dietary preferences. In the simplest terms, browsers are classified as those ruminants who rely on concentrated diets of leaves and inflorescences from herbaceous dicots such as forbs and shrubs, and are characterized by small, simple stomach chambers (Hofmann and Stewart 1972; Gordon and Illius 1994). Grazers are classified as those ruminants that rely on a bulk diet primarily composed of grasses, and are characterized by larger, more complex stomach chambers (Gordon and Illius 1994). Intermediate feeders are those ruminants that rely on a mixture of both browse and graze.

As a species, caribou are often classified as intermediate feeders that nevertheless require feed with high nutritional content and limited fiber (Hofmann 1989). In summer, when forage plants are still metabolically active, caribou feed almost exclusively on the aerial organs of vascular plants (e.g. shoots, flowers, catkins), and avoiding stems and grasses. In winter, when vascular plants enter dormancy and above-ground phytomass lignifies, caribou transition to a diet composed largely of sedges and graminoids with lower lignin content (Hofmann 1989, 2000). Barren-ground caribou (*Rangifer tarandus groenlandicus*) migrate extensively to exploit different food resources in summer and winter, while other subspecies of *Rangifer*, such as Peary caribou on Banks Island are less wide-ranging and have limited feeding options during winter.

Unlike for muskoxen, there are few studies of dietary variation by age and sex in caribou, and no published studies exist for caribou on Banks Island. Analysis of rumen content in Peary caribou on Banks Island (Shank et al. 1978) indicated that sedges (*Carex* spp., *Eriophorum* spp.) and other grasses (*Gramineae* spp.) accounted for 50-70% of rumen content throughout the year, with highest percentages during the early and late winter. Forbs, particularly *Astragalus alpinus*, accounted for only ~ 15% of rumen content, except

in late November, when proportions of *Astragalus alpinus* and *Dryas integrifolia* both increased (Shank et al. 1978). Studies of fecal pellet content in Peary caribou on Banks Island by Larter and Nagy (1997, 2004) suggested somewhat different dietary compositions. Dwarf willow (*Salix arctica*) comprised approximately sixty percent of feces content during summer, with sedges, legumes (*Astragalus alpinus, Oxytropis* spp.) and non-leguminous forbs making up the remaining forty percent. In winter, willow tissue content in feces decreased, and the proportions of legumes and saxifrages increased. Averaged across all months, sedges accounted for approximately 25% of fecal content. Larter and Nagy (1997) suggest that lichen intake by Peary caribou on Banks Island is minimal due to its limited availability. Personal observations in 2014, however, suggest that yellow lichen (*Cetraria tilesii*) is abundant in both the northern and southern parts of the island. Further, Trevor Lucas, one of our research partners in Sachs Harbour, and a professional hunting guide on Banks Island suggests that caribou consume yellow lichen in abundance throughout the year (Trevor Lucas 2014, personal communication).

Forchhammer et al. (2002) classify muskoxen as generalist browsers, though Hofmann (2000:72,78) stated previously that the digestive system of muskoxen "developed in accordance with that of a typical grazer or roughage feeder" and the species is "equipped with a very robust [grazer] digestive system". Like most grazers, muskoxen have large, complex gastrointestinal tracts that allow them to extract energy from large volumes of high fiber, high protein forage. Oakes et al. (1992) matched feces to individual muskoxen on Banks Island, and were therefore able to differentiate fecal samples by age and sex. Contrary to the results of Larter and Nagy (1997) discussed below, Oakes et al. (1992) found that shrub (*Salix arctica, Dryas integrifolia*) content in muskox feces was relatively low regardless of age or sex. Oakes et al. (1992) also found that adult female muskoxen had significantly greater proportions of forbs in their feces than adult males, who had significantly greater proportion of sedges and rushes in their feces than adult females. The feces of yearlings contained significantly greater proportions of shrubs than subadults and adults of either sex (Oakes et al. 1992:610). When all non-adults were pooled, they had a significantly greater proportion of shrub leaves (as opposed to other parts) in their feces than adults of both sexes (Oakes et al. 1992:610).

Larter and Nagy (1997, 2004) found that across months, sedges comprised about 30-50% of fecal content, while dwarf willow accounted for the remaining ~ 40%. In agreement with Oakes et al. (1992), Larter and Nagy (1997) also found that sedges and grasses accounted for most of the adult male diet, while sedges and forbs dominated the diet in non-lactating adult females, subadults, and calves. Contrary to nutritional expectations, the diets of lactating adult females were similar to adult males, with sedges and grasses making up the majority of their diets. Yearlings primarily consumed forbs and grasses, though they also consumed the most shrubs of any group.

Based on the available data, there is clearly potential for dietary overlap between caribou and muskoxen, particularly in the consumption of sedges and dwarf willow. Although sedges are abundant on Banks Island (Larter and Nagy 2001a), Larter and Nagy (1997) also noted that as winters on Banks Island have become warmer, snowfall and thaw/refreeze events both increased. In low, wet areas where sedges are abundant, ice crusts formed from refrozen snowmelt can limit access to vegetation, potentially forcing muskoxen onto hillsides to feed on dormant willow. Larter and Nagy (1997) hypothesized that increased consumption of dormant willow by the growing muskox population may subsequently limit the ability of the plant to flower in the following summer, therefore increasing competition for aerial tissues during summers.

2.1.2 Potential Issues with Existing Dietary Interpretations

Research based on fecal and rumen content has been invaluable for understanding modern caribou and muskox dietary ecology. There are potential drawbacks to both approaches, however. Several studies (Gill et al. 1983; Holechek and Valdez 1985; Bartolomé et al. 1995) indicate that certain forage types can be under- and over-represented in herbivore fecal material, and rumen contents may vary based on the digestibility of different forages. Based on analysis of rumen content, Thing et al. (1987) found that graminoids are typically underrepresented in the feces of muskoxen due to their high digestibility. Additionally, several lines of evidence suggest that the ruminant digestive process itself skews the isotopic compositions of tissue and waste such that they may not accurately reflect dietary composition. Several studies have shown that ruminants are unable to digest the lignin portion of forage material effectively, if at all (Eldsen and Phillipson 1948; Gill et al. 1983).

Because of its low digestibility, lignin or forage with high lignin content may be overrepresented in feces or the rumen.

Additionally, although fecal and rumen studies are useful for making inferences about modern caribou and muskox diet, we have no archaeological fecal samples with which to investigate whether and how caribou and muskox diets have varied over time. As we argue in Chapter 3, the boom-and-bust demographic cycles experienced by caribou and muskoxen may have a relatively recent origin, which has implications for archaeological interpretations about Banks Island. To develop an understanding of caribou and muskox ecology over the *longue durée* (Balée 1998, 2006; Crumley 2007), we need an analytical approach that can be applied to modern and archaeological caribou and muskoxen alike.

2.1.3 Stable Isotope Analysis in Terrestrial Herbivore Ecology

In this paper, we use stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope analysis of forage species, bone collagen, and crown dentin collagen to reconstruct the diets of modern caribou and muskoxen from Banks Island. Specifically, we address two research questions: (1) Is there overlap in specific forage items consumed by modern caribou and muskoxen on Banks Island? (2) If so, does dietary overlap occur only seasonally, or throughout the year?

Stable isotope analysis is an established method of reconstructing diet and environmental conditions during an animal's life. The $\delta^{13}C$ and $\delta^{15}N$ of different forage species varies with photosynthetic fixation of CO_2 and source nitrogen, respectively, and these differences are passed up the food chain. It is generally accepted that the carbon in dietary protein is preferentially routed to proteinaceous tissues like bone collagen, while for instance, bone structural carbonate $\delta^{13}C$ represents the $\delta^{13}C$ of CO_2 derived from all dietary macronutrients (protein, carbohydrates, and lipids) (Gannes et al. 1998; Hedges and van Klinken 2000; Koch 2007). Consequently, lower protein dietary items should only minimally influence the isotopic compositions of proteinaceous tissues like bone collagen.

Preferential representation of dietary protein in bone collagen $\delta^{13}C$ does occur in carnivores and omnivores, where dietary protein is generally so abundant that it can be utilized

exclusively for tissue growth and maintenance (Krueger and Sullivan 1984; Lee-Thorp et al. 1989; Ambrose and Norr 1993; Tieszen and Fagre 1993). In this case, dietary essential and nonessential amino acids are routed directly to proteinaceous body tissues, or are deaminated to synthesize nonessential amino acids (Hare et al. 1991; Tieszen and Fagre 1993). The tissues of vegetation, however, are composed almost entirely of carbohydrates, and generally contain low amounts of protein. Krueger and Sullivan (1984) suggest that many of the amino acids that compose vegetative protein are not useful for faunal tissue growth or maintenance. Herbivores must therefore either synthesize amino acids necessary for tissue development *de novo* from carbohydrates (Krueger and Sullivan 1984; Ambrose and Norr 1993; Dewhurst et al. 2000; Atasoglu et al. 2004) or employ other macronutrient-maximizing strategies like coprophagy (Hörnicke and Björnhag 1980; Peterson and Wunder 1997; van Geel et al. 2011). In ruminant herbivores, synthesis of both nonessential and essential amino acids from carbohydrates is accomplished through microbial fermentation in the rumen. Here, cellulose is converted by microflora into both volatile fatty acids (VFAs) for energy, and amino acids for protein synthesis (Hungate 1966; Batzli et al. 1981; Sørmo et al. 1997; Mathiesen et al. 2000). The stable isotopic composition of bone collagen in herbivores like caribou and muskoxen should therefore reflect all assimilated forage sources, not just those with high crude protein contents.

An isotopic approach to caribou and muskox dietary ecology has several advantages. Collagen is probably the most commonly studied tissue in faunal stable isotope ecology and its extraction and analysis is simple and relatively inexpensive. This opens the door to future long-term caribou and muskox monitoring projects in the Arctic using stable isotope analysis. The rate of tissue turnover in bone collagen is also much slower than blood, hair, or muscle (Tieszen et al. 1983). Consequently, isotopic compositions of bulk bone collagen can be used to make inferences about ecological trends over longer periods, which are complimentary to, and potentially more informative than data from fecal and rumen content studies.

Dentin develops from the dentinoenamel junction (DEJ) in sequential, cone-like layers that extend from the apex of the tooth crown towards the roots (Carlson 1990; Hillson 2000; Zazzo et al. 2006) (Figure 2.2). Unlike dentin from tooth roots, primary dentin (i.e. dentin

apposited during tooth crown development) is not resorbed or remodeled after apposition (Gage et al. 1989; Lowenstam and Weiner 1989; Balasse 2003). The $\delta^{13}C$ and $\delta^{15}N$ of crown dentin collagen ($\delta^{13}C_{dc}$, $\delta^{15}N_{dc}$) therefore provides a level of temporal isotopic resolution that is more refined than – but still directly comparable to – bulk bone collagen $\delta^{13}C$ and $\delta^{15}N$, and has the potential to reveal seasonal, or at least intra-annual, variation in diet. Bone and teeth are also generally resistant to chemical alteration, and as we demonstrate in Chapter 3, preservation of hard tissues from Arctic archaeological sites is excellent. In that chapter, we also demonstrate that the isotopic compositions of bones and teeth from the earliest, most ephemeral sites on Banks Island can be compared with those from later assemblages, as well as modern bone and tooth samples from this chapter, to provide otherwise unobtainable information about the deep ecological histories of these species.

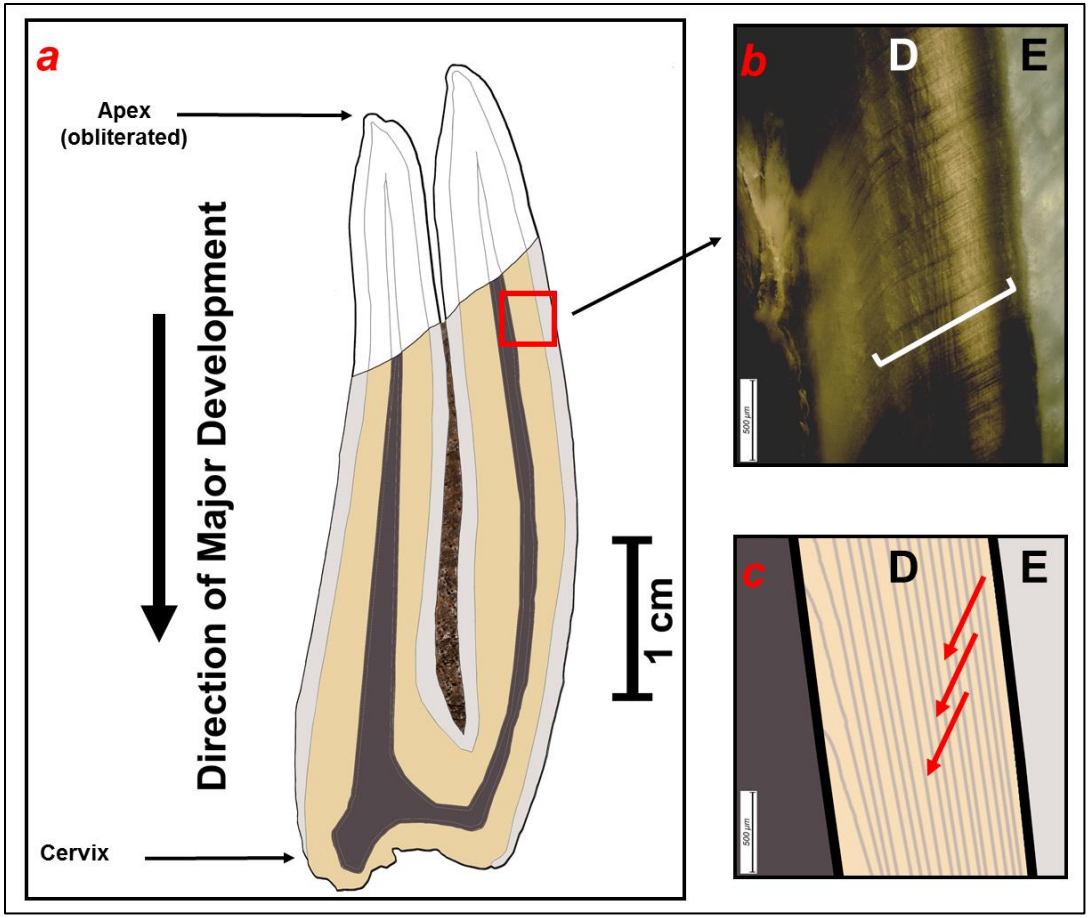


Figure 2.2. Diagram of a typical hypsodont tooth crown. **(*a*)** buccolingual cross-section showing apical section obliterated through occlusal wear; **(*b*)** image of the dentinoenamel junction (DEJ) in a muskox M2, taken at 5x magnification using differential interference contrast (DIC) microscopy. "E" is enamel and "D" is dentin; small, near-horizontal lines (white bracket) are individual dentin tubules; **(*c*)** idealized illustration of diagram *b*, depicting sequentially-developed dentin cones (gray lines). Red arrows indicate the direction of successive dentin apposition away from the DEJ.

2.2 Materials

2.2.1 Bone and Dentin Collagen

Skeletal remains of muskoxen that died relatively recently – as evidenced by the presence of hair or soft tissue on the bones – were present at several archaeological sites we visited in 2014. We collected bone and tooth samples from these remains when possible and include them in our modern bone dataset. Additionally, skeletal samples from adult caribou and muskoxen harvested in the spring and fall of 2015 and 2016 by Trevor Lucas, our research associate in Sachs Harbour, were shipped frozen from Banks Island.

Included in our analysis are isotopic and elemental data for modern caribou and muskox bone collagen from a pilot project on Banks Island (Masoner, White, Hodgetts and Longstaffe, unpublished data). These bone samples were obtained in 2010 and their collagen was prepared and analyzed in the same manner as bone samples from 2014, 2015, and 2016. We also include bone collagen carbon and nitrogen isotope data for five Peary caribou published by Drucker et al. (2012). These caribou were harvested on Banks Island in 1970 and 1975, and their reported $\delta^{13}C_{bc}$ are corrected to those of our modern caribou by –1.43‰ and –1.32‰, respectively, using equations from Verburg (2007). Bone sample information is listed in Tables 2.1 and 2.2. Tooth sample information is listed in Tables 2.3 and 2.4.

Table 2.1. Isotopic, elemental, and percent collagen content data for caribou bulk bone collagen samples.

Sample ID	Harvest Date	Taxon	Element	$\delta^{13}C$ (‰, VPDB)	$\delta^{15}N$ (‰, AIR)	C%	N%	Atomic C:N Ratio	Wt% Coll
BKS-001†	2010	Caribou	Cranium	–21.9	+2.9	42.8	16.1	3.1	
BIBS15-67§	2015	Caribou	Cranium	–22.1	+4.1	45.2	16.5	3.2	20.2
BIBS15-68	2015	Caribou	Cranium	–21.8	+3.2	45.3	16.8	3.2	19.1
BIBS16-19§	2016	Caribou	Mandible	–21.5	+4.5	44.7	16.3	3.2	21.6
BIBS16-20	2016	Caribou	Rib	–21.9	+3.7	44.4	16.3	3.2	21.7
BIBS16-40	2016	Caribou	Rib	–22.0	+3.6	45.9	16.8	2.4	22.0
BIBS16-41	2016	Caribou	Mandible	–21.7	+3.0	44.3	16.3	2.7	18.9
BIBS16-42	2016	Caribou	Humerus	–22.1	+3.4	45.6	16.7	3.5	15.3
BIBS16-43	2016	Caribou	Rib	–22.3	+5.0	44.6	16.4	2.3	22.2
BIBS16-44	2016	Caribou	Rib	–22.7	+5.5	44.5	16.4	2.4	21.6
BNK-7*	1970	Caribou	Mandible	–21.6	+3.2				
BNK-18*	1970	Caribou	Mandible	–21.6	+3.5				
BNK-4**	1975	Caribou	Mandible	–22.0	+3.7				
BNK-11**	1975	Caribou	Mandible	–22.3	+3.1				
BNK-15**	1975	Caribou	Mandible	–22.4	+3.6				

† From pilot study

* Data from Drucker et al. (2012); $\delta^{13}C$ has been corrected by –1.43‰

** Data from Drucker et al. (2012); $\delta^{13}C$ has been corrected by –1.32‰

§ Dentin collagen sampled from tooth belonging to this individual

Table 2.2. Isotopic, elemental, and percent collagen content data for muskox bulk bone collagen samples.

Sample ID	Harvest Date	Taxon	Element	$\delta^{13}C$ (‰, VPDB)	$\delta^{15}N$ (‰, AIR)	C%	N%	Atomic C:N Ratio	Wt% Coll
BKS-0190†	2010	Muskox	Mandible	–22.6	+4.5	42.9	16.3	3.1	
BKS-0191†	2010	Muskox	Cranium	–22.3	+3.7	40.4	15.1	3.1	
BIBS14-168‡		Muskox	Tibia	–22.1	+3.9	44.1	16.0	3.2	18.0
BIBS14-169‡§		Muskox	Mandible	–23.4	+4.0	43.4	15.8	3.2	20.8
BIBS14-445‡§		Muskox	Mandible	–22.7	+5.4	46.1	16.9	3.2	21.1
BIBS16-9	2016	Muskox	Mandible	–22.9	+4.8	43.3	15.9	3.2	25.7
BIBS16-10	2016	Muskox	Mandible	–22.8	+4.4	43.3	15.9	3.2	23.5
BIBS16-11	2016	Muskox	Mandible	–22.7	+3.9	43.4	16.0	3.2	22.5
BIBS16-12	2016	Muskox	Mandible	–22.5	+4.6	43.5	16.0	3.2	24.1
BIBS16-13	2016	Muskox	Mandible	–22.7	+4.0	43.5	16.0	3.2	23.1
BIBS16-14	2016	Muskox	Mandible	–22.3	+4.0	44.0	16.2	3.2	23.8
BIBS16-15	2016	Muskox	Mandible	–22.7	+4.6	44.6	16.5	3.2	22.2
BIBS16-16	2016	Muskox	Mandible	–23.0	+4.0	44.6	16.5	3.2	23.2
BIBS16-17	2016	Muskox	Mandible	–22.3	+4.3	43.8	16.1	3.2	22.8
BIBS16-18	2016	Muskox	Mandible	–22.2	+5.1	44.4	16.4	3.2	25.9

† From pilot study

‡ Recently deceased individual collected at or near archaeological site

§ Dentin collagen sampled from tooth belonging to this individual

Table 2.3. Isotopic, elemental, and percent collagen content data for crown dentin microbulk collagen samples from caribou.

Sample ID	Taxon	Microbulk Sample	$\delta^{13}C$ (‰, VPDB)	$\delta^{15}N$ (‰, AIR)	C%	N%	Atomic C:N Ratio	Wt% Coll
BIBS15-67 M2	Caribou	DC1	–21.0	+4.0	43.2	15.5	3.3	8.7
		DC2	–21.1	+4.5	44.9	16.3	3.2	14.0
BIBS16-19 dp4	Caribou	BULK	–21.1	+6.2	42.5	15.3	3.2	12.3
BIBS16-19 M1	Caribou	DC1	–21.3	+6.2	42.7	15.3	3.3	5.4
		DC2	–21.5	+6.1	42.7	15.4	3.2	11.4
		DC3	–21.2	+6.2	43.8	15.9	3.2	14.6
BIBS16-19 M2	Caribou	DC1	–21.9	+6.0	43.1	15.7	3.2	5.6
		DC2	–21.3	+5.7	43.3	15.5	3.3	8.3

Table 2.4. Isotopic, elemental, and percent collagen content data for crown dentin microbulk collagen samples from muskoxen.

Sample ID	Taxon	Microbulk Sample	$\delta^{13}C$ (‰, VPDB)	$\delta^{15}N$ (‰, AIR)	C%	N%	Atomic C:N Ratio	Wt% Coll
BIBS14-169 M1	Muskox	DC1	–22.9	+7.9	42.8	15.6	3.2	14.5
		DC2	–22.6	+7.7	44.8	16.3	3.2	14.4
		DC3	–22.8	+8.0	44.9	16.4	3.2	14.5
		DC4	–22.5	+7.9	45.3	16.5	3.2	16.0
BIBS14-169 M2	Muskox	DC1	–22.8	+7.9	42.2	15.3	3.2	14.3
		DC2	–23.0	+7.8	44.5	16.2	3.2	14.0
		DC3	–23.0	+7.5	45.1	16.4	3.2	14.3
		DC4	–23.3	+7.6	45.5	16.6	3.2	14.4
		DC5	–22.3	+7.6	45.7	16.5	3.2	18.1
BIBS14-169 M3	Muskox	DC1	–22.8	+7.5	41.8	15.0	3.3	14.7
		DC2	–22.5	+7.5	44.2	16.1	3.2	13.6
		DC3	–22.7	+7.5	43.1	15.6	3.2	12.6
		DC4	–23.2	+7.5	44.3	16.2	3.2	13.5
		DC5	–22.8	+7.5	45.4	16.5	3.2	12.5
		DC6	–23.6	+7.4	44.6	16.1	3.2	14.2
		DC7	–23.6	+7.5	45.6	16.5	3.2	17.0
BIBS14-169 P4	Muskox	DC1	–22.5	+7.5	39.9	14.4	3.2	9.1
		DC2	–22.9	+7.5	44.7	16.1	3.2	12.0
		DC3	–22.9	+7.5	44.6	16.3	3.2	12.0

		DC4	–23.4	+7.6	45.3	16.4	3.2	14.1
		DC5	–23.8	+7.5	44.5	16.3	3.2	16.6
		DC6	–23.1	+6.8	45.9	16.6	3.2	18.9
BIBS14-445 M1	Muskox	DC1	–22.3	+7.2	42.2	15.4	3.2	11.0
		DC2	–22.4	+7.3	43.8	15.9	3.2	14.3
		DC3	–22.0	+7.4	44.9	16.3	3.2	15.2
		DC4	–22.1	+7.5	44.7	16.3	3.2	16.8
		DC5	–21.7	+7.2	44.7	16.4	3.2	18.7
BIBS14-445 M2	Muskox	DC1	–22.1	+6.9	41.8	15.0	3.2	13.9
		DC2	–21.9	+6.9	43.4	15.8	3.2	12.8
		DC3	–21.9	+6.9	43.3	15.8	3.2	6.4
		DC4	–22.5	+6.7	43.5	15.8	3.2	14.0
		DC5	–21.2	+6.6	44.8	16.4	3.2	13.3
		DC6	–21.5	+7.6	45.4	16.5	3.2	17.2

2.2.2 Forage Plants

We collected 49 samples of important forage species from 18 genera at 13 different sites on Banks Island (Figure 2.1, Table 2.5) during June 2014 and May to July 2015. We used illustrated volumes by Porsild (1957) and Polunin (1959) as well as the "Flora of the Canadian Arctic Archipelago" interactive key for the DELTA Intkey program (http://delta-intkey.com) to make taxonomic identifications. Forage functional group classifications follow the scheme outlined in Table 2.6. To abate microbial degradation, forage samples were stored in a ventilated field tent and allowed to air-dry for at least two weeks before shipment to the University of Western Ontario in paper bags. These forage samples were supplemented by isotopic and elemental data from 25 forage samples collected in 2010 as part of the pilot project.

Table 2.5. Taxonomic and collection site information for forage samples from Banks Island.

Sample ID	Scientific Name	Common Name	Functional Group	Collection Site		Elev (m)
				Northing (WGS 84)	Westing (WGS 84)	
OjRk-1						
14VS-1	*Oxytropis arctobia*		Leguminous Forb			
14VS-2	*Dryas integrifolia*	Mountain Avens	Rose/Heath			
14VS-4	*Salix arctica*	Arctic Willow	Willow			
14VS-5	*Saxifraga eschscholtzii*	Cushion Saxifrage	Non-leguminous Forb	71.52539	123.66239	80
14VS-6	*Eriophorum callitrix*	Cottongrass	Sedge			
14VS-7	*Salix arctica*	Arctic Willow	Willow			
14VS-8	*Saxifraga eschscholtzii*	Cushion Saxifrage	Non-leguminous Forb			
Agvik (OkRn-1)						
14VS-19	*Dryas integrifolia*	Mountain Avens	Rose/Heath	71.80317	124.64729	12
Emegak Lake Area						
14VS-10	*Eriophorum latifolium*	Broad-leaved Cottongrass	Sedge	71.80383	124.61708	31
14-VS-11	*Dupontia* spp.	Tundragrass	Grass			
14VS-12	*Salix arctica*	Arctic Willow	Willow			
14VS-13-1	*Cetraria tilesii*	Yellow Lichen	Lichen			
14VS-13-2	*Thamnolia vermicularis*	Worm Lichen	Lichen			
14VS-14	*Petasites frigidus*	Frigid Colt's foot	Non-leguminous Forb			
14VS-15	*Eriophorum latifolium*	Broad-leaved Cottongrass	Sedge			
14VS-16	*Carex aquatilis stans*	Water Sedge	Sedge			

14VS-17	*Oxytropis arctobia*		Leguminous Forb			
14VS-18	*Alopecurus magellanicus*	Alpine Foxtail	Grass			
Area ~ 4 km east of Kellett Point						
15VS-2BC	*Salix arctica*	Arctic Willow	Willow			
15VS-4BC	*Dryas octopetala*	Mountain Avens	Rose/Heath			
15VS-3BC	*Thamnolia vermicularis*	Worm Lichen	Lichen	71.96114	125.72725	16
15VS-1BC	*Saxifraga oppositifolia*		Non-leguminous Forb			
15VS-5BC	*Dryas octopetala*	Mountain Avens	Rose/Heath			
Mary Sachs Lake Area						
15VS-1LK	*Eriophorum angustifolium*	Cottongrass	Sedge			
15VS-3LK-1	*Cetraria tilesii*	Yellow Lichen	Lichen			
15VS-3LK-2	*Thamnolia vermicularis*	Worm Lichen	Lichen	71.97276	125.57301	
15VS-4LK	*Salix arctica*	Arctic Willow	Willow			
15VS-5LK	*Cassiope tetragona*	Arctic White Heather	Rose/Heath			
Green Cabin Area						
15VS-205	*Saxifraga eschscholtzii*	Cushion Saxifrage	Non-leguminous Forb	73.22864	119.53942	
15VS-204	*Oxytropis arctica*		Leguminous Forb	73.22875	119.54522	
15VS-206	*Dryas integrifolia*	Mountain Avens	Rose/Heath	73.22878	119.53958	37
15VS-207	*Salix arctica*	Arctic Willow	Willow			
15VS-208	*Carex aquatilis stans*	Water Sedge	Sedge	73.23094	119.54769	50
15VS-209-1	*Thamnolia vermicularis*	Worm Lichen	Lichen	73.23094	119.54586	48
15VS-209-2	*Sphagnum squarrosum*	Sphagnum Moss	Moss			
15VS-210	*Oxytropis arctobia*		Leguminous Forb	73.23167	119.54661	45

15VS-203-1	*Cetraria tilesii*	Yellow Lichen	Lichen	73.38419	119.91361	41
15VS-203-2	*Thamnolia vermicularis*	Worm Lichen	Lichen			
15VS-202	*Cetraria tilesii*	Yellow Lichen	Lichen	73.38503	119.91361	41
15VS-201	*Eriophorum callitrix*	Cottongrass	Sedge	73.38531	119.91361	44
		Char Lake (PjPx-2)				
14VS-9	*Poaceae* spp.	Grass	Grass	73.65775	119.93520	16
		Head Hill (PlPx-1) Area				
15VS-215	*Oxytropis* spp.		Leguminous Forb	73.83658	119.98372	57
15VS-216	*Astragalus alpinus*	Alpine Milk Vetch	Leguminous Forb	73.83719	119.98742	73
15VS-214-1	*Cetraria tilesii*	Yellow Lichen	Lichen			
15VS-214-2	*Thamnolia vermicularis*	Worm Lichen	Lichen	73.83761	119.98550	70
15VS-214-3	*Sphagnum squarrosum*	Sphagnum Moss	Moss			
15VS-211	*Salix arctica*	Arctic Willow	Willow			
15VS-213	*Carex aquatilis stans*	Water Sedge	Sedge	73.83906	119.98936	77
15VS-213-2	*Sphagnum squarrosum*	Sphagnum Moss	Moss			
		Mercy Bay Area				
15VS-219-1	*Cetraria tilesii*	Yellow Lichen	Lichen			
15VS-219-2	*Thamnolia vermicularis*	Worm Lichen	Lichen	74.10558	119.05497	9
15VS-219-3	*Sphagnum squarrosum*	Sphagnum Moss	Moss			
15VS-218	*Carex aquatilis stans*	Water Sedge	Sedge			
15VS-220	*Saxifraga cernua*	Bulblet Saxifrage	Non-leguminous Forb	74.10561	119.05419	8
15VS-220-2	*Sphagnum squarrosum*	Sphagnum Moss	Moss			
15VS-221	*Astragalus alpinus*	Alpine Milk Vetch	Leguminous Forb			

15VS-217	*Thamnolia vermicularis*	Worm Lichen	Lichen	74.10650	119.05169	2
		HMS *Investigator* Cache Area				
P1†	*Dryas octopetala*	Mountain Avens	Rose/Heath	74.18798	119.08961	
P10†	*Pedicularis lanata*	Wooly Lousewort	Non-leguminous Forb			
P11A†	*Papaver radicatum*	Arctic Poppy	Non-leguminous Forb			
P12†	*Poaceae* spp.	Grass	Grass			
P13†	*Saxifraga cernua*	Bulblet Saxifrage	Non-leguminous Forb			
P14†	*Leymus arenarius*	Lyme Grass	Grass			
P15†	*Cassiope tetragona*	Arctic White Heather	Rose/Heath			
P2A†	*Saxifraga hirculus*	Marsh Saxifrage	Non-leguminous Forb			
P3†	*Salix arctica*	Arctic Willow	Willow			
P4†	*Oxyria digyna*	Mountain Sorrel	Non-leguminous Forb			
P5†	*Thamnolia vermicularis*	Worm Lichen	Lichen			
P6†	*Oxytropis arctica*	Arctic Oxytrope	Leguminous Forb			
P8†	*Poaceae* spp.	Grass	Grass			
P9†	*Saxifraga oppositifolia*	Purple Saxifrage	Non-leguminous Forb			

† From pilot study

Table 2.6. Functional group classification scheme for forage samples.

Herbs (Non-woody Vascular Plants)		**Shrubs (Woody Vascular Plants)**	**Mosses (Non-vascular Plants)**	**Lichens (Composite Organisms)**
Monocotyledonous Graminoids	**Dicotyledonous Forbs**			
True Grasses (*Gramineae*)	Non-leguminous	Dwarf Willow	Sphagnum Moss	Lichens
Sedges (*Cyperaceae*)	Leguminous (*Fabaceae*)	Rose/Heath		

2.3 Methods

2.3.1 Sample Preparation

After shipment to the University of Western Ontario, frozen bone samples were thawed and soft tissue was removed with a scalpel. Defleshed bone samples were immediately placed in a 60°C oven with several beakers of fresh desiccant and allowed to desiccate for approximately 24 hours. After drying, ~ 1 g of bone was removed from each sample using a Dremel® rotary tool. Whenever possible, we selected only cortical bone for analysis because the rate of tissue turnover is slightly slower than in trabecular bone (Cox and Sealy 1997; Hill and Orth 1998; Hedges et al. 2007). An additional subsample was removed for DNA analysis (Rodrigues et al. forthcoming). Because fresh bone contains substantial amounts of oils and fats, samples were rinsed three times in 2:1 chloroform-methanol prior to crushing. After drying overnight in a fumehood, samples were crushed to <0.85mm, and bulk collagen was extracted using a modified version of the protocol described by Longin (1971). Briefly, this process involves the removal of lipids and any residual soft-tissue with three rinses in 2:1 chloroform-methanol, demineralization in 0.50 M HCl, removal of humic and fulvic acids in 0.1 M NaOH, solubilization in weak acid (10^{-3} M HCl), and evaporation of water to yield dry collagen. The second set of rinses in 2:1 chloroform-methanol was included to remove any residual lipids. Additionally, although there should be no humic or fulvic acids in fresh bone, we included the NaOH treatment for comparability with archaeological bone samples (Chapter 3).

Sequential dentin "microbulk"[7] collagen samples were obtained from tooth crowns using the following method. First, selected teeth were extracted from mandibles or maxillae, cleaned of dust, debris, and residual cementum using ultrapure water, a toothbrush, and a dental scaler, and allowed to dry under continuous air flow in a fume hood. The size of the

[7]Since it is not possible to obtain collagen from individual dentin appositional layers with the sampling methodology we employ here, the isotopic compositions of each sequential dentin sample reflect the averaged isotopic compositions of multiple, cross-cut dentin appositional layers. We use the term "microbulk" to distinguish from studies where whole-tooth, homogenized dentin samples are analyzed. See Section 2.4.9 for further discussion.

muskox teeth exceeded all commercially-available embedding molds, and we instead employed inexpensive silicone cigarette cases purchased from a variety store as reusable embedding molds with excellent results. The teeth were fully embedded in epoxy resin (Struers EpoFix®) (Figure 2.3b) and the resultant epoxy "blocks" were allowed to harden for at least a week. After curing, we used a Buehler® IsoMet™ low-speed saw to produce two 250 μm-thick buccolingual thick sections (henceforth the "A-section" and "B-section") through the highest point of the least worn tooth loph (Figure 2.3c). After microsampling enamel from each A-section for related research (see Chapter 4; B-sections were used exclusively for the analysis of tooth enamel $\delta^{13}C$ and $\delta^{18}O$ in that chapter as well), we used a second, smaller sectioning machine to divide each tooth crown into ~ 5 mm transverse "slices" (Figure 2.3d, e). Because the degree of occlusal wear in each tooth varies, the root-enamel junction (REJ) (i.e. the cervix) of each tooth crown was used as a common "anchor point" for each sampling "grid" of 5 mm transverse sections.

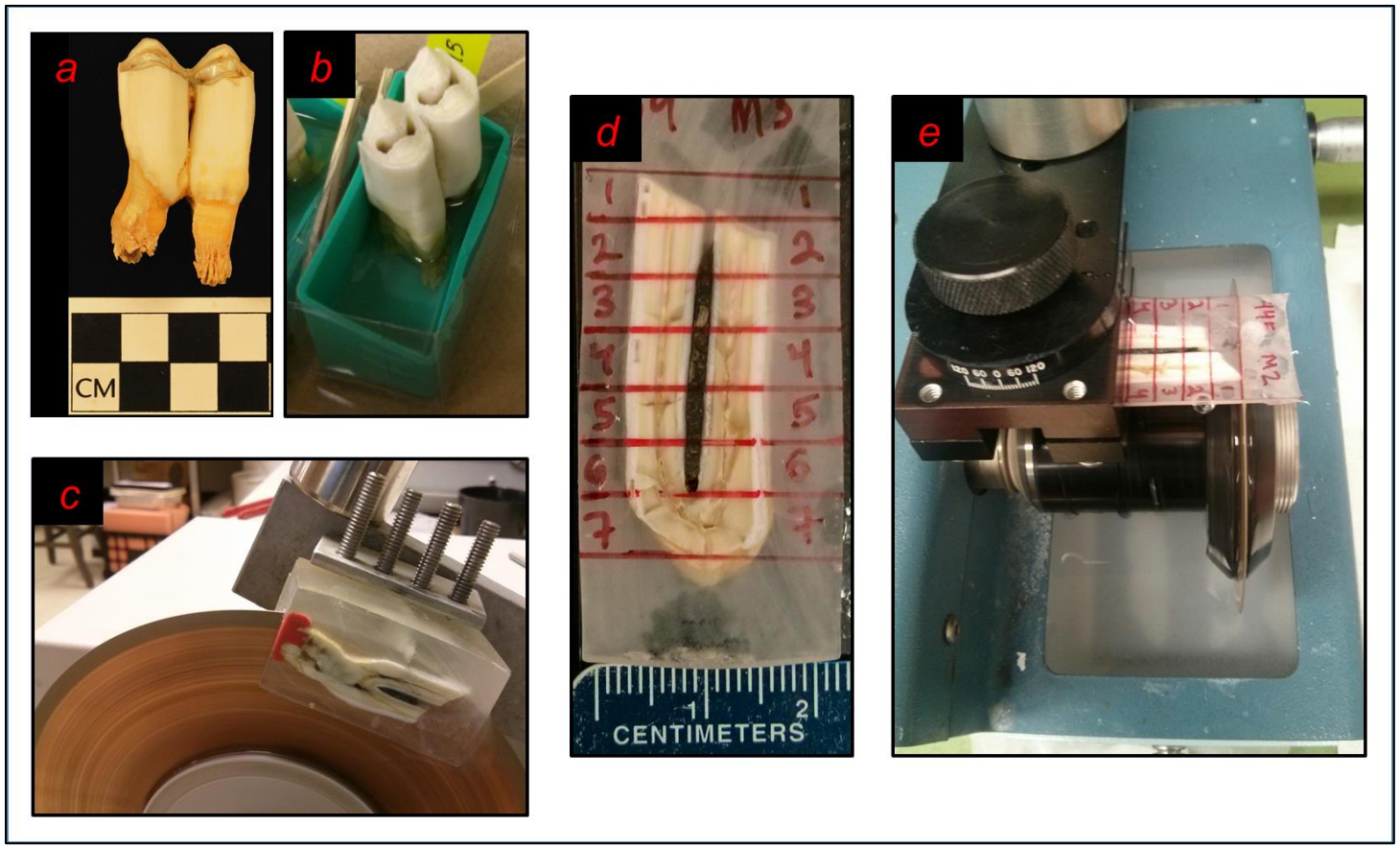


Figure 2.3. The dentin collagen sampling process: **(*a*)** intact tooth after being removed, cleaned, and dried; **(*b*)** embedding in epoxy resin using silicone molds; **(*c*)** obtaining one of two thick sections from the epoxy block; the first section (the "A-section") is used for obtaining dentin samples (red material is modeling clay used to position tooth during embedding); **(*d*)** an A-section marked for transverse sectioning; numbers correspond to sequential dentin sample IDs. Each section is approximately 5 mm in height with the sampling "grid" anchored at the root-enamel junction (REJ); **(*e*)** obtaining sequential dentin samples from an A-section using the second sectioning machine.

Large fragments of enamel and epoxy were mechanically removed from each transverse slice, and collagen was extracted from each sequential dentin sample following the same methods used for bone collagen extraction, with one notable exception. We did not crush the dentin samples to a uniform size as we did for bone samples because: (1) samples were very small and crushing inevitably results in the loss of small amounts of sample material; and (2) allowing the dentin samples to demineralize as small chunks ensured that residual epoxy could be removed from samples with tweezers later in the collagen extraction process. Like the modern bone samples, dentin samples were rinsed in three rounds of 2:1 chloroform-methanol prior to obtaining dry weights and beginning the collagen extraction process. However, whereas with modern bone samples the purpose of these pre-rinses was to remove excess oil, fat, and marrow, they were applied to dentin collagen samples to dissolve residual epoxy.

Following Szpak et al. (2013) and Tahmasebi (2015), we subdivided forage samples by tissue types (e.g. roots, root crowns, stems, leaves, inflorescences). We then rinsed the samples of soil and other exogenous materials with distilled water and dried them at 90°C for ~ 24 hours. Samples were then ground to a homogenous size using a Wig-L-Bug® grinding mill. Because forage samples were not subjected to additional treatments after drying and grinding, we did not create methodological duplicates. Forage samples from the pilot project were prepared and analyzed in the same manner as samples collected in 2014 and 2015.

2.3.2 Isotopic Analysis and Determination of Elemental Weight Percentage

All isotopic analyses, including those from the pilot project, were performed at the Laboratory for Stable Isotope Science (LSIS) at the University of Western Ontario using a Costech™ Elemental Combustion System interfaced with either a Thermo Scientific™ DELTA^{plus} XL® or Thermo Scientific™ DELTA V Plus® isotope ratio mass spectrometer operating in continuous flow mode. All isotopic compositions are reported in per mil (‰) using delta notation (δ) (Equation 2.1):

$$\delta = \left[\frac{R_{Sample}}{R_{Standard}} - 1\right]$$

[Equation 2.1]

where *R* is the ratio of heavy to light isotopes in the analyte. Carbon isotope compositions are calibrated to Vienna Pee Dee Belemnite (VPDB) and nitrogen isotope compositions are calibrated to atmospheric N_2 (AIR) using USGS40 (L-glutamic acid; accepted $\delta^{13}C$ and $\delta^{15}N$ –26.39‰ and –4.52‰, respectively) and USGS41 (L-glutamic acid; accepted $\delta^{13}C$ and $\delta^{15}N$ +37.63‰ and +47.57‰, respectively) as reference standards (Qi et al. 2004). For forage, bone collagen, and dentin collagen analyses, an internal keratin standard (MP Biomedicals Inc., Cat No. 90211, Lot No. 9966H), and an international standard (IAEA-CH-6) were used to measure analytical accuracy. For nitrogen-only isotope analyses of forage tissues, the internal keratin standard, and an international standard (NIST-1547) were used to measure analytical accuracy.

For each sample, weight percent carbon (C%) and nitrogen (N%) were not measured directly but were calculated using Equation 2.2:

$$\frac{\frac{\%E_{Standard} * Amplitude_{Sample}}{Amount_{Sample}}}{K-Factor}$$

[Equation 2.2]

where "$\%E_{Standard}$" equals the accepted elemental (C or N) weight percentage of the reference standard (here, either USGS-40 or USGS-41), "$Amplitude_{Sample}$" equals the amplitude of ions with a mass-to-charge (m/z) ratio of 44 (for carbon) or 28 (for nitrogen) measured in the sample, and "$Amount_{Sample}$" equals the sample weight (in mg). The "*K-factor*", used to correct for instrumental mass discrimination, and is derived from Equation 2.3:

$$\frac{Average\ Amplitude_{Standard}}{Average\ Amount_{Standard}}$$

[Equation 2.3]

where "*Average Amplitude*$_{Standard}$" equals the average amplitude of ions with a mass-to-charge (m/z) ratio of 44 (for carbon) or 28 (for nitrogen) measured in all analyses of a reference standard (here, either USGS-40 or USGS-41) during the analytical session, and "*Average Amount*$_{Standard}$" equals the average weight (in mg) of all reference standards (again, either USGS-40 or USGS-41) analyzed during the analytical session.

For each batch of bone and dentin collagen samples (typically 20 to 24 samples each), we created two method duplicates to assess the effect of the collagen extraction process on the reproducibility of sample isotopic and elemental values. Because forage plant samples were not processed prior to analysis aside from washing and drying, no forage sample method duplicates were created. For all analyses (including forage samples) we also analyzed duplicate samples (i.e. instrumental duplicates) at regular intervals during each analytical session to monitor instrument precision. The standard deviation of method duplicates and instrumental duplicates reported here reflect the differences between the average value (δ^{13}C, δ^{15}N, C%, N%) of all method or instrumental duplicates, and the average value (δ^{13}C, δ^{15}N, C%, N%) of their parent samples.

Unlike in bone collagen, the proportion of carbon in wild vegetation is generally much higher than the proportion of nitrogen. Because of this, accurate δ^{13}C and δ^{15}N for forage samples cannot typically be obtained in a single analytical session. Instead, forage samples are first analyzed for their carbon isotope compositions under normal EA-CF-IRMS operating conditions. The mass 28 amplitudes, however, are too low to produce accurate δ^{15}N and are ignored, but the calculated N% data are used to determine, on a sample-by-sample basis, the quantity of sample necessary to obtain reproducible nitrogen isotope data. Forage samples are then reweighed to match this typically much larger target weight, and a $Mg(ClO_4)_2$ trap is installed on the capillary running from the EA to the IRMS to trap CO_2 from the combusted sample. The combination of a higher sample weight and CO_2 trap

permits an appropriate volume of NO_x to be combusted from the sample and converted to N_2 without oversaturating the detector with large amounts of combusted CO_2 sample gas.

2.3.3 Bayesian Dietary Mixing Models Using MixSIAR

Over the last several decades, the study of dietary niche using stable isotope data has matured rapidly, and there is a broad constellation of linear and Bayesian mixing models available with which to estimate the proportional contributions of multiple sources to a mixture. Here, sources correspond to forage isotopic compositions and mixtures correspond to bone collagen isotopic compositions, though mixing models have a wide range of applications (Stock and Semmens 2013). Each mixing model has specific advantages and disadvantages (see Phillips et al. 2014 for a broad review of recent advances). We use the MixSIAR package (version 3.1) (Semmens et al. 2013) for R (version 3.3.2) (R Development Core Team 2009) to develop Bayesian dietary mixing models. MixSIAR is based on the MixSIR mixing model (Moore and Semmens 2008) and the SIAR package for R (Parnell et al. 2010). MixSIAR utilizes the Markov chain Monte Carlo (MCMC) algorithm to estimate the probability of different source contributions (here, forage isotopic and elemental compositions) to a mixture (here, bone collagen isotopic and elemental compositions) and propagate uncertainty around that estimate. The major advantage of MixSIAR is that it integrates many of the significant contributions from recent mixing models into a single, adaptable framework (Semmens et al. 2013). MixSIAR requires three inputs: consumer isotopic data, source isotopic (and if desired, elemental) data, and trophic discrimination factors (TDFs) (sometimes also referred to as "trophic enrichment factor" (TEF) or "trophic fractionation factor" (TFF).

While it represents a significant advancement in the access to, and ease-of-use of dietary mixing models, MixSIAR will generally fit a model even if input data are nonsensical, and there is considerable room for error caused by incorrect model parameters (Inger et al. no date; Phillips et al. 2014). MixSIAR is sensitive to similarities in source isotopic compositions, and uncertainty in the mixing model increases when source groups include less than twenty samples. These issues are relevant because our source isotopic data come from terrestrial forage species that utilize the C_3 photosynthetic pathway. Phillips et al. (2014) suggest determining whether source data should be aggregated prior to analysis,

though *a posteriori* source aggregation of source chains is also possible in R (Stock and Semmens 2013). Generally, a K nearest-neighbors randomization test (kNN) with various *post hoc* adjustments (Ben-David et al. 1997; Rosing et al. 1998; Drever et al. 2000; Kadye and Booth 2012; Matsubayashi et al. 2014) is used to test for significant difference in multiple isotopic tracers between sources (but see Lubetkin and Simenstad (2004) for a squared nearest neighbor difference (NND^2) approach). Geange et al. (2011) also discuss methods for transforming ratio and percentage data (such as C% or N%) into continuous variables for statistical analysis.

Because we obtained forage samples from both the southern and northern parts of Banks Island (Figure 2.1), we used Mann-Whitney *U* tests (Ben-David et al. 1998) to evaluate whether there were statistically significant geographic differences in the $\delta^{13}C$ and $\delta^{15}N$ of the same forage species or functional groups. Although the Mann-Whitney *U* test can only be used to test for significant differences in a *single* factor between two groups (here, a single isotope tracer), simple coding in R permits the $\delta^{13}C$ and $\delta^{15}N$ of multiple groups in the same dataset to be quickly evaluated with multiple, separate Mann-Whitney *U* tests. We applied this method to test for north-south variation in *Cetraria*, *Thamnolia*, pooled lichens, sedges, grasses, pooled sedges and grasses (graminoids), willow, rose/heath, and pooled willow and rose/heath (shrubs), legumes, non-leguminous forbs, and pooled legumes and non-leguminous forbs (forbs). Although Phillips et al. (2014) note that the ability of mixing models to discriminate between sources begins to decline with more than six or seven sources, we ran the mixing model simulations with maximum source divisions, and aggregated some sources afterwards.

The largest source of uncertainty and potential error in dietary mixing models is the trophic discrimination factor (TDF). Early work documented persistent but variable shifts in $\delta^{13}C$ and $\delta^{15}N$ between consumers and dietary sources (DeNiro and Epstein 1981; Sullivan and Krueger 1981; Krueger and Sullivan 1984; Minigawa and Wada 1984; van der Merwe 1989; Ambrose and Norr 1993). In larger mammals, the trophic enrichment in ^{13}C between bone collagen and diet ($\Delta^{13}C_{coll\text{-}diet}$) generally falls between +4-6‰, while the enrichment in ^{15}N between bone collagen and diet ($\Delta^{15}N_{coll\text{-}diet}$) falls between +3-5‰ (Sullivan and Krueger 1981; Krueger and Sullivan 1984; van der Merwe 1989; Koch 1998). Recent

research demonstrates, however, that TDFs vary significantly with phylogeny (Vanderklift and Ponsard 2003; Caut et al. 2009; Cherel et al. 2014). Further, TDF estimates derived from controlled feeding experiments may not be applicable to wild populations because TDFs, especially for nitrogen, vary with the quality of dietary protein (Fantle et al. 1999; Oelbermann and Scheu 2002; Robbins et al. 2005, 2010; Greer et al. 2015). Bond and Diamond (2011) find that Bayesian mixing models are highly sensitive to the TDFs used, which means that mixing models may produce misleading mixing solutions with inaccurate TDFs (Caut et al. 2008). This leaves researchers with two options: (1) use published, experimentally-derived TDFs for the same or similar species, with knowledge that they may not reflect "wild" TDFs, or: (2) perform a meta-analysis of relevant, published consumer and source isotopic data and attempt to create TDF estimates from these data.

Recently, Healy et al. (2016) developed the Stable Isotope Discrimination Estimation in R (SIDER) package for R (https://github.com/healyke/SIDER). SIDER provides a TDF estimate for a given species by utilizing a generalized linear mixed model (GLMM) to incorporate variation based on phylogeny, physiology, and ecology in a large meta-dataset of published isotopic data included in the package. The MCMC algorithm is then used to propagate uncertainty around the TDF estimate. The mean and standard deviation of the probability distribution for the imputed TDF estimate can then be incorporated into mixing models. Healy et al. (2016) demonstrate that SIDER-imputed TDF estimates are within 0.2‰ of experimentally-derived TDFs. A Bayesian approach to TDF estimation is especially attractive in the study of caribou and muskoxen. Both species likely have unique physiological adaptations to the Arctic environment that may result in actual TDFs distinct from large-bodied ruminants from temperate regions. We used SIDER (version 0.9) in R (version 3.3) for TDF imputations. Three Markov chains, each with a length of three million iterations, were constructed from the GLMM-derived TDF estimate. We discarded

(i.e. "burned")[8] the first 1,500,000 iterations in each chain, and saved only every 500th iteration[9] after the burn-in period.

We used two criteria included in the SIDER package to assess the Markov chains: effective sample size (ESS) (Kong 1992; Liu 1996), and the Gelman-Rubin convergence diagnostic (Gelman and Rubin 1992a, 1992b; Gelman et al. 2013). ESS simply evaluates whether, after accounting for burn-in and thinning, the number of remaining iterations in the chain is sufficient to estimate the target posterior distribution (Lanfear et al. 2016; Martino et al. 2017). An ESS of 200 is generally accepted as the minimum necessary to measure model efficiency, and an ESS of >10000 is considered ideal (Lanfear et al. 2016). The simplest way to ensure sufficient ESS is to increase chain length. Under the model parameters listed above, each chain has an ESS of 18000. The Gelman-Rubin diagnostic detects the failure of chains to converge on the target distribution (Brooks and Gelman 1998). The Gelman-Rubin diagnostic ($\hat{R}$) approaches one (1) from above (i.e. decreases to 1) when the pooled within-chain variance is greater than between-chain variance. A high $\hat{R}$ value therefore suggests that within-chain variance could be further reduced through continued simulation (i.e. longer chain length). Following Gelman et al. (2013) and Stock and Semmens (2016), we rejected chains whose $\hat{R}$ values exceed 1.1. Additionally, because SIDER runs were relatively inexpensive in terms of computational time, averaging ~ 40 minutes to execute, we repeated each of the four TDF runs four times to test for significant differences in the imputed TDF estimates.

---

[8] "Burn-in" is an informal term for the common practice of discarding a subjective number of iterations at the start of a Markov chain. Because the MCMC algorithm randomly "walks" around a distribution, it is always possible that the chain will start in low-probability regions before wandering towards high probability regions representative of the sample distribution. In relatively short Markov chains, initial iterations will subsequently bias the estimated posterior probability distribution. Nevertheless, there is no mathematical or theoretical motivation for burn-in, and Geyer (2011) for instance, advocates for simply running longer Markov chains instead, where the effect of initial iterations on the probability distribution becomes negligible.

[9] "Thinning" describes the process of discarding all but every *k*th iteration in a Markov chain to avoid autocorrelation between model parameters (SAS Institute Inc. 2011) and to reduce processing time (Gelman and Shirley 2011). Although Geyer (1992), MacEachern and Berliner (1994), and Link and Eaton (2012) suggest that thinning is counter-productive, we observed no difference between test mixing model runs with and without thinning, except that the non-thinned run cost about an extra day of processing time.

We fit the dietary mixing model in using individual source (forage) isotopic and elemental data (as opposed to averages and SD values) and SIDER-derived TDFs. For all mixing model simulations, three Markov chains, each with a length of three million iterations, were constructed from the data. As with our SIDER imputations, we discarded the first 1.5 million iterations in each chain, as well as every 500th iteration after the burn-in period[10]. As suggested by Stock and Semmens (2016), we used a multiplicative error structure in the model, which takes into account variability in consumer isotope data due to sampling (i.e. "process error") and interindividual differences in inherent processes like digestibility, assimilation, and metabolism (i.e. "residual error") in consumers (Jackson et al. 2009; Semmens et al. 2009; Stock and Semmens 2016). Although it is common practice to perform multiple independent runs of a Bayesian simulation to check for appropriate convergence and mixing, the computational expense to run each mixing model was significant. Using the run parameters described above, a dedicated computer (Microsoft® Windows® 7 64-bit, Intel® Core™ i3 2.2GHz, 16GB RAM) required between 72 and 84 hours to run each mixing model.

We assessed whether the model failed to approach convergence using the Gelman-Rubin diagnostic (Gelman and Rubin 1992a, 1992b; Gelman et al. 2013), as well as the Geweke diagnostic (Geweke 1992). The Geweke diagnostic provides evidence against efficient convergence by comparing the mean and asymptotic variance of spectral density in non-overlapping segments or "windows" (usually the first 10 percent (after burn-in) and last 50 percent) of the chain for each variable. In chains that approach convergence early in the run, the variance in spectral density should be low and the means of the two chain windows should not differ significantly. The Geweke test statistic, the *Z*-score, is a measure of standard deviation, and *Z*-score values at the extremes of the normal distribution (greater than two standard deviations) suggest that for the given variable, the chain did not approach convergence early in the post-burn-in period. Following Stock and Semmens (2013), we

[10]Experimental mixing model runs with longer Markov chains (five million iterations), and a longer burn-in period (1.75 million iterations) with a different computer (Microsoft® Windows® 7 64-bit, Intel® Core™ i5 2GHz, 8GB RAM) did not produce significantly different posterior probability distributions.

rejected the chain if more than five percent of the chain variables had absolute *Z*-scores higher than 1.96.

2.4 Results

2.4.1 Bone Collagen

Modern bone samples were analyzed alongside archaeological bone collagen samples in ten analytical sessions. Across 72 analyses of the internal keratin standard, δ^{13}C was –24.10±0.16‰ (accepted value = –24.04‰); and δ^{15}N was +6.40±0.13‰ (accepted value = +6.36‰). Across 28 analyses of IAEA-CH-6 δ^{13}C was –10.44±0.07‰ (accepted δ^{13}C = –10.45‰; Hut 1987). Including data from the pilot study, the standard deviation of bone collagen samples analyzed as instrumental duplicates (n = 3) was δ^{13}C = ±0.0‰, δ^{15}N = ±0.1‰, C% = ±0.1, and N% = ±0.1. The standard deviation of bone collagen samples analyzed as method duplicates (n = 3) was δ^{13}C = ±0.0‰, δ^{15}N = ±0.1‰, C% = ±0.1, and N% = ±0.1.

The collagen content, as a percentage of sample weight ("wt% coll") for bones from recently (estimate <15 years) deceased muskoxen (*n* = 3) averaged 20.0% (min = 18.0%; max = 21.1%). Percent collagen content for fresh caribou and muskox bone (*n* = 16) averaged 22.9% (min = 19.1%; max = 25.9%). Percent collagen content for the pilot project samples (*n* = 2) were not available; we assume that they are comparable to fresh bone samples. These collagen weight percent values are typical of the range observed in modern bone (wt% coll = ~ 20 to 30%) (Schoeninger et al. 1989; Ambrose 1990; Ambrose and Norr 1993; van Klinken 1999; Jørkov et al. 2007). Elemental abundances of carbon (C%) and nitrogen (N%) in all bone samples averaged 44.0% (min = 40.4%, max = 46.1%) and 16.2% (min = 15.1%, max = 16.9%), respectively. Atomic C:N ratios averaged 3.2 (min = 3.1; max = 3.2). Elemental abundances and atomic C:N ratios are both within commonly accepted ranges for isotopically unaltered bone collagen (C% = 15.3 to 47.0%; N% = 5.5 to 17.3%; atomic C:N = 2.9 to 3.6) (DeNiro 1985; Ambrose 1990; van Klinken 1999).

The $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ of modern caribou and muskoxen from Banks Island are listed in Tables 2.1 and 2.2, and illustrated in Figure 2.4. Including data from Drucker et al. (2012), δ^{13}C averaged –22.0‰ (min = –22.7‰, max = –21.5‰) for caribou and –22.6‰ (min = –

23.4‰, max = –22.1‰) for muskoxen. The δ^{15}N of modern bone collagen samples averaged +3.7‰ (min = +2.9‰, max = +5.5‰) for caribou, and +4.4‰ (min = +3.7‰, max = +5.4‰) for muskoxen.

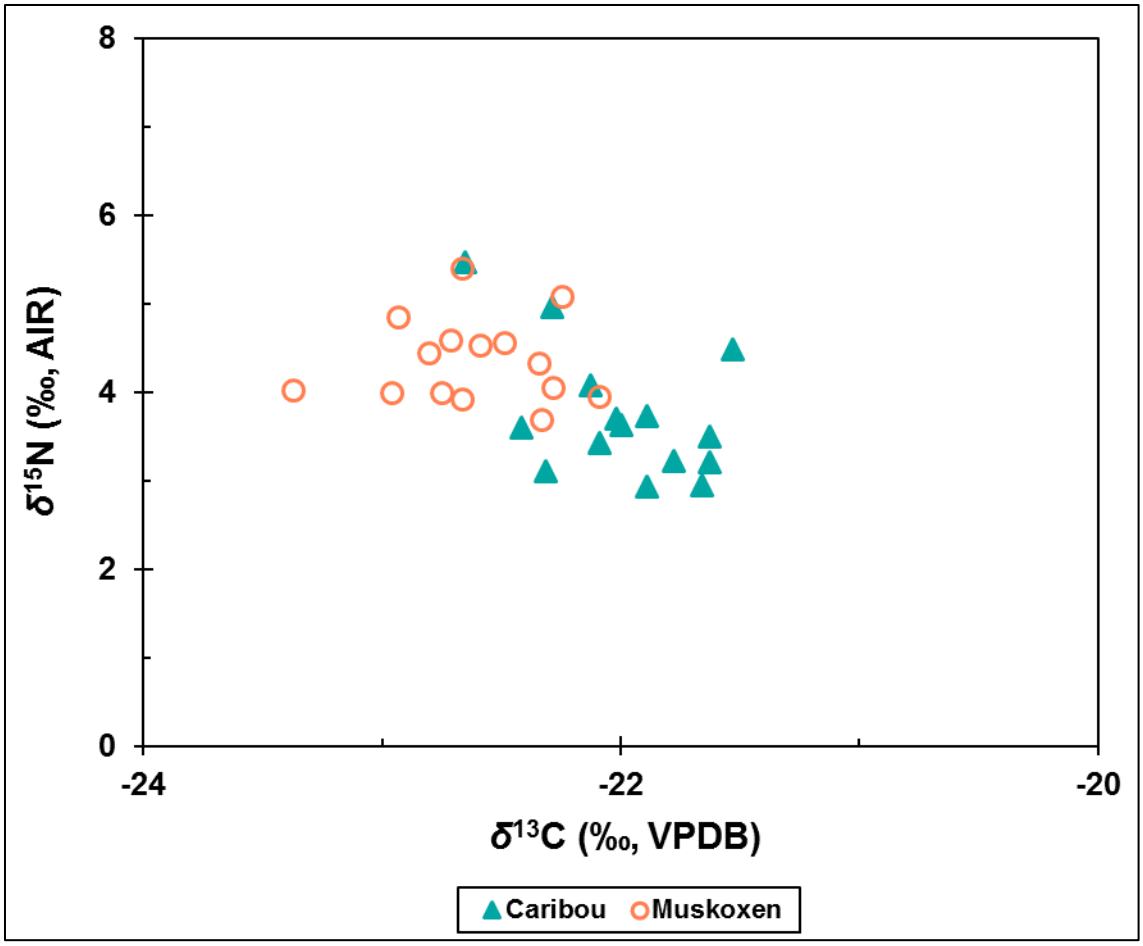


Figure 2.4. Bulk bone collagen δ^{15}N vs. δ^{13}C from modern caribou and muskox on Banks Island.

2.4.2 Variation in Forage Sample $\delta^{13}C$ and $\delta^{15}N$

Forage sample were analyzed for their $\delta^{13}C$ and $\delta^{15}N$ in six analytical sessions each. Across 34 analyses of the internal keratin standard (accepted $\delta^{13}C$ and $\delta^{15}N$ = –24.04‰ and +6.36‰, respectively) in carbon-only analytical sessions, $\delta^{13}C$ was –24.06±0.06‰. Across 38 analyses of the internal keratin standard in nitrogen-only analytical sessions, $\delta^{15}N$ was +6.46±0.14‰. Across 21 analyses of IAEA-CH-6 (accepted $\delta^{13}C$ = –10.45‰; Hut 1987)), $\delta^{13}C$ was –10.45±0.09‰. Across 25 analyses of NIST-1547 (accepted $\delta^{15}N$ = +1.98‰), $\delta^{15}N$ was +1.96±0.15‰. Including data from the pilot study, the standard deviation of forage samples analyzed as instrumental duplicates (n = 20) is $\delta^{13}C$ = ±0.1‰, $\delta^{15}N$ = ±0.2‰, C% = ±0.2, and N% = ±0.2.

Carbon and nitrogen isotopic and elemental data for all forage sample tissues are listed in Table 2.7 and their $\delta^{13}C$ and $\delta^{15}N$ are illustrated in Figure 2.5. Even though the forage species in our analysis all utilize the C_3 photosynthetic pathway, forage $\delta^{13}C$ ranges from –31.5 to –23.1‰. Likewise, forage $\delta^{15}N$ ranges from –8.7 to +9.4‰. When averaged, carbon (C%) and especially nitrogen (C%) contents vary markedly by forage species and functional group (Table 2.8). Lichens tend to have the lowest average N content by weight (0.4%), and consequently the highest average atomic C:N ratio (average = 101.7), while forbs (particularly leguminous forbs) have the highest average N content by weight (3.0%) and therefore the lowest atomic C:N ratio (average = 21.6).

Table 2.7. Isotopic and elemental data for forage samples from Banks Island. Samples are ordered alphabetically by functional group. Subsamples are denoted by lowercase letters.

Sample ID	Scientific Name	Tissue	$\delta^{13}C$ (‰, VPDB)	$\delta^{15}N$ (‰, AIR)	C%	N%	Atomic C:N Ratio
		Grass					
14VS-18a	*Alopecurus magellanicus*	Stems	–25.2	+4.8	42.1	1.9	25.8
14VS-18b		Inflorescences	–24.8	+6.2	41.7	2.7	18.1
14-VS-11a	*Dupontia* spp.	Roots	–25.6	+6.3	41.0	2.2	21.3
14-VS-11b		Root crowns	–26.5	+6.5	43.4	2.1	24.0
14-VS-11c		Stems/blades	–25.2	+7.4	40.8	2.7	17.4
14VS-11d		Spikelets	–27.6	–3.2	42.8	0.9	57.1
P14†	*Leymus arenarius*	Whole	–27.0	–2.8	42.8	1.3	37.4
14VS-9a	*Poaceae* spp.	Roots	–27.4	–3.3	37.1	0.9	48.4
14VS-9b		Root crowns	–28.7	–2.7	41.5	0.9	52.1
14VS-9c		Stems	–27.3	–2.6	41.8	0.8	60.4
14VS-9d		Spikelets	–26.7	+8.4	44.1	3.0	16.9
14VS-9e		Green stems	–28.2	–4.3	41.7	2.4	20.0
P12†	*Poaceae* spp.	Whole	–27.2	+1.5	41.5	1.9	26.0
P8†	*Poaceae* spp.	Whole	–27.0	+3.1	41.8	1.4	33.8
		Leguminous Forb					
15VS-216a	*Astragalus alpinus*	Roots	–31.0	–1.4	44.0	2.6	19.6

15VS-216b		Stems	–29.0	–2.0	44.4	2.4	21.8
15VS-216c		Leaves	–30.3	–1.0	40.2	4.2	11.1
15VS-216d		Flowers	–28.6	–1.1	44.2	3.3	15.8
15VS-221a		Roots	–29.8	–1.4	44.6	3.3	15.5
15VS-221b	*Astragalus alpinus*	Stems	–28.1	–1.5	43.8	2.8	18.3
15VS-221c		Leaves	–30.2	–1.0	41.5	3.8	12.8
15VS-221d		Flowers	–29.1	–0.5	44.0	3.6	14.3
15VS-204a		Roots	–30.3	–1.7	49.3	0.8	67.7
15VS-204b	*Oxytropis arctica*	Stems	–29.1	–1.7	44.5	2.7	18.9
15VS-204c		Leaves	–29.9	–1.4	43.0	3.7	13.5
15VS-204d		Flowers	–27.1	–1.2	34.6	2.8	14.4
P6a†		Stems	–27.1	–1.6	40.4	2.5	19.1
P6b†	*Oxytropis arctica*	Leaves	–28.7	–0.9	35.8	4.4	9.4
P6c†		Seedpod	–25.7	–0.6	42.0	4.7	10.5
14VS-17a		Branches	–28.1	–0.7	38.7	2.2	20.8
14VS-17b	*Oxytropis arctobia*	Leaves	–27.4	–1.6	38.3	1.6	27.1
14VS-17c		Stems	–26.9	–1.8	40.6	1.3	37.5
14VS-17d		Seed pods	–26.9	+0.5	41.2	1.7	28.5
14VS-1a		Roots	–25.8	–1.2	45.0	3.1	16.9
14VS-1b	*Oxytropis arctobia*	Stems	–25.8	–1.0	43.4	3.5	14.5
14VS-1c		Leaves	–26.2	–0.7	44.0	4.2	12.1
14VS-1d		Flowers	–25.1	–0.4	44.8	4.0	13.0

15VS-210a		Roots	–28.8	–0.9	46.0	2.7	19.8
15VS-210b		Branches	–29.4	–1.8	45.2	1.7	30.4
15VS-210c	*Oxytropis arctobia*	Leaves	–29.4	–1.2	42.2	2.4	20.2
15VS-210d		Aerial stems	–28.6	–2.0	43.6	1.5	35.0
15VS-210e		Seed pods	–28.2	–0.3	44.1	4.1	12.4
15VS-215a		Root crowns	–28.3	–0.9	44.6	2.8	18.6
15VS-215b		Stems	–27.6	–1.5	44.2	2.1	24.1
15VS-215c	*Oxytropis* spp.	Leaves	–29.3	+0.3	43.9	4.8	10.6
15VS-215d		Seed pods	–28.1	+0.6	41.8	4.3	11.5
15VS-215e		Seed pods	–26.2	+1.0	43.4	4.1	12.2
		Lichen					
14VS-13-1	*Cetraria tilesii*	Whole	–23.1	–6.0	38.4	0.4	110.3
15VS-202	*Cetraria tilesii*	Whole	–24.5	–8.3	35.9	0.5	83.3
15VS-203-1	*Cetraria tilesii*	Whole	–24.7	–6.1	36.4	0.3	131.8
15VS-214-1	*Cetraria tilesii*	Whole	–25.6	–7.6	40.3	0.4	123.2
15VS-219-1	*Cetraria tilesii*	Whole	–25.4	–8.1	38.2	0.4	114.6
15VS-3LK-1	*Cetraria tilesii*	Whole	–24.6	–7.9	40.5	0.3	161.1
14VS-13-2	*Thamnolia vermicularis*	Whole	–27.6	–2.4	38.2	0.6	77.9
15VS-203-2	*Thamnolia vermicularis*	Whole	–27.3	–7.0	40.6	0.4	108.6
15VS-209-1	*Thamnolia vermicularis*	Whole	–27.8	–5.5	40.0	0.5	101.0

15VS-214-2	*Thamnolia vermicularis*	Whole	–27.3	–4.9	37.3	0.6	78.2
15VS-217	*Thamnolia vermicularis*	Whole	–27.6	–7.1	35.6	0.5	86.5
15VS-219-2	*Thamnolia vermicularis*	Whole	–28.0	–7.0	40.2	0.6	78.9
15VS-3BC	*Thamnolia vermicularis*	Whole	–26.9	–7.4	39.4	0.4	102.9
15VS-3LK-2	*Thamnolia vermicularis*	Whole	–28.3	–3.7	42.5	0.5	97.5
P5†	*Thamnolia vermicularis*	Whole	–27.8	–8.7	42.2	0.5	92.0
		Moss					
15VS-209-2	*Sphagnum squarrosum*	Whole	–30.2	–2.6	30.2	0.7	49.6
15VS-213-2	*Sphagnum squarrosum*	Whole	–29.2	+0.5	37.8	0.9	46.9
15VS-214-3	*Sphagnum squarrosum*	Whole	–29.9	–4.1	28.3	0.7	44.0
15VS-219-3	*Sphagnum squarrosum*	Whole	–29.1	–3.9	29.9	0.9	38.6
15VS-220-2	*Sphagnum squarrosum*	Whole	–30.5	+5.1	35.9	2.0	21.0
		Non-leguminous Forb					
P4c†	*Oxyria digyna*	Flowers	–28.1	+1.7	43.2	3.2	15.6
P11a†	*Papaver radicatum*	Stems	–29.6	+2.7	40.5	1.6	30.3
P11b†		Leaves	–29.4	+5.6	40.0	2.6	18.2
P11c†		Flowers	–29.6	+4.3	44.0	3.6	14.2
P10†	*Pedicularis lanata*	Whole	–29.8	–2.4	42.5	1.0	48.3
14VS-14a	*Petasites frigidus*	Stems	–26.5	+1.8	40.1	1.0	46.0
14VS-14b		Leaves	–28.4	+2.4	40.1	2.3	20.5

14VS-14c		Inflorescences	–26.1	+2.5	44.9	2.0	26.3
15VS-220a		Roots	–29.8	–1.5	41.7	2.1	23.7
15VS-220b		Bulbils	–29.3	–1.9	41.9	1.1	43.6
15VS-220c	*Saxifraga cernua*	Stems	–29.5	+0.2	42.9	0.4	130.5
15VS-220d		Leaves	–30.5	+1.0	37.7	0.9	46.4
15VS-220e		Flowers	–28.7	+5.5	40.6	1.1	43.6
P13a†		Stems	–27.6	–2.6	40.8	0.4	129.6
P13b†	*Saxifraga cernua*	Leaves	–29.7	–2.5	38.2	1.0	44.3
P13d†		Seeds	–28.4	–1.8	40.3	1.6	29.3
14VS-5a		Leaves	–29.7	+1.8	37.3	1.2	35.5
14VS-5b	*Saxifraga eschscholtzii*	Stems	–26.6	+2.1	41.8	1.7	28.6
14VS-5c		Flowers	–29.2	+4.1	43.4	3.2	15.6
14VS-8a		Leaves	–29.4	–1.8	44.8	0.9	56.1
14VS-8b	*Saxifraga eschscholtzii*	Basal buds	–27.1	+1.4	36.1	1.1	38.6
14VS-8c		Dead leaves	–30.1	–1.8	41.0	1.0	45.9
14VS-8d		Flowers	–26.2	+3.3	43.5	2.4	21.5
15VS-205a		Leaves	–30.3	–1.3	51.2	1.1	53.6
15VS-205b	*Saxifraga eschscholtzii*	Leaves	–29.9	–1.3	44.7	1.1	46.3
15VS-205c		Leaves	–30.3	–0.7	43.6	1.3	38.4
15VS-205d		Leaves	–29.7	–0.9	40.4	1.3	37.0
P2a†	*Saxifraga hirculus*	Stems	–25.9	–1.1	43.0	1.2	43.3
15VS-1BC	*Saxifraga oppositifolia*	Whole	–27.9	–1.4	32.1	0.9	43.5

P9†	*Saxifraga oppositifolia*	Whole	–30.1	–0.5	42.5	1.3	37.8
		Rose/Heath					
15VS-5LKa	*Cassiope tetragona*	Stems	–29.3	–6.8	48.9	0.7	78.1
15VS-5LKb		Leaves	–28.9	–5.4	48.8	0.8	67.1
P15†	*Cassiope tetragona*	Whole	–31.1	–3.6	47.2	0.8	73.3
14VS-19a	*Dryas integrifolia*	Roots	–30.1	+1.9	47.1	1.0	52.8
14VS-19b		Stems	–30.7	+1.3	48.7	0.9	63.0
14VS-19c		Green leaves	–31.5	+1.1	47.0	2.1	26.7
14VS-19d		Brown leaves	–31.5	+0.9	46.2	1.1	50.1
14VS-2a	*Dryas integrifolia*	Stems	–29.5	–2.6	48.8	0.8	70.9
14VS-2b		Leaves	–30.3	–4.6	46.2	1.8	30.5
15VS-206a	*Dryas integrifolia*	Branches	–31.0	–1.1	46.2	0.9	57.8
15VS-206b		Leaves	–30.8	–2.2	44.4	1.6	31.6
15VS-206c		Aerial stems	–28.9	–1.9	44.2	2.4	21.9
15VS-206d		Flowers	–28.3	–0.9	30.7	1.9	19.2
15VS-4BCa	*Dryas octopetala*	Branches	–29.1	–4.0	45.2	0.9	58.5
15VS-4BCb		Stems	–27.9	–6.0	45.8	0.8	68.5
15VS-4BCc		Leaves	–30.3	–6.0	49.2	2.3	24.6
15VS-4BCd		Flowers	–30.0	–5.3	47.4	2.7	20.5
15VS-5BCa	*Dryas octopetala*	Branches	–30.1	–0.7	48.2	0.8	66.2
15VS-5BCb		Stems	–28.6	–1.7	44.9	1.2	43.2

15VS-5BCc	*Dryas octopetala*	Leaves	–30.0	–1.4	47.8	2.5	22.5
15VS-5BCd		Flowers	–29.0	–1.1	40.5	2.2	21.8
P1a†		Stems	–30.2	–2.9	43.4	1.1	47.7
P1b†		Flowers	–30.2	–2.8	45.7	1.3	40.1
P1c†		Leaves	–30.8	–2.9	46.7	1.8	29.5
P1f†		Flowers	–29.7	–2.1	57.5	2.3	29.2
		Sedge					
14VS-16a	*Carex aquatilis stans*	Roots	–24.8	+5.0	44.8	0.9	60.3
14VS-16b		Root crowns	–26.4	+5.0	44.7	1.3	39.9
14VS-16c		Stems	–26.4	+5.2	43.6	2.5	20.1
14VS-16d		Inflorescences	–26.1	+5.0	44.9	2.0	25.6
15VS-208a	*Carex aquatilis stans*	Roots	–27.9	+2.5	37.7	1.3	33.0
15VS-208b		Root crowns	–27.5	+2.0	40.5	0.9	50.5
15VS-208c		Leaves	–28.0	+0.4	45.0	3.0	17.7
15VS-208d		Stems	–26.3	+2.3	43.8	2.2	23.4
15VS-208e		Inflorescences	–26.5	+3.0	44.9	2.1	24.8
15VS-213a	*Carex aquatilis stans*	Roots	–26.8	+1.6	45.3	0.7	72.9
15VS-213b		Root crowns	–26.8	+0.9	46.9	0.9	60.4
15VS-213c		Leaves	–28.2	+0.5	46.7	2.6	21.2
15VS-213d		Stems	–25.0	+0.1	45.6	1.3	40.8
15VS-213e		Inflorescences	–26.0	+0.8	45.4	1.7	31.9
15VS-218a	*Carex aquatilis stans*	Root crowns	–27.8	–2.8	38.5	0.9	49.0

15VS-218b		Leaves	–28.0	–3.2	42.4	1.8	26.9
15VS-218c		Stems	–26.4	–3.8	43.3	1.3	39.5
15VS-218d		Inflorescences	–27.4	–1.8	42.3	1.9	26.2
15VS-1LKa	*Eriophorum angustifolium*	Stems	–27.4	+3.7	43.3	0.3	146.1
15VS-1LKb		Bolls	–27.0	+6.1	42.9	1.5	32.6
14VS-6b	*Eriophorum callitrix*	Bolls	–25.5	+6.8	42.2	3.1	15.8
15VS-201a		Roots	–26.9	+3.9	41.5	0.6	83.6
15VS-201b		Root crowns	–27.1	+4.5	43.0	0.5	105.2
15VS-201c	*Eriophorum callitrix*	Leaves	–26.8	+4.7	44.5	0.6	85.4
15VS-201d		Stems	–26.9	+4.1	44.4	0.7	78.5
15VS-201e		Bolls	–26.0	+4.7	43.8	1.9	26.4
14VS-10a	*Eriophorum latifolium*	Stems	–24.4	+2.9	42.8	1.3	39.9
14VS-10b		Bolls	–24.6	+4.3	43.2	2.0	25.7
14VS-15a	*Eriophorum latifolium*	Stems	–25.1	+6.7	44.0	1.5	33.1
14VS-15b		Bolls	–23.9	+8.4	45.0	2.3	23.0
		Willow					
14VS-12a		Roots	–29.4	+0.5	47.1	0.7	73.6
14VS-12b	*Salix arctica*	Branches	–29.7	–0.7	47.7	0.6	90.0
14VS-12c		Catkins	–26.8	–0.3	45.2	1.3	41.9
14VS-12d		Leaves	–30.6	–1.4	43.4	3.2	15.7
14VS-4a	*Salix arctica*	Stems	–28.6	–0.6	48.1	1.0	58.6
14VS-4b		Leaves	–27.8	+0.4	47.5	2.8	19.8

14VS-4c		Catkins	–26.7	+0.4	45.3	1.8	29.7
14VS-4d		Branches	–27.6	+0.6	48.1	0.7	75.6
14VS-7a		Stems	–27.8	+1.2	47.3	0.7	77.2
14VS-7b	*Salix arctica*	Leaves	–27.9	+1.6	48.3	3.4	16.8
14VS-7c		Catkins	–26.0	+2.4	43.6	3.1	16.3
15VS-207a		Roots	–29.0	–2.5	45.6	0.8	70.2
15VS-207b	*Salix arctica*	Branches	–28.8	–3.4	47.4	1.0	53.2
15VS-207c		Leaves	–28.9	–2.7	45.4	3.2	16.6
15VS-207d		Catkins	–28.1	–3.0	38.8	1.7	27.4
15VS-211a		Roots	–29.5	–3.7	47.6	1.2	48.0
15VS-211b	*Salix arctica*	Branches	–28.9	–5.2	50.5	0.7	80.8
15VS-211c		Leaves	–29.9	–4.6	45.5	2.6	20.3
15VS-211d		Catkins	–30.4	–4.4	48.3	0.9	64.1
15VS-2BCa		Roots	–27.6	–0.8	43.3	1.0	50.6
15VS-2BCb		Branches	–29.9	–1.0	49.2	0.7	80.0
15VS-2BCc	*Salix arctica*	Green branches	–28.5	–1.5	50.6	1.0	58.7
15VS-2BCd		Leaves	–27.9	–0.9	48.4	3.6	15.6
15VS-2BCe		Catkins	–27.7	0.0	44.7	3.4	15.5
15VS-4LKa		Roots	–27.9	–1.3	46.0	0.8	68.0
15VS-4LKb	*Salix arctica*	Branches	–26.9	–1.9	46.5	0.3	164.2
15VS-4LKc		Green branches	–28.0	–3.5	48.8	0.9	61.6
P3a[†]	*Salix arctica*	Stems	–28.5	–3.1	46.8	1.1	50.1

P3b†	Leaves	–28.3	–2.3	48.0	1.2	47.6
P3c†	Flowers	–27.1	–2.5	39.8	1.7	28.0

† From pilot study

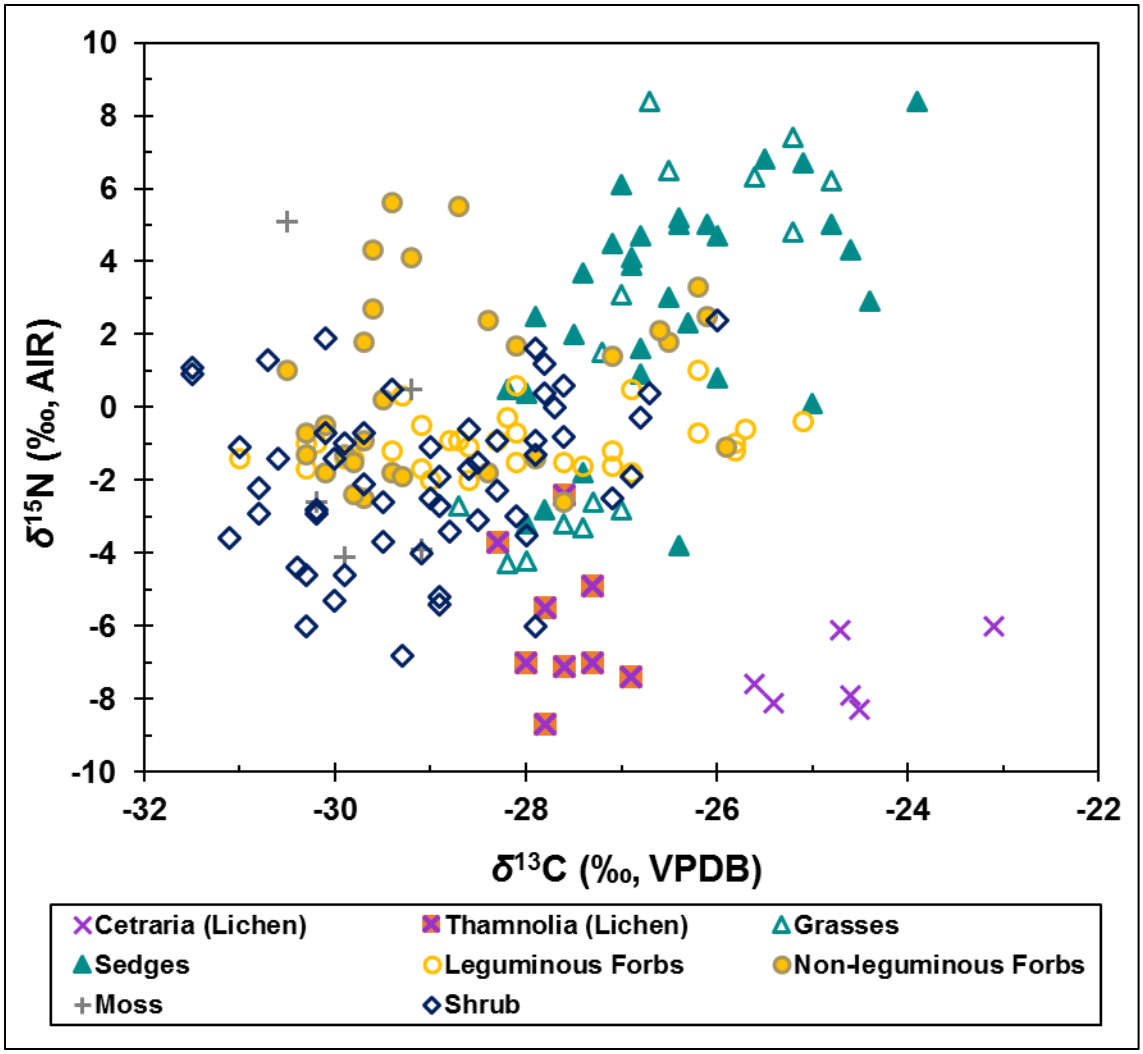


Figure 2.5. The δ^{15}N vs. δ^{13}C of all tissue subsamples from different forage plants collected on Banks Island in 2014 and 2015.

Table 2.8. Mean C% and N% of forage samples from Banks Island, their mean atomic C:N ratios, and sample size.

Functional Group	Mean C%	Mean N%	Mean Atomic C:N	*n*
Cetraria tilesii	38.3	0.4	116.8	6
Thamnolia vermicularis	39.6	0.5	90.4	9
All Lichen	38.9	0.4	101.7	15
Moss	32.4	1.1	35.7	5
Non-leguminous Forbs	41.5	1.5	31.8	30
Leguminous Forbs	42.8	3.0	16.5	33
All Forbs	42.1	2.3	21.6	63
Grass	42.1	1.8	27.1	15
Sedge	43.6	1.5	32.9	30
All Graminoids	42.9	1.7	29.7	45
Rose/Heath	45.9	1.5	36.5	25
Dwarf Willow	46.4	1.6	34.6	30
All Shrubs	46.2	1.5	35.5	55

2.4.3 Geographic Variation in Forage Sample $\delta^{13}C$ and $\delta^{15}N$

The results of Mann-Whitney *U* tests for geographic differences in forage $\delta^{13}C$ and $\delta^{15}N$ (Table 2.9) suggest that there are statistically significant ($p < 0.05$) variations in both the $\delta^{13}C$ and $\delta^{15}N$ of sedges, graminoids, and willow between southern and northern parts of Banks Island. The $\delta^{13}C$ of legumes, non-leguminous forbs, and forbs is significantly different between the southern and northern parts of the island (p = 0.00, 0.01, 0.00, respectively), and when willow and rose/heath are aggregated, there is a statistically significant difference in $\delta^{15}N$ (p = 0.01). Conversely, lichen $\delta^{13}C$ and $\delta^{15}N$ does not vary geographically on Banks Island. In all cases where there is significant geographic variation in isotopic compositions, the trend is towards lower $\delta^{13}C$ and/or $\delta^{15}N$ at higher latitudes. This is probably related to the difference in climatic regimes between the southern and northern parts of the island (Chapter 4), and enrichments in both ^{13}C and ^{15}N associated with water use efficiency and reduced water availability in forage in colder, more arid locales (Farquhar et al. 1982, 1989; Handley and Raven 1992; Handley et al. 1999; Barbour and Farquhar 2000). Subsequently, forage sources were divided into 13 categories for the initial dietary mixing model analyses: *Cetraria tilesii*; grass; moss; northern legume; northern non-leguminous forb; northern sedge; northern willow, rose/heath; southern legume; southern non-leguminous forb; southern sedge; southern willow; and *Thamnolia vermicularis*.

Table 2.9. Results of Mann-Whitney *U* tests comparing isotopic compositions of forage samples from northern and southern sites. Moss samples were only collected at northern sites and were therefore not tested.

Functional Group	*p*-values	
	$\delta^{13}C$	$\delta^{15}N$
Cetraria tilesii	0.27	0.53
Thamnolia vermicularis	0.90	0.30
All Lichen	0.67	0.22
Non-leguminous Forb	0.01*	0.20
Leguminous Forb	0.00*	0.59
All Forb	0.00*	0.07
Grass	0.23	0.23
Sedge	0.00*	0.00*
All Graminoid	0.00*	0.00*
Rose/Heath	0.66	0.66
Dwarf Willow	0.03*	0.00*
All Shrub	0.20	0.01*

* Denotes a statistically significant difference in the isotopic compositions of samples from northern and southern collection sites at the 0.05 significance level.

2.4.4 Bayesian-Imputed Trophic Discrimination Factors (TDFs)

In all four SIDER runs (caribou $\Delta^{13}C_{coll\text{-}diet}$, muskox $\Delta^{13}C_{coll\text{-}diet}$, caribou $\Delta^{15}N_{coll\text{-}diet}$, and muskox $\Delta^{15}N_{coll\text{-}diet}$), Gelman-Rubin values for all levels were <1.1 and each chain had an effective sample size of 18000.

Based on the SIDER model parameters used, we obtained $\Delta^{13}C_{coll\text{-}diet}$ and $\Delta^{15}N_{coll\text{-}diet}$ of +4.7 ±1.5‰ and +3.3 ±1.1‰, respectively, for caribou and $\Delta^{13}C_{coll\text{-}diet}$ and $\Delta^{15}N_{coll\text{-}diet}$ estimates of +2.6 ±1.8‰ and +3.7 ±1.3‰, respectively, for muskoxen. Additionally, these TDF estimates varied by less than 0.03‰ across repeated SIDER runs, further suggesting that the chains approached convergence and were adequately mixed. We also experimented with MixSIAR models utilizing other carbon and nitrogen TDFs (Szpak et al. 2012; Appendix A, Supplemental Table A1 and A2). We consider species-specific TDF values imputed by SIDER, however, to provide a more effective measure of uncertainty surrounding TDF estimates than generalized TDF parameters obtained through the meta-analysis of TDFs from taxa from other habitats and trophic levels (e.g. Szpak et al. 2012). Our discussion that follows will therefore refer to the mixing model solutions that used Bayesian-derived rather than generalized TDFs.

2.4.5 Estimates of Source Contributions to Caribou Bone Collagen Isotopic Compositions – Maximum Source Divisions

Model diagnostics suggest that the Markov chains approached convergence. All 29 variables in the caribou dietary mixing model had Gelman-Rubin values of <1.01, and only a single variable had an absolute *Z*-score higher than 1.96 (residual proportion, chain 2, Z = -2.510). Figure 2.6 presents the average $\delta^{13}C$ and $\delta^{15}N$ and standard deviations of all forage sources, adjusted to the $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ of modern caribou collagen using the SIDER TDFs. The pairs plot (Figure 2.7) displays the posterior probability distributions of each forage source (diagonal panes), pairwise densities (upper right panes), and pairwise numerical correlation coefficients (lower left panes) for each forage source. Larger correlation coefficients (in larger font) indicate that the mixing model struggles to differentiate between the source pairs (Inger et al. no date), and that if possible, the two sources should be aggregated. Figure 2.7 demonstrates that the only significant correlation

is between southern legumes (*SLegume*) and yellow lichens (*Cetraria*), which have a moderate-to-strong negative correlation (r = -0.66). The pairwise density plot for this source pair, however, demonstrates that although a negative correlation exists, the relationship is not strongly linear. For this reason, and because legumes and lichens are distant both phylogenetically as well as isotopically, we did not aggregate them.

Estimates of the proportional contribution of each forage source to caribou bone collagen are presented in Figure 2.8 and Table 2.10. For clarity, the posterior probability distributions in Figure 2.8 are rescaled to equal one. Figure 2.8 and Table 2.10 both suggest that *Cetraria* and southern sedges make the largest contributions to caribou bone collagen (median dietary proportions = 19% and 18%, respectively), while southern legumes and northern sedges have smaller median dietary proportions (9% and 7%, respectively). All other sources have median values of 5% percent or less. As anticipated, the probability distributions of all but a few forage resources (rose/heath, moss, and northern non-leguminous forbs, willows and legumes) are large when no source aggregation is used.

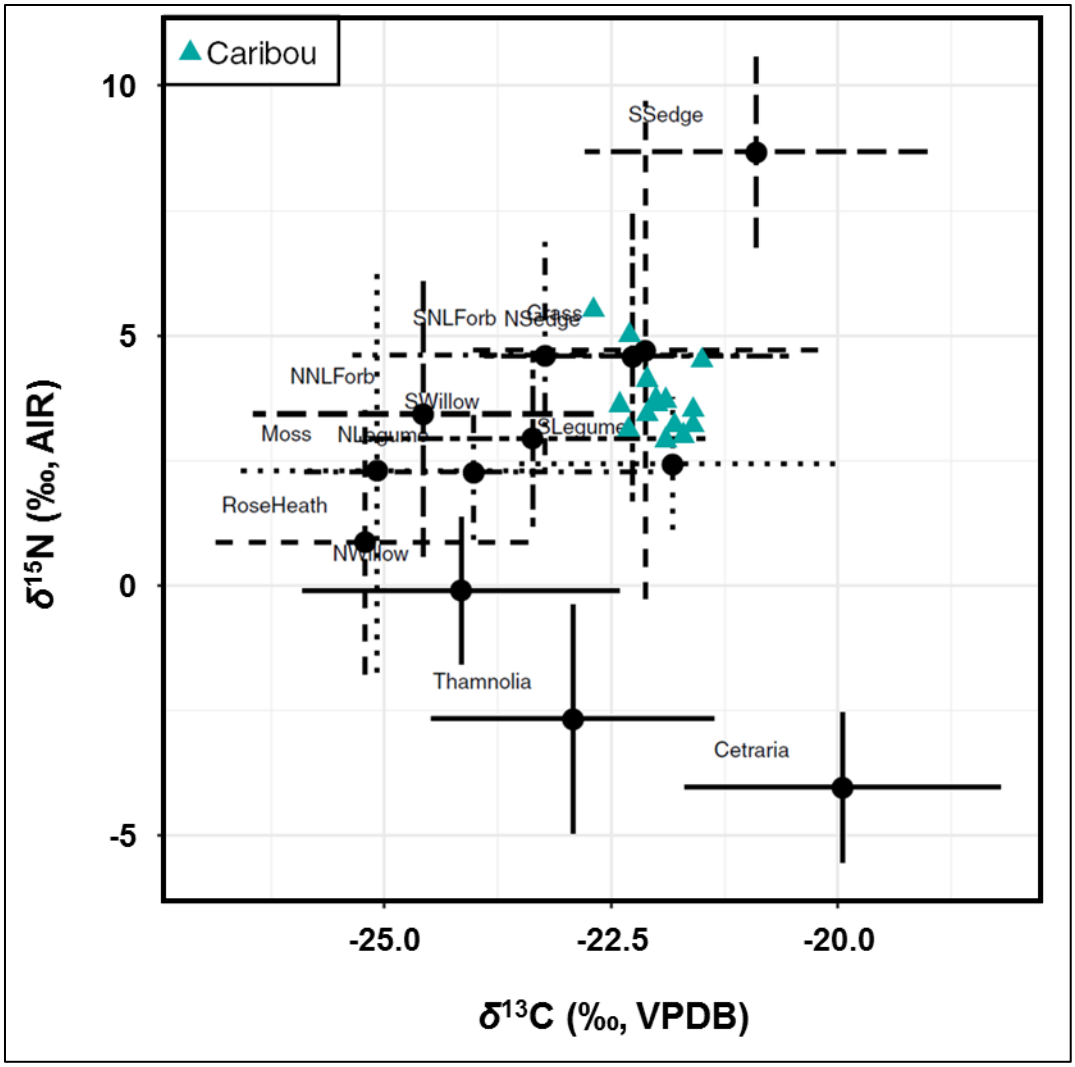


Figure 2.6. Average $\delta^{15}N$ vs. $\delta^{13}C$ and standard deviations of all forage sources, adjusted to the $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ of modern caribou bone collagen (teal triangles) using the SIDER-imputed TDFs.

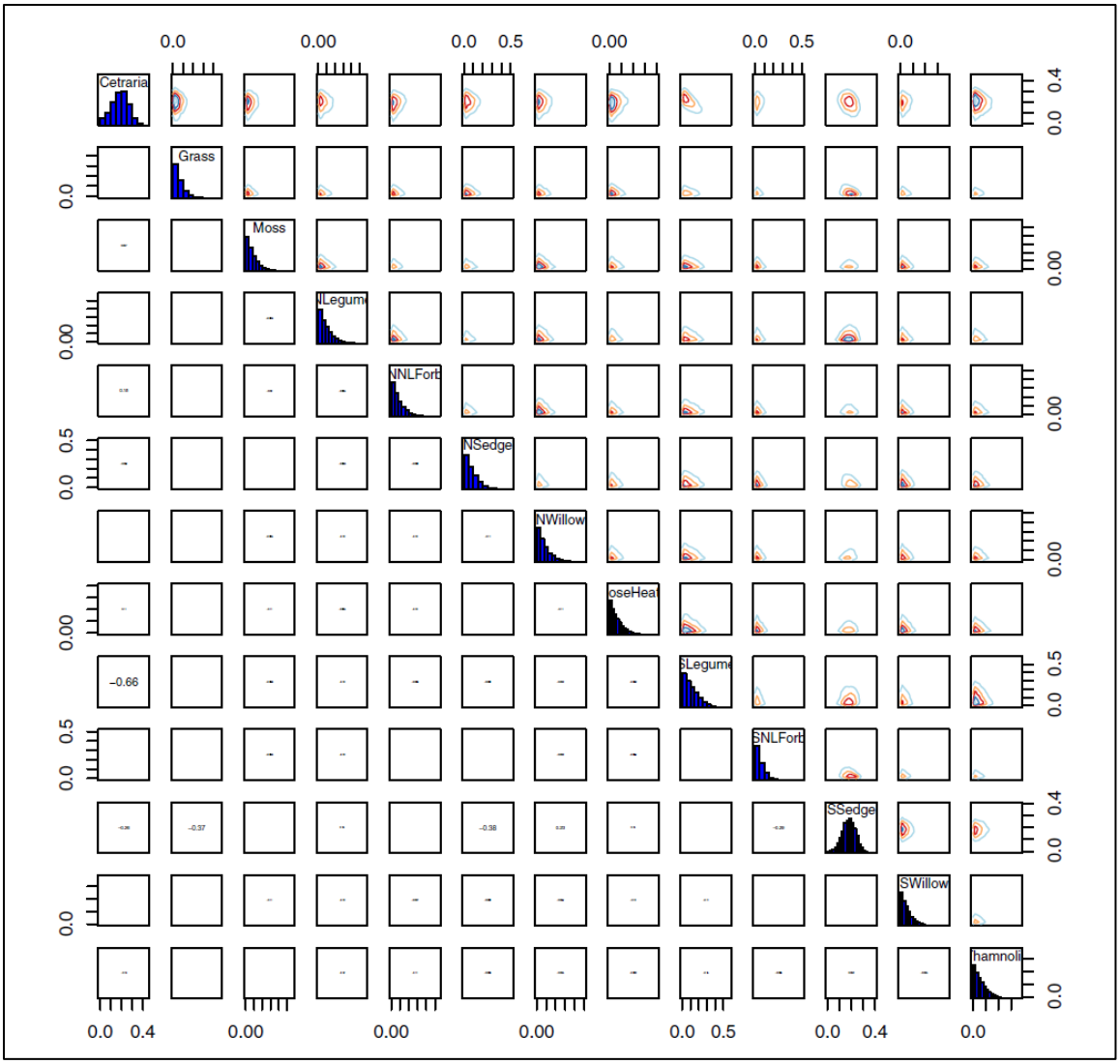


Figure 2.7. Pairs plot for all forage sources in the caribou dietary mixing model. Posterior probability distributions for individual forage sources (in blue) are shown in the diagonal panes. Pairwise densities plots are shown in the upper right panes. Numerical correlation coefficients are shown in the lower left panes; font size is deliberately scaled to correlation size to draw the reader's attention only to instances of high correlation between sources.

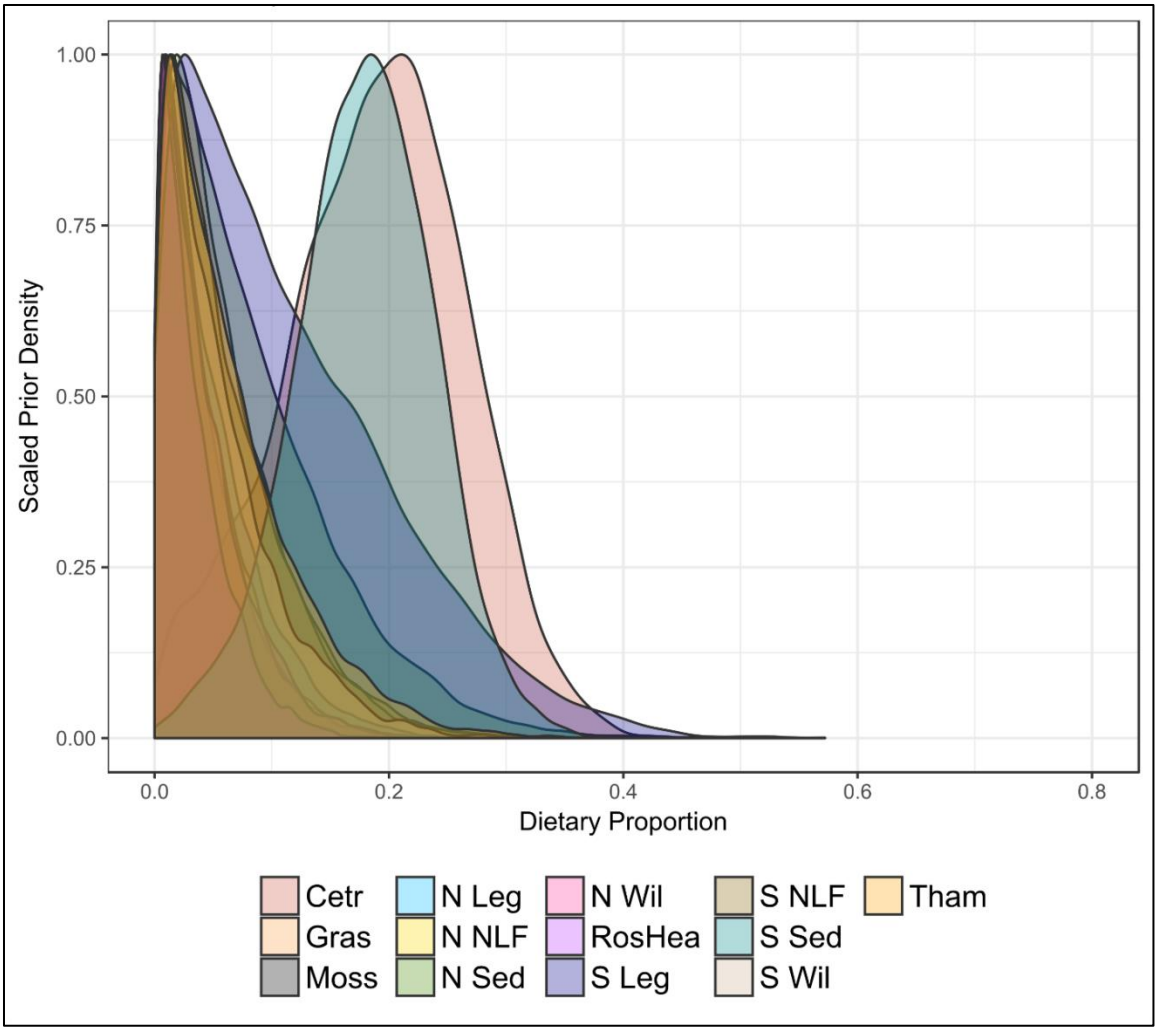


Figure 2.8. Posterior probability distributions of all forage sources to caribou bone collagen. Forage items are: *Cetraria tilesii* (Cetr); grasses (Gras); moss (Moss); northern legumes (N Leg); northern non-leguminous forbs (N NLF); northern sedges (N Sed); northern willow (N Wil); rose/heath (RosHea); southern legumes (S Leg); southern non-leguminous forbs (S NLF); southern sedges (S Sed); southern willow (S Wil); and *Thamnolia vermicularis* (Tham). The figure suggests that *Cetraria tilesii*, southern sedges, and likely southern legumes are largest contributors to modern caribou bone collagen carbon and nitrogen isotope compositions.

Table 2.10. Mean and median values and 95% credible intervals of the posterior probability distributions of all forage sources, indicating the estimated proportional contribution of each forage source to caribou bone collagen isotopic compositions on Banks Island. Values correspond to the histograms in Figures 2.7 and 2.8.

Forage Source	Median (%)	Mean (%)	95% CI
Rose/Heath	0.03	0.03	0.00 – 0.11
Moss	0.03	0.04	0.00 – 0.13
Northern Non-leguminous Forb	0.03	0.04	0.00 – 0.14
Northern Dwarf Willow	0.03	0.04	0.00 – 0.14
Northern Leguminous Forb	0.04	0.04	0.00 – 0.15
Southern Dwarf Willow	0.04	0.05	0.00 – 0.18
Grass	0.05	0.06	0.00 – 0.18
Southern Non-leguminous Forb	0.05	0.06	0.00 – 0.19
Thamnolia vermicularis	0.05	0.06	0.00 – 0.21
Northern Sedge	0.07	0.08	0.00 – 0.25
Southern Legume	0.09	0.12	0.00 – 0.33
Southern Sedge	0.18	0.18	0.06 – 0.29
Cetraria tilesii	0.19	0.19	0.03 – 0.33

2.4.6 Estimates of Source Contributions to Caribou Bone Collagen Isotopic Compositions – Aggregated Source Divisions

Following DeVries et al. (2016) we aggregated the original 13 posterior probability distributions into eight categories: moss, grass, *Thamnolia vermicularis*, non-leguminous forbs, shrubs, legumes, *Cetraria tilesii*, and sedge. Other aggregations are either nonsensical because they group clearly distinct forage types (as is case with *Cetraria* and *Thamnolia*), or did not reduce the probability distribution ranges. Figure 2.9 presents the average $\delta^{13}C$ and $\delta^{15}N$ and standard deviations of aggregated forage sources, adjusted to the $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ of modern caribou collagen using the SIDER TDFs.

Estimates of the proportional contribution of aggregated forage types to caribou bone collagen are presented in Figure 2.10 and Table 2.11. When aggregated, the median dietary proportion of sedge increases to 26%, while the proportional estimate for *Cetraria tilesii*, which is not aggregated with any other forage source, remains the same (19%). The median dietary proportions of legumes, shrubs, and non-leguminous forbs all increase. Probability distribution ranges for all aggregated forage sources except sedges remain large, even at relatively large sample sizes, as with shrubs. Large probability distribution ranges are probably unavoidable given that caribou and muskoxen feed from a single trophic level, the forage sources we include share a common photosynthetic pathway, and only two isotope systems are used.

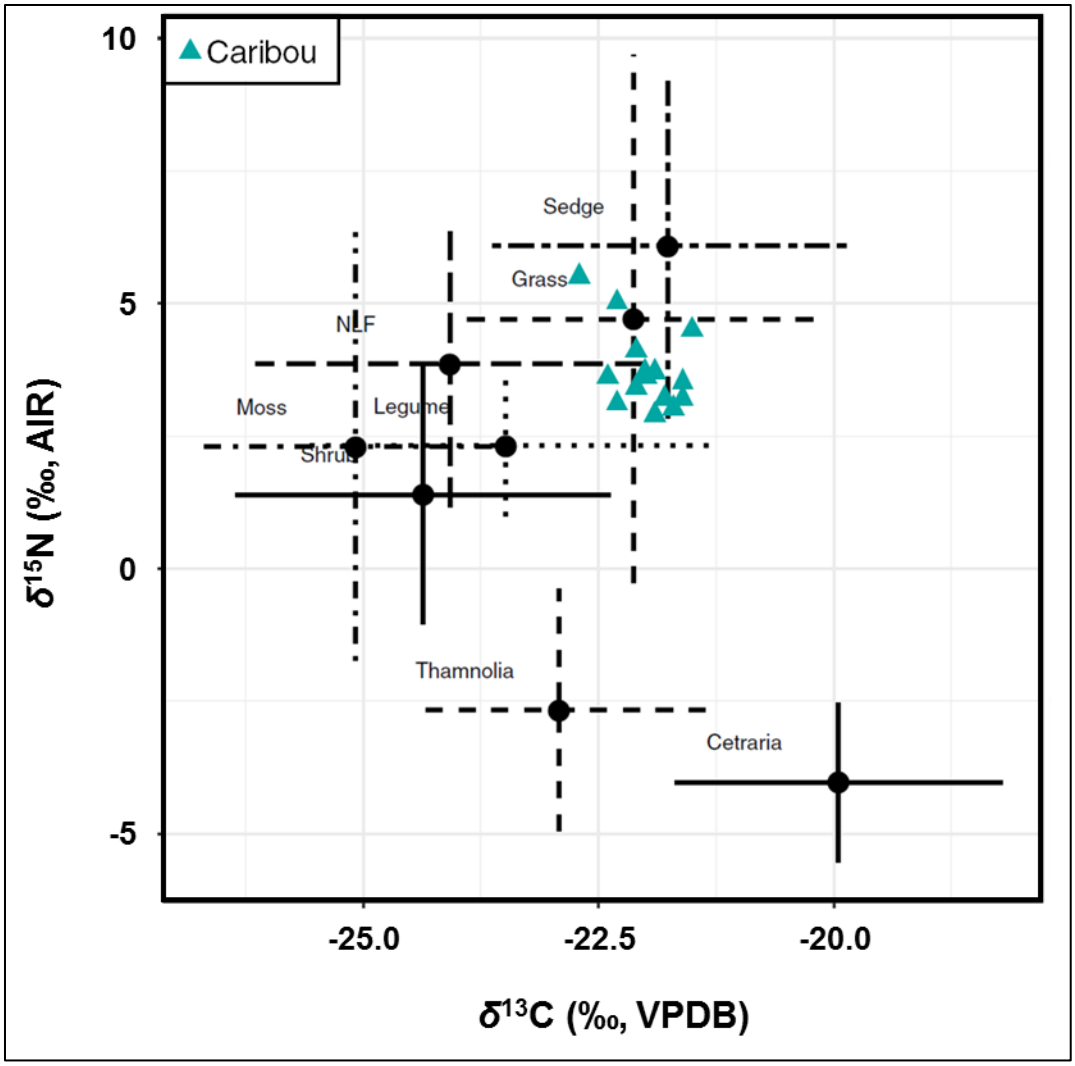


Figure 2.9. Average $\delta^{15}N$ vs. $\delta^{13}C$ and standard deviations of aggregated forage sources, adjusted to the $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ of modern caribou (teal triangles) using the SIDER-imputed TDFs.

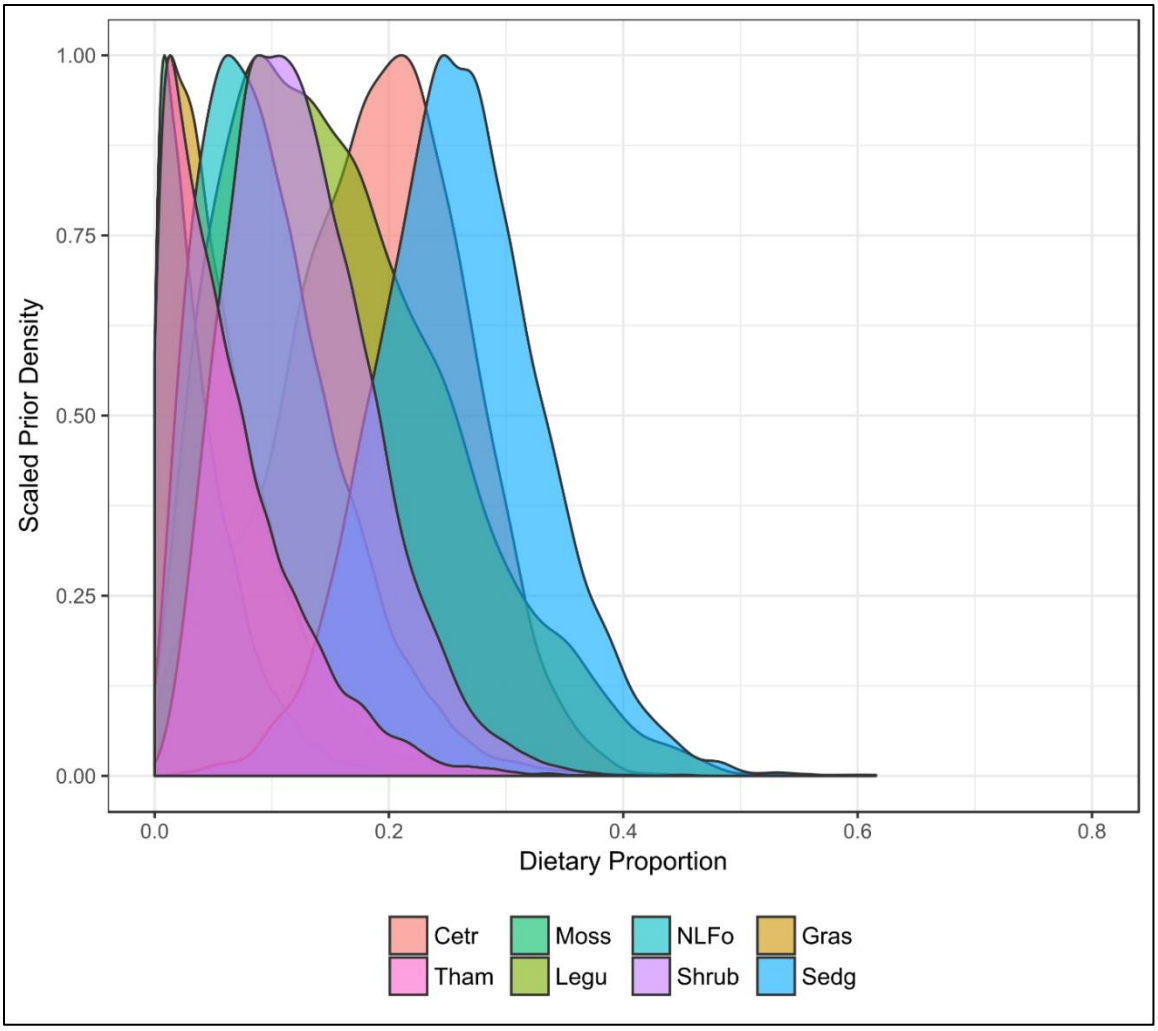


Figure 2.10. Posterior probability distributions of aggregated forage sources to caribou bone collagen. Forage items are: *Cetraria tilesii* (Cetr); *Thamnolia vermicularis* (Tham); moss (Moss); legumes (Legu); non-leguminous forbs (NLFo); shrubs (Shrub); grasses (Gras); sedges (Sedg). The figure suggests that, with *a posteriori* source aggregation, the proportional contributions of legumes, shrubs, and non-leguminous forbs, respectively, to caribou bone collagen carbon and nitrogen isotope compositions increase.

Table 2.11. Mean and median values and 95% credible intervals of the posterior probability distributions of aggregated forage sources, indicating the estimated proportional contribution of each forage source to caribou bone collagen isotopic compositions on Banks Island. Values correspond to the histograms in Figure 2.10.

Forage Source	Median (%)	Mean (%)	95% CI
Moss	0.03	0.04	0.00 – 0.13
Grass	0.05	0.06	0.00 – 0.18
Thamnolia vermicularis	0.05	0.06	0.00 – 0.21
Non-leguminous Forb	0.09	0.10	0.01 – 0.24
Shrub	0.12	0.13	0.03 – 0.26
Leguminous Forb	0.15	0.16	0.02 – 0.38
Cetraria tilesii	0.19	0.19	0.03 – 0.33
Sedge	0.26	0.26	0.13 – 0.41

2.4.7 Estimates of Source Contributions to Muskox Bone Collagen Isotopic Compositions – Maximum Source Divisions

Model diagnostics for the muskox dietary mixing model also suggest that all Markov chains approached convergence. All 29 variables have Gelman-Rubin values of <1.05, and only two variables in two chains have absolute *Z*-scores higher than 1.96 (northern sedge, chain 1, $Z = 3.270$; moss, chain 2, $Z = -2.414$).

The average $\delta^{13}C$ and $\delta^{15}N$ and standard deviations of all forage sources, adjusted to the $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ of modern muskoxen collagen using the SIDER TDFs are displayed in Figure 2.11. The pairs plot for muskoxen (Figure 2.12) reveals moderate negative correlation coefficients between southern legumes and *Cetraria tilesii* ($r = -0.54$), and between grass and southern sedges ($r = -0.54$). The pairwise density plots for these forage sources indicate that neither negative correlation is strongly linear, and again we did not aggregate legumes and *Cetraria tilesii*. We did, however, aggregate grass with southern and northern sedges.

Estimates of the proportional contribution of each forage source to muskox bone collagen are presented in Figure 2.13 and Table 2.12. Again, the posterior probability distributions in Figure 2.13 have been rescaled to 1 for clarity. The mixing model suggests that *Cetraria tilesii* makes the largest contribution to muskox bone collagen (median dietary proportion = 41%), followed by southern sedges (median dietary proportion = 21%). All other forage sources have median source contributions of less than 5%. As with caribou, however, the range of posterior probabilities for many of the forage sources (especially *Cetraria tilesii*) is very large.

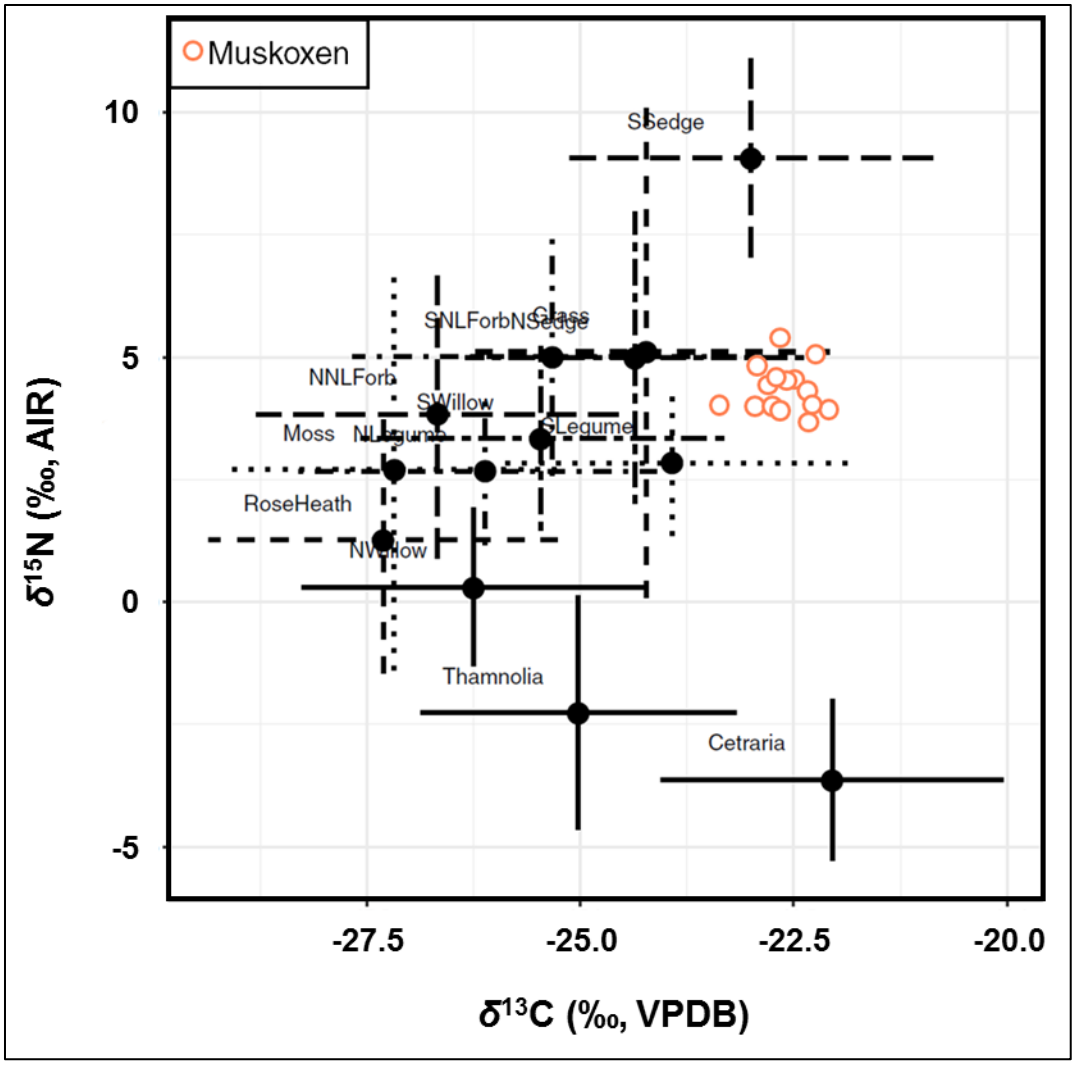


Figure 2.11. Average δ^{15}N vs. δ^{13}C and standard deviations of all forage sources, adjusted to the $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ of modern muskox bone collagen (pink circles) using the SIDER-imputed TDFs.

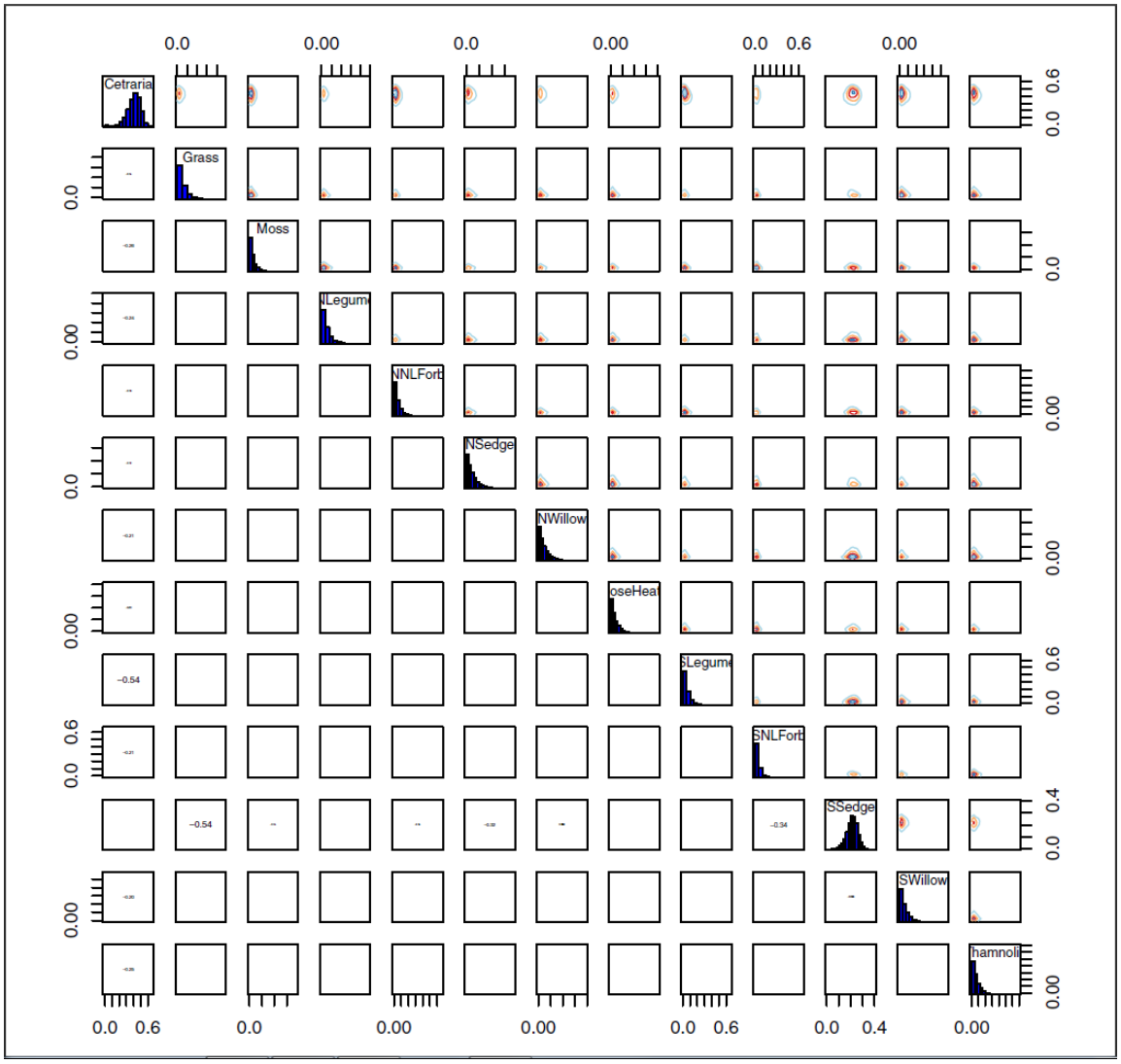


Figure 2.12. Pairs plot for all forage sources in the muskox dietary mixing model. Posterior probability distributions for individual forage sources (in blue) are shown in the diagonal panes. Pairwise densities plots are shown in the upper right panes. Numerical correlation coefficients are shown in the lower left panes; font size is deliberately scaled to correlation size to draw the reader's attention only to instances of high correlation between sources.

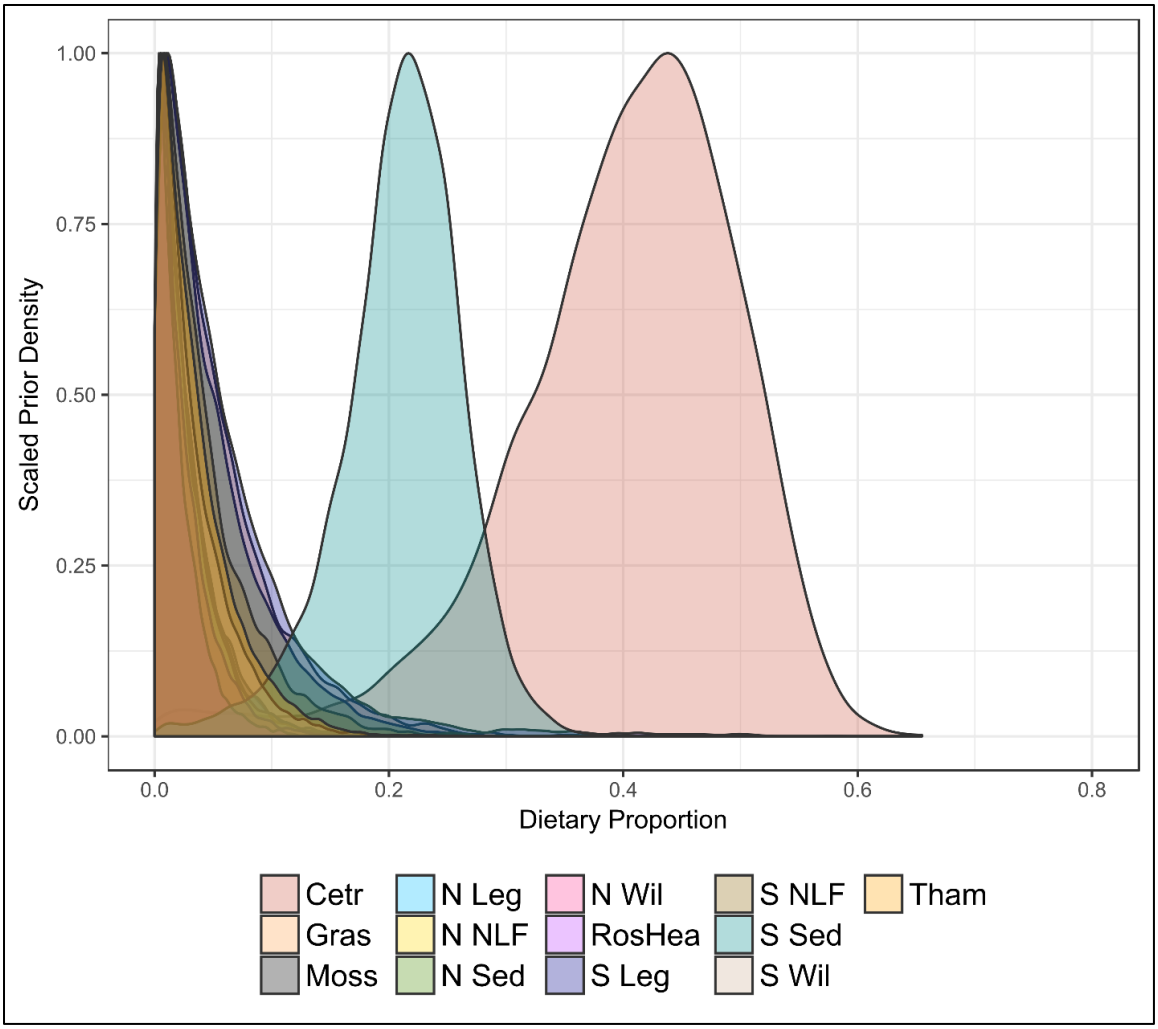


Figure 2.13. Posterior probability distributions of all forage sources to muskox bone collagen. Forage items are: *Cetraria tilesii* (Cetr); grasses (Gras); moss (Moss); northern legumes (N Leg); northern non-leguminous forbs (N NLF); northern sedges (N Sed); northern willow (N Wil); rose/heath (RosHea); southern legumes (S Leg); southern non-leguminous forbs (S NLF); southern sedges (S Sed); southern willow (S Wil); and *Thamnolia vermicularis* (Tham). The figure suggests that *Cetraria tilesii* and southern sedges, are largest contributors to modern muskox bone collagen carbon and nitrogen isotope compositions.

Table 2.12. Mean and median values and 95% credible intervals of the posterior probability distributions of all forage sources, indicating the estimated proportional contribution of each forage source to muskox bone collagen isotopic compositions on Banks Island. Values correspond to the histograms in Figures 2.12 and 2.13.

Forage Source	Median (%)	Mean (%)	95% CI
Rose/Heath	0.01	0.02	0.00 – 0.07
Northern Dwarf Willow	0.02	0.02	0.00 – 0.09
Northern Non-leguminous Forb	0.02	0.03	0.00 – 0.10
Northern Leguminous Forb	0.02	0.03	0.00 – 0.09
Moss	0.02	0.03	0.00 – 0.10
Southern Dwarf Willow	0.02	0.03	0.00 – 0.11
Thamnolia vermicularis	0.03	0.03	0.00 – 0.12
Southern Non-leguminous Forb	0.03	0.04	0.00 – 0.15
Northern Sedge	0.03	0.05	0.00 – 0.17
Grass	0.04	0.05	0.00 – 0.18
Southern Legume	0.04	0.06	0.00 – 0.23
Southern Sedge	0.21	0.21	0.09 – 0.30
Cetraria tilesii	0.41	0.40	0.15 – 0.55

2.4.8 Estimates of Source Contributions to Muskox Bone Collagen Isotopic Compositions – Aggregated Source Divisions

The posterior probability distributions of forage sources were aggregated into the same groups as in caribou. Figure 2.14 displays the average $\delta^{13}C$ and $\delta^{15}N$ and standard deviations of aggregated forage sources, adjusted to the $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ of modern muskoxen using the SIDER TDFs. Estimates of the proportional contribution of aggregated forage types to muskox bone collagen are presented in Figure 2.15 and Table 2.13. Again, the median dietary proportion of *Cetraria tilesii* remains the same, while the median dietary proportion of sedge increases slightly to 26%. The median dietary proportions of all other aggregated forage sources remain below 10% (though 95% credible intervals range as high as 26% for legumes).

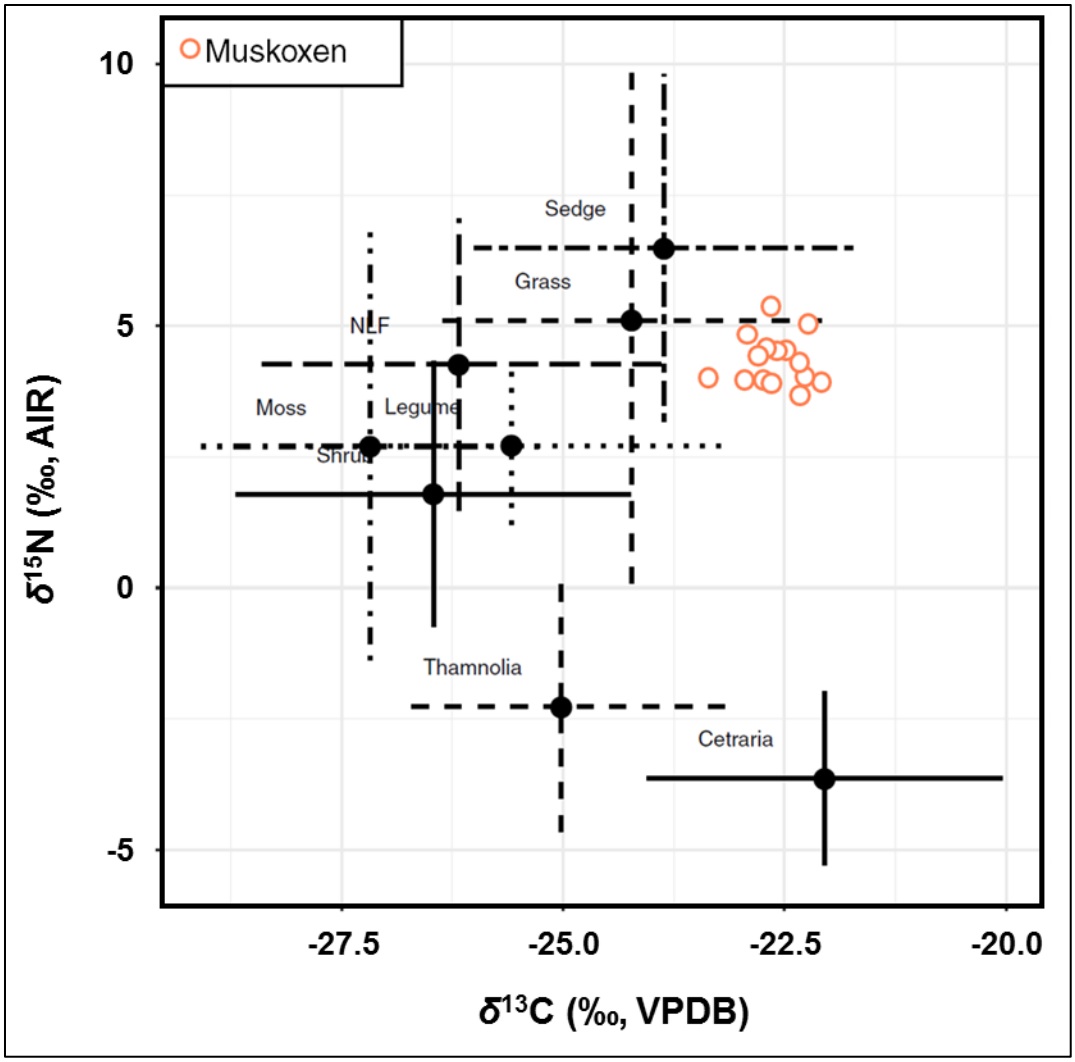


Figure 2.14. Average δ^{15}N vs. δ^{13}C and standard deviations of aggregated forage sources, adjusted to the $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ of modern muskox (pink circles) using the SIDER-imputed TDFs.

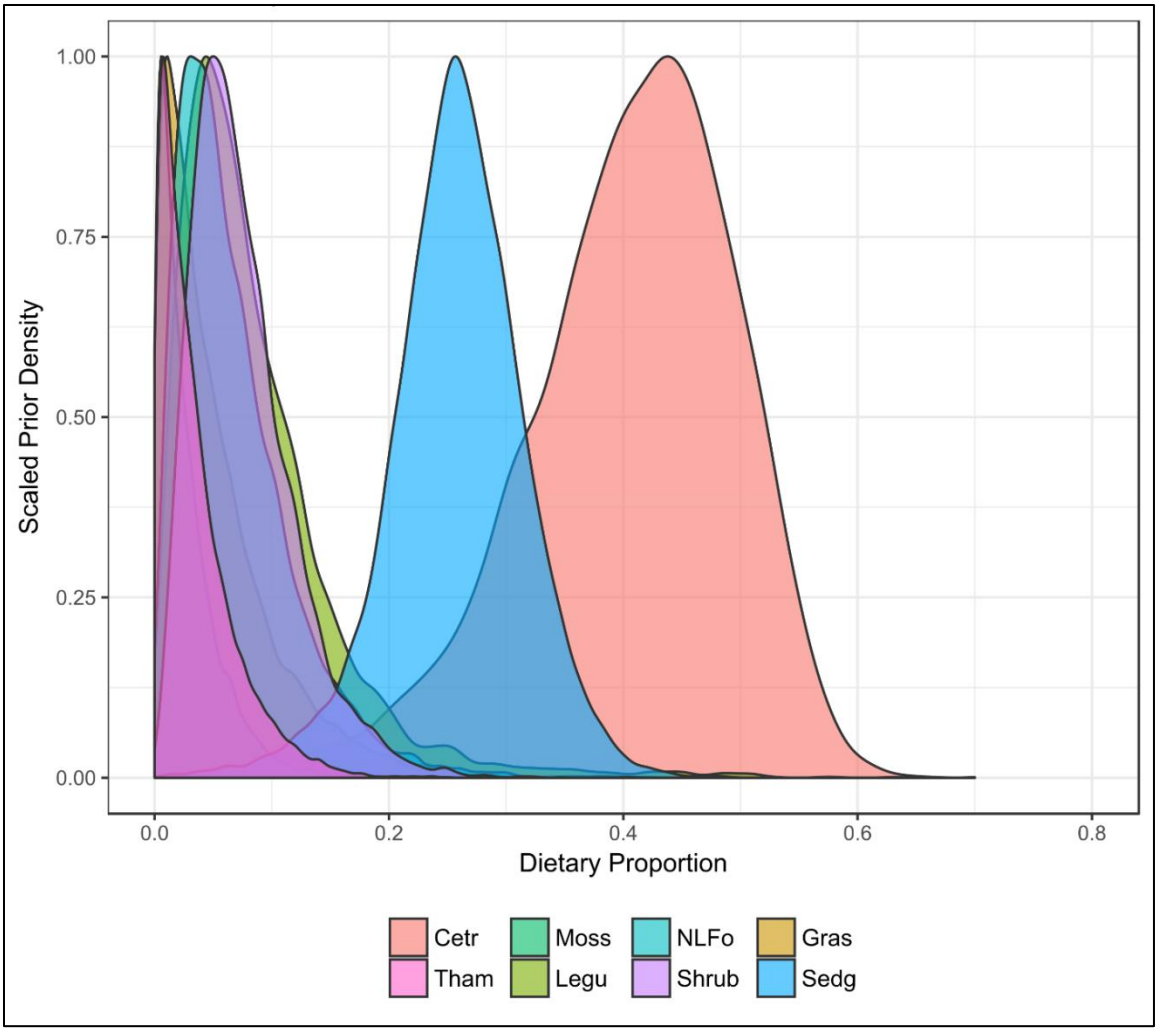


Figure 2.15. Posterior probability distributions of aggregated forage sources to muskox bone collagen. Forage items are: *Cetraria tilesii* (Cetr); *Thamnolia vermicularis* (Tham); moss (Moss); legumes (Legu); non-leguminous forbs (NLFo); shrubs (Shrub); grasses (Gras); sedges (Sedg). The figure suggests that, even with *a posteriori* source aggregation, *Cetraria tilesii* and southern sedges, respectively, remain the largest contributors to modern muskox bone collagen carbon and nitrogen isotope compositions.

Table 2.13. Mean and median values and 95% credible intervals of the posterior probability distributions of aggregated forage sources, indicating the estimated proportional contribution of each forage source to muskox bone collagen isotopic compositions on Banks Island. Values correspond to the histograms in Figure 2.15.

Forage Source	Median (%)	Mean (%)	95% CI
Moss	0.02	0.03	0.00 – 0.10
Thamnolia vermicularis	0.03	0.03	0.00 – 0.12
Grass	0.04	0.05	0.00 – 0.18
Non-leguminous Forb	0.06	0.07	0.01 – 0.19
Shrub	0.07	0.07	0.01 – 0.18
Leguminous Forb	0.07	0.09	0.01 – 0.26
Sedge	0.26	0.26	0.13 – 0.37
Cetraria tilesii	0.41	0.40	0.15 – 0.55

2.4.9 Dentin Collagen $\delta^{13}C$ and $\delta^{15}N$ Results

Modern dentin collagen samples were analyzed with archaeological dentin collagen samples in two analytical sessions. Across 29 analyses of the internal keratin standard (accepted $\delta^{13}C$ and $\delta^{15}N$ = –24.04‰ and +6.36‰, respectively) $\delta^{13}C$ was –24.03±0.3‰ and $\delta^{15}N$ was 6.37±0.1‰. Across eight analyses of IAEA-CH-6 (accepted $\delta^{13}C$ = –10.45‰; Hut 1987), $\delta^{13}C$ was –10.88±0.4‰. The standard deviation of modern dentin collagen samples analyzed as instrumental duplicates (n = 4) is $\delta^{13}C$ = ±0.0‰, $\delta^{15}N$ = ±0.1‰, C% = ±0.1, and N% = ±0.0. The standard deviation of dentin collagen samples analyzed as method duplicates (n = 3) is $\delta^{13}C$ = ±0.1‰, $\delta^{15}N$ = ±0.4‰, C% = ±0.5, and N% = ±0.2.

The percent collagen content of dentin from recently deceased muskoxen (*n* = 33 microbulk samples from 6 teeth) averaged 14.2% (min = 6.4%; max = 18.9%) (Table 2.4). Teeth from muskoxen harvested in 2016 were not sampled due to scheduling constraints. Percent collagen content for dentin from caribou harvested in 2015 and 2016 (*n* = 8 microbulk samples from 4 teeth) averaged 10.0% (min = 5.4%; max = 14.6%) (Table 2.3). Relative to bone samples, the percent collagen content of dentin samples is relatively low. We suggest that these values do not reflect poor collagen quality, but rather, are the result of the sample preparation method. Before obtaining starting weights for dentin collagen microbulk samples, we mechanically removed as much enamel as possible, and rinsed each transverse crown section in 2:1 chloroform-methanol to remove the epoxy used to stabilize the sample for sectioning. Nevertheless, some enamel and epoxy remained affixed to the samples when they were weighed. Residual epoxy was debrided during the second round of rinses in 2:1 chloroform-methanol by replacing normal vial caps with glue-free, PTFE-faced screw caps[11] and agitating vigorously with a vortex mixer. Any epoxy remaining after this step was removed during the demineralization stage, using clean tweezers to remove epoxy fragments from the softened dentin. All residual enamel was dissolved

[11]Chloroform-methanol will dissolve the glue affixing the cap-liner to normal vial caps, contaminating the sample.

during demineralization. In short, the measured dentin contents are probably inaccurate because starting sample weights were too high because of epoxy and enamel that were subsequently removed during the collagen extraction process. In addition, because we did not crush transverse crown samples to a uniform size prior to collagen extraction, the starting weights of methodological duplicates were somewhat different than those of the sample from which they derived.

Evidence of dentin collagen quality comes from carbon and nitrogen abundances, and their associated atomic C:N ratios (Tables 2.3 and 2.4). Abundances of carbon (C%) and nitrogen (N%) across all dentin samples averaged 43.9% (min = 38.5%, max = 45.9%) and 15.9% (min = 13.7%, max = 16.7%), respectively. Atomic C:N ratios across all dentin samples averaged 3.2 (min = 3.2; max = 3.3). As with our bone collagen samples, these abundances and atomic C:N ratios for dentin collagen are both within commonly accepted ranges for isotopically unaltered bone collagen (C% = 15.3 to 47.0%; N% = 5.5 to 17.3%; atomic C:N = 2.9 to 3.6) (DeNiro 1985; Ambrose 1990; van Klinken 1999).

The carbon and nitrogen isotope compositions, respectively, of caribou and muskox sequential microbulk dentin collagen samples are presented alongside summary data discussed above in Tables 2.3 and 2.4, and are illustrated in Figures 2.16 and 2.17. Microbulk sample IDs follow the major axis of crown development. Although the isotopic data are arranged in order of gross tooth development (dp4, M1, M2, M3, P4) we emphasize that, because of occlusal wear and potential overlap in development, the pattern of isotopic variation is not continuous between teeth. Teeth that were too small or too worn to obtain more than a single dentin sample, as in caribou teeth, are designated “bulk”.

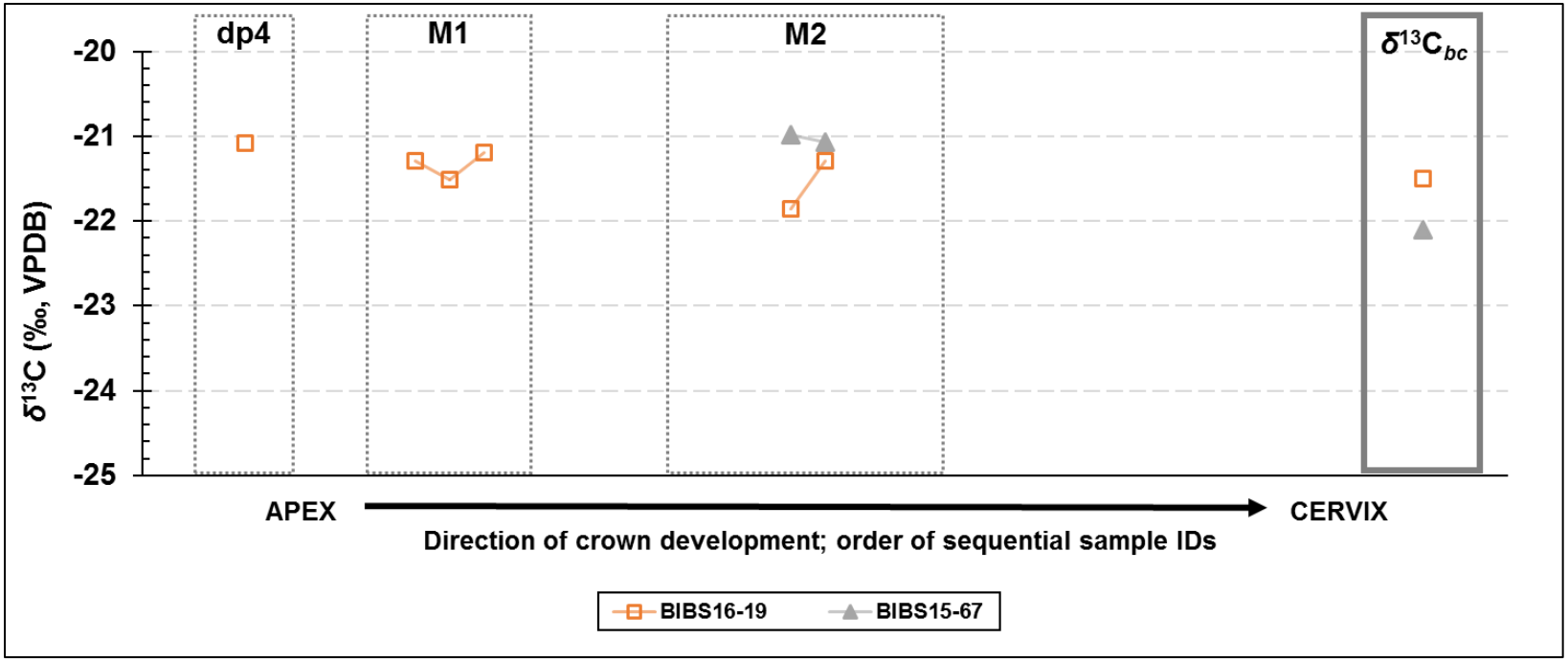


Figure 2.16. Values of $\delta^{13}C_{dc}$ in teeth from two modern caribou: BIBS16-19 (unfilled orange squares) and BIBS15-67 (filled gray triangles). Teeth are displayed in approximate developmental order (dp4, M1, M2). The last dentin sequential sample of each crown is always taken from the 5 mm closest to the root-enamel junction (REJ). The $\delta^{13}C$ of bulk bone collagen from both caribou are shown for comparison at far right.

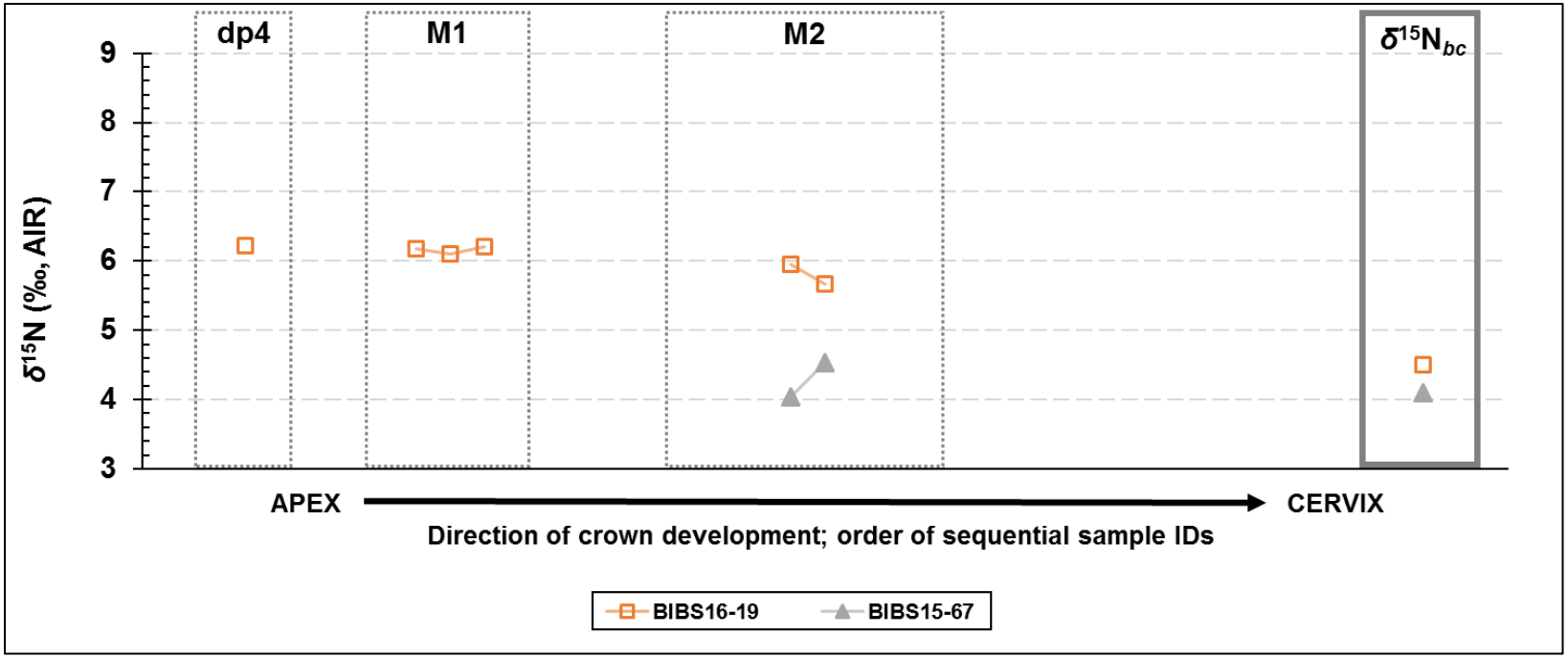


Figure 2.17. Values of $\delta^{15}N_{dc}$ in teeth from two modern caribou: BIBS16-19 (unfilled orange squares) and BIBS15-67 (filled gray triangles). Teeth are displayed in approximate developmental order (dp4, M1, M2). The last dentin sequential sample of each crown is always taken from the 5 mm closest to the root-enamel junction (REJ). The $\delta^{15}N$ of bulk bone collagen from both caribou are shown for comparison at far right.

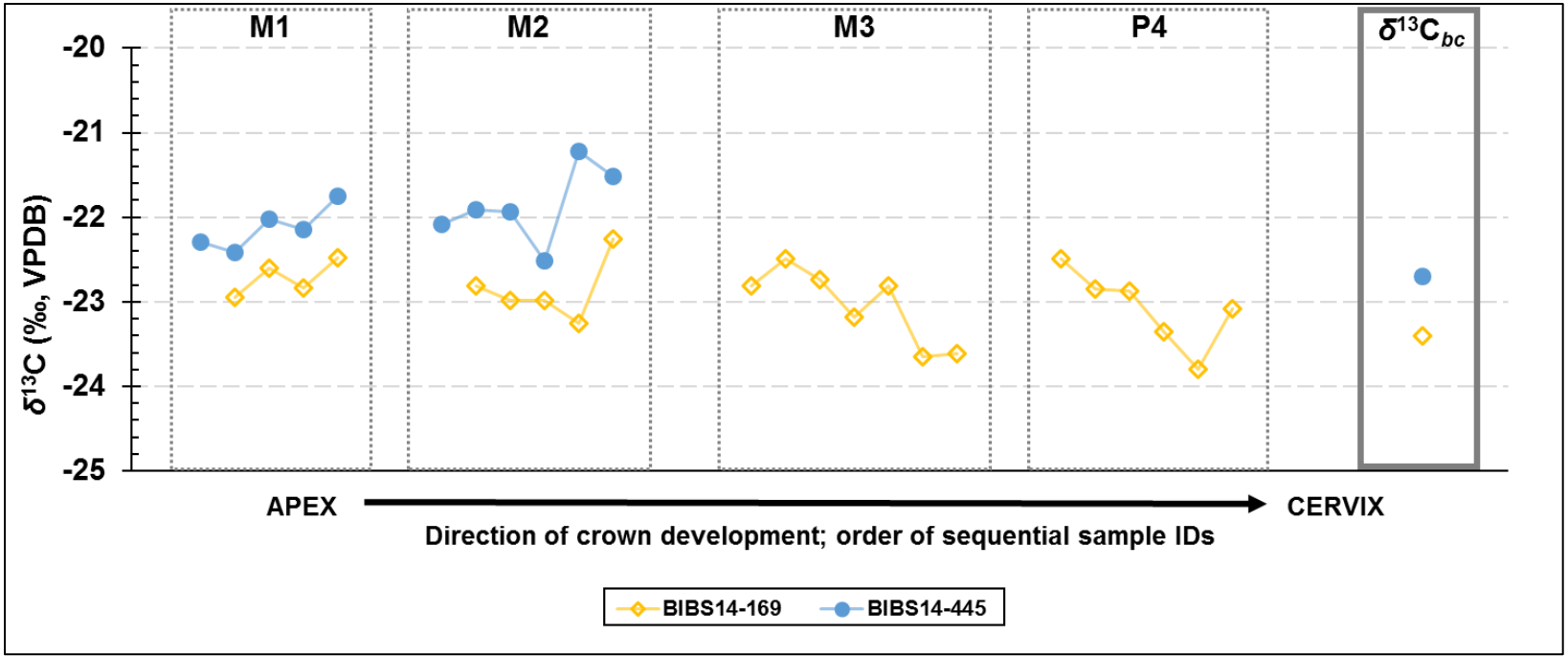


Figure 2.18. Values of $\delta^{13}C_{dc}$ in teeth from two modern muskoxen: BIBS14-169 (unfilled shapes) and BIBS14-445 (filled shapes). Teeth are displayed in approximate developmental order (M1, M2, M3 and P4). The last sequential sample of each tooth is always taken from the dentin closest to the junction of the crown and root. The $\delta^{13}C$ of bulk bone collagen from both muskoxen are shown for comparison at far right.

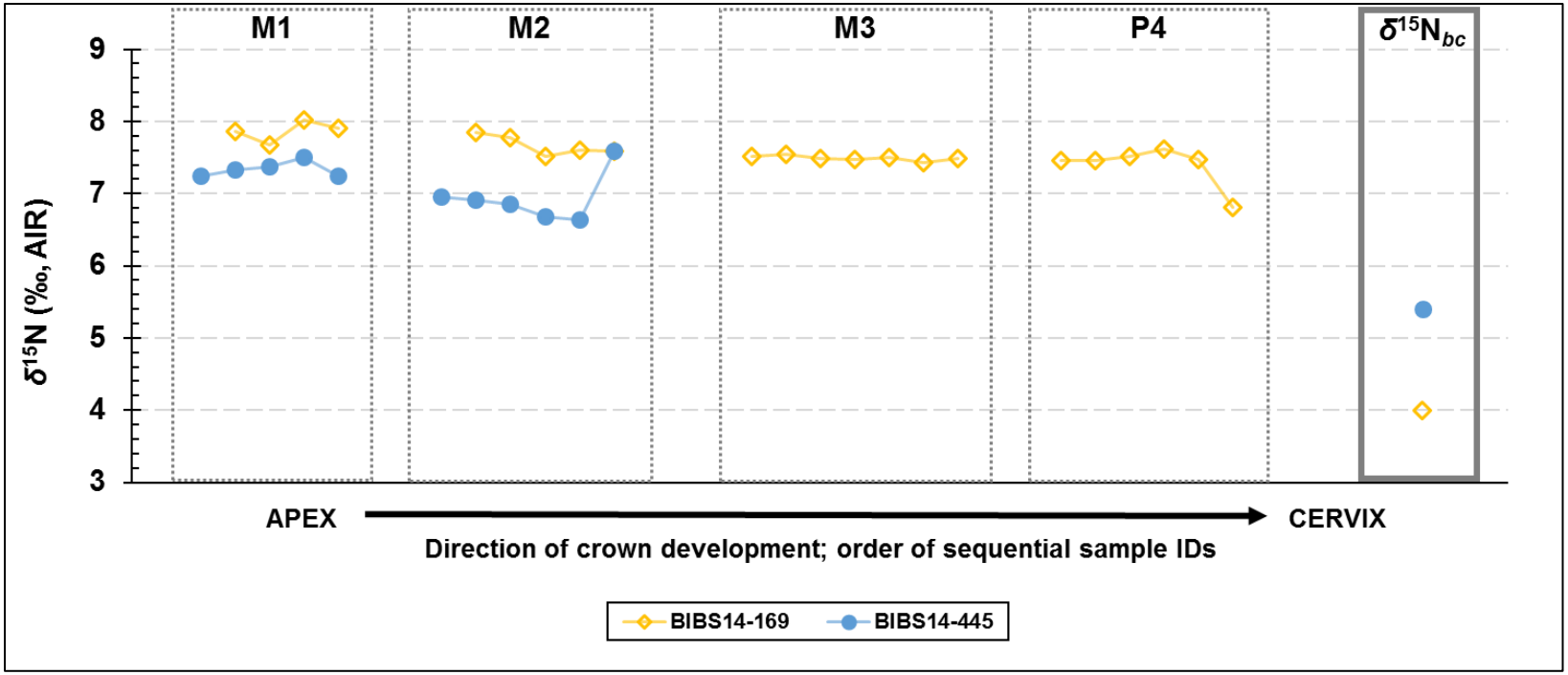


Figure 2.19. Values of $\delta^{15}N_{dc}$ in teeth from two modern muskoxen: BIBS14-169 (unfilled shapes) and BIBS14-445 (filled shapes). Teeth are displayed in approximate developmental order (M1, M2, M3 and P4). The last sequential sample of each tooth is always taken from the dentin closest to the junction of the crown and root. The $\delta^{15}N$ of bulk bone collagen from both muskoxen are shown for comparison at far right.

The intra-tooth average $\delta^{13}C_{dc}$ of all caribou dentin microbulk samples is nearly uniform (average = –21.3‰, min = –21.9‰, max = –21.0‰), although the intra-tooth average $\delta^{13}C_{dc}$ of BIBS16-19 M2 is slightly lower than that of BIBS15-67 M2 (Figure 2.16, Table 2.14). Intra-tooth average $\delta^{15}N_{dc}$ is also relatively invariable: across the three teeth sampled from BIBS16-19, intra-tooth average $\delta^{15}N_{dc}$ is +6.1‰ (min = +5.7‰, max = +6.2‰) (Figure 2.17, Table 2.15). Conversely, the intra-tooth average $\delta^{15}N_{dc}$ of BIBS15-67 M2 (+4.3‰) is nearly two per mil lower than that of BIBS16-19 M2 (+5.9‰) (Table 2.15). In all, caribou crown dentin collagen isotopic data are relatively uninformative of seasonal dietary changes. This is due largely to the sampling approach we used: caribou teeth, even molars, are relatively small and it was not possible to extract more than two microbulk samples from each tooth. Additionally, Figure 2.2b demonstrates that the sequential dentin "cones" (Balasse et al. 2001) are nearly vertical in caribou and muskox teeth. Consequently, our method of dividing the tooth crown into 5 mm segments perpendicular to the tooth major axis cuts across multiple dentin appositional layers, significantly attenuating any seasonal isotopic variability recorded in the dentin.

Caribou dentin collagen samples do provide useful information about *inter-tooth* isotopic variation, and isotopic differences between dentin and bone collagen. Isotopically-attenuated dentin collagen should reflect averaged dietary $\delta^{13}C$ and $\delta^{15}N$ over the months or possibly years when the tooth crown developed. Conversely, the isotopic compositions of bone collagen should reflect average dietary isotopic compositions during approximately the last decade of life (Tieszen et al. 1983; Pate 1994). Since dentin collagen should have the same tissue-diet spacing as bone collagen (Koch 2007), tooth-averaged $\delta^{13}C_{dc}$ and $\delta^{15}N_{dc}$ can be compared to bone collagen $\delta^{13}C$ and $\delta^{15}N$ to make inferences about dietary changes between early and adult life.

Offsets between caribou dentin and bone collagen isotopic compositions ($\Delta^{13}C_{dc\text{-}bc}$ and $\Delta^{15}N_{dc\text{-}bc}$) are presented in Tables 2.14 and 2.15. In BIBS16-19 dp4, the $\Delta^{13}C_{dc\text{-}bc}$ is 0.4‰ and this offset decreases by half in the M1 (0.2‰) and half again in the M2 (0.1‰). This is not the case for BIBS15-67 M2: tooth-averaged $\delta^{13}C_{dc}$ is 1.1‰ higher than $\delta^{13}C_{bc}$ from the same individual, even though, using BIBS16-19 as an example, we might expect only

a minimal $\Delta^{13}C_{dc\text{-}bc}$ offset in an M2. This pattern is reversed for nitrogen. The $\Delta^{15}N_{dc\text{-}bc}$ for BIBS16-19 is 1.7‰ in both the dp4 and M1, and declines to 1.3‰ in the M2, while the $\Delta^{15}N_{dc\text{-}bc}$ for BIBS15-67 M2 is only 0.2‰.

Table 2.14. Summary data for caribou dentin collagen $\delta^{13}C$, and dentin collagen-bone collagen $\delta^{13}C$ offsets.

Sample ID	Taxon	Microbulk Sample	$\delta^{13}C_{dc}$ (‰, VPDB)	Intra-tooth Average $\delta^{13}C_{dc}$ (‰, VPDB)	$\delta^{13}C_{bc}$ (‰, VPDB)	$\Delta^{13}C_{dc\text{-}bc}$		
						dp4	M1	M2
BIBS15-67 M2	Caribou	DC1	–21.0	–21.0	–22.1			+1.1
		DC2	–21.1					
BIBS16-19 dp4	Caribou	BULK	–21.1	–21.1		+0.4		
BIBS16-19 M1	Caribou	DC1	–21.3	–21.3	–21.5		+0.2	
		DC2	–21.5					
		DC3	–21.2					
BIBS16-19 M2	Caribou	DC1	–21.9	–21.6				+0.1
		DC2	–21.3					

Table 2.15. Summary data for caribou dentin collagen $\delta^{15}N$, and dentin collagen-bone collagen $\delta^{15}N$ offsets.

Sample ID	Taxon	Microbulk Sample	$\delta^{15}N_{dc}$ (‰, AIR)	Intra-tooth Average $\delta^{15}N_{dc}$ (‰, AIR)	$\delta^{15}N_{bc}$ (‰, AIR)	$\Delta^{15}N_{dc\text{-}bc}$		
						dp4	M1	M2
BIBS15-67 M2	Caribou	DC1	+4.0	+4.3	+4.1			+0.2
	Caribou	DC2	+4.5					
BIBS16-19 dp4	Caribou	BULK	+6.2	+6.2		+1.7		
BIBS16-19 M1	Caribou	DC1	+6.2	+6.2	+4.5		+1.7	
	Caribou	DC2	+6.1					
	Caribou	DC3	+6.2					
BIBS16-19 M2	Caribou	DC1	+6.0	+5.9				+1.3
	Caribou	DC2	+5.7					

Intra-tooth variation in $\delta^{13}C_{dc}$ is limited in all muskox teeth (average = –22.6‰, min = –23.8‰, max = –21.2‰) (Figure 2.18, Table 2.16). The M1s and M2s from BIBS14-169 and BIBS14-445 display similar patterning in $\delta^{13}C_{dc}$ with a ~ 0.5‰ offset between them. Intra-tooth variation in dentin $\delta^{13}C$ is greatest in BIBS169 P4, where $\delta^{13}C_{dc}$ declines from –22.5‰ to –23.8‰ before increasing to –23.1‰. Given that BIBS14-169 was collected at Umingmak (PjRa-2), in the northern part of the island and BIBS14-445 was collected farther south at Sunnguqpaaluk (PdRi-1), and that the $\delta^{13}C$ of some forage guilds/species varies geographically, the $\delta^{13}C_{dc}$ of teeth from both individuals could represent the same seasonal variation with a geographic offset. Intra-tooth average $\delta^{15}N_{dc}$ across all muskox teeth is +7.4‰ (min = +6.6‰, max = +8.0‰) with very little intra-tooth variation (Figure 2.19, Table 2.17). In both muskoxen, $\delta^{15}N_{dc}$ is nearly uniform across teeth except for a 0.7‰ decline between the last two microbulk collagen samples of BIBS14-169 P4, and a +1‰ increase between the last two microbulk collagen samples of BIBS14-445 M2. The very slight decline in $\delta^{15}N_{dc}$ is shared in the M2s of both muskoxen, though the intra-tooth average $\delta^{15}N_{dc}$ of BIBS14-169 M2 is ~ 1‰ higher than that of BIBS14-445 M2 (Table 2.17).

Offsets between muskox crown dentin collagen and bone collagen isotopic compositions ($\Delta^{13}C_{dc\text{-}bc}$ and $\Delta^{15}N_{dc\text{-}bc}$) are presented in Tables 2.16 and 2.17. In BIBS14-169 M1, the $\Delta^{13}C_{dc\text{-}bc}$ is +0.7‰, and declines to +0.5‰ in the M2 and +0.3‰ in the P4 (the difference between the $\Delta^{13}C_{dc\text{-}bc}$ of the M2 and M3 is within the range of instrument error) (Table 2.16). The $\Delta^{13}C_{dc\text{-}bc}$ of BIBS14-445 M1 and M2 are +0.6‰ and +0.8‰, respectively. Similarly, there is a decline in the $\Delta^{15}N_{dc\text{-}bc}$ across the teeth of BIBS14-169 from +3.9‰ in the M1 to +3.4 in the P4 (Table 2.17). There is also a decline in $\Delta^{15}N_{dc\text{-}bc}$ in the teeth of BIBS14-445 from +1.9‰ in the M1 to +1.5‰ in the M2.

Table 2.16. Summary data for muskox dentin collagen $\delta^{13}C$, and dentin collagen-bone collagen $\delta^{13}C$ offsets.

Sample ID	Taxon	Microbulk Sample	$\delta^{13}C_{dc}$ (‰, VPDB)	Intra-tooth Average $\delta^{13}C_{dc}$ (‰, VPDB)	$\delta^{13}C_{bc}$ (‰, VPDB)	$\Delta^{13}C_{dc\text{-}bc}$			
						M1	M2	M3	P4
BIBS14-169 M1	Muskox	DC1	–22.9	–22.7		+0.7			
		DC2	–22.6						
		DC3	–22.8						
		DC4	–22.5						
BIBS14-169 M2	Muskox	DC1	–22.8	–22.9			+0.5		
		DC2	–23.0						
		DC3	–23.0						
		DC4	–23.3						
		DC5	–22.3						
BIBS14-169 M3	Muskox	DC1	–22.8	–23.0	–23.4			+0.4	
		DC2	–22.5						
		DC3	–22.7						
		DC4	–23.2						
		DC5	–22.8						
		DC6	–23.6						
		DC7	–23.6						
BIBS14-169 P4	Muskox	DC1	–22.5	–23.1					+0.3
		DC2	–22.9						

		DC3	–22.9				
		DC4	–23.4				
		DC5	–23.8				
		DC6	–23.1				
		DC1	–22.3				
		DC2	–22.4				
BIBS14-445 M1	Muskox	DC3	–22.0	–22.1		+0.6	
		DC4	–22.1				
		DC5	–21.7				
		DC1	–22.1		–22.7		
		DC2	–21.9				
		DC3	–21.9				
BIBS14-445 M2	Muskox	DC4	–22.5	–21.9			+0.8
		DC5	–21.2				
		DC6	–21.5				

Table 2.17. Summary data for muskox dentin collagen $\delta^{15}N$, and dentin collagen-bone collagen $\delta^{15}N$ offsets.

Sample ID	Taxon	Microbulk Sample	$\delta^{15}N_{dc}$ (‰, AIR)	Intra-tooth Average $\delta^{15}N_{dc}$ (‰, AIR)	$\delta^{15}N_{bc}$ (‰, AIR)	$\Delta^{15}N_{dc\text{-}bc}$			
						M1	M2	M3	P4
BIBS14-169 M1	Muskox	DC1	+7.9	+7.9	+4.0	+3.9			
		DC2	+7.7						
		DC3	+8.0						
		DC4	+7.9						
BIBS14-169 M2	Muskox	DC1	+7.9	+7.7			+3.7		
		DC2	+7.8						
		DC3	+7.5						
		DC4	+7.6						
		DC5	+7.6						
BIBS14-169 M3	Muskox	DC1	+7.5	+7.5				+3.5	
		DC2	+7.5						
		DC3	+7.5						
		DC4	+7.5						
		DC5	+7.5						
		DC6	+7.4						
		DC7	+7.5						
BIBS14-169 P4	Muskox	DC1	+7.5	+7.4					+3.4
		DC2	+7.5						

		DC3	+7.5				
		DC4	+7.6				
		DC5	+7.5				
		DC6	+6.8				
		DC1	+7.2				
		DC2	+7.3				
BIBS14-445 M1	Muskox	DC3	+7.4	+7.3		+1.9	
		DC4	+7.5				
		DC5	+7.2				
		DC1	+6.9		+5.4		
		DC2	+6.9				
		DC3	+6.9				
BIBS14-445 M2	Muskox	DC4	+6.7	+6.9			1.5
		DC5	+6.6				
		DC6	+7.6				

2.5 Discussion

2.5.1 Caribou Bone Collagen Isotopic Compositions and Diet on Banks Island

The proportional density estimates of sedges and forbs in Figure 2.8 and Table 2.10 agree with both caribou fecal pellet (Larter and Nagy 1997, 2004) and rumen content (Shank et al. (1978) studies on Banks Island. Unlike the isotopically-derived proportional density estimates, however, fecal and rumen analyses also suggest that shrubs are a primary component of caribou diet on Banks Island during the summer. Given the relatively high protein content of shrubs during the growing season (Larter and Nagy 2001b, 2002), even seasonal consumption should lead to some representation in bone collagen isotopic composition.

Contrary to the isotopically-derived proportional density estimates, fecal and rumen studies also suggest minimal lichen consumption by caribou on Banks Island; Larter and Nagy (1997, 2001b, 2004) and other researchers (Klein 1992; Miller and Gunn 2003) argue that lichen phytomass in the Canadian Arctic Archipelago is too low to support significant browsing. Such consumption, however, is not unprecedented in other regions. Kelsall (1968) and Skoog (1968) both suggest that the incisors of caribou are probably not morphologically adapted for cutting through the tissues of woody plants, and are better suited for plucking lichens and sedges from the ground surface. Traditional ecological knowledge from Banks Island also strongly suggests that caribou forage on yellow lichen year-round (Trevor Lucas, personal communication). Both the migratory mainland caribou herds of Canada (Klein 1991), and Scandinavian reindeer (Gaare and Skogland 1975; Staaland and Sæbø 1987; Mathiesen et al. 2000) forage heavily on lichens during the winter. Thomas et al. (1999) also note that caribou on nearby Melville Island consume lichen throughout the year.

Although lichen phytomass on Banks Island is apparently low, Larter and Nagy (2001a) found that lichens were among the most frequently occurring forage in the southern region of Banks Island, especially in upland and stony barrens, where caribou tend to range

(Parker 1978; Vincent and Gunn 1981). In any case, limited lichen phytomass may not be an issue for caribou, who tend to move quickly between feeding areas.

2.5.2 Muskox Bone Collagen Isotopic Compositions and Diet on Banks Island

The relatively high proportional estimate of *Cetraria tilesii* in muskox diet (Figure 2.13 and Table 2.12) is also unexpected. Traditional ecological knowledge on Banks Island suggests that muskoxen mainly forage on sedges and other graminoids, and do not eat lichen (Nagy 1999; Trevor Lucas, personal communication), and almost all other data on muskox diet agree with this view. Again, Oakes et al. (1992) suggested that, of the vascular plant content in muskox feces on Banks Island during the late spring and summer of 1987, sedges and rushes accounted for nearly half of the vascular plant content, grasses and forbs accounted for another ~ 30% and 20%, respectively. Likewise, fecal content analyses (Larter and Nagy 1997, 2001c, 2004) suggest that muskox diet on Banks Island consists of a 60-40% mix of sedges and willow year-round, with minor contributions from legumes during the summer. As with caribou, lichen fragments were not found in any muskox fecal pellets analyzed by Larter and Nagy (1997, 2004) or Oakes et al. (1992).

There is physiological precedent for limited yellow lichen consumption by muskoxen: Fruticose lichens contain high levels of plant secondary substances (Rundel 1978; Hidalgo 2005; Sundset et al. 2010), particularly usnic acid (Culberson 1977; Palo 1993; Bjerke and Dahl 2002) that are typically poisonous to animals. Because of the presence of these substances, few other animals besides caribou and reindeer consume such lichens. Recent work (Sundset et al. 2008, 2010; Glad et al. 2014) demonstrates that the caribou gut microbiome is not only capable of neutralizing usnic acid, but may be able to metabolize it. Salgado-Flores et al. (2016), however, have recently established that the bacterial and archaeal microflora of the muskox rumen are more closely related to those of caribou than to those of other ruminant herbivores. This similarity in rumen microfloral profiles suggests that muskoxen may be able to process lichen in the same way as caribou. Muskoxen in Alaska are known to consume lichen regularly (Palmer 1944; Thing et al. 1987; Ihl and Klein 2001; Gustine et al. 2011; Ihl, unpublished data) apparently without adverse effects.

2.5.3 Potential Confounding Factors

The high proportional estimates of lichen contribution to caribou and muskox bone collagen challenge the results of many dietary studies specific to caribou and muskoxen on Banks Island. Consideration of other potential factors is therefore warranted before exploring the implications of lichen consumption further. As detailed in Section 2.4.7, several diagnostic tests affirm the performance of the Markov chains used in the mixing models, and multiple runs on different computers, and with different run parameters all produced essentially the same mixing model results.

One possible biasing factor is that our muskox bone samples were taken from animals harvested in the southwestern part of Banks Island. The seasonal movements of muskoxen are presumably limited (Nagy 1999; Tener 1965) and forage isotopic compositions on Banks Island vary geographically (Section 2.4.3). Muskoxen from the northern parts of Banks Island could have diets and bone collagen stable isotopic compositions different from the southwestern muskoxen, and therefore also the caribou in this study.

Initially, we suspected that isotopically-distinct but protein-poor lichen species could be biasing the mixing models, but this is accounted for when C and N abundances are included in the model. Although lichens contain almost no crude protein (Table 2.8; Spencer and Krumboltz 1929; Scotter 1972; White 1983; Larter and Nagy 2001b, 2002), they are rich in glucose and other fermentable carbohydrates (Skogland 1990; Svihus and Holand 2000; Sundset et al. 2010). Since the $\delta^{13}C$ of herbivore bone collagen should reflect the $\delta^{13}C$ of all forage sources, including those with little crude protein, there is no methodological issue with using bulk bone collagen and bulk forage isotopic data in the mixing model.

Another possibility is that the models are underdetermined due to the number of forage source divisions and low isotopic variability between them (Parnell et al. 2010). Pairwise correlations (Section 2.4.7) suggest that with Markov chains of sufficient length, the mixing models can distinguish sources from one another. The large posterior probability ranges for many of the forage sources, however, demonstrate that many potential mixing solutions are possible. Given that herbivores only feed from a single trophic level, and all forage sources we sampled utilize the C_3 photosynthetic pathway, this is difficult to avoid.

Still, *a posteriori* aggregation does not drastically change estimated proportional forage contributions to caribou or muskox bone collagen. In some cases (e.g. northern and southern non-leguminous forbs), aggregation increases uncertainty by combining isotopically-distinct forage types.

Although we sampled from as broad a range of potential forage species as possible, it may be that the exclusion of some forage types significantly affects the mixing models. For instance, we did not sample any rush (*Luzula* spp.) or horsetail (*Equisetum* spp.) species. As monocots, we expect that the stable isotopic compositions of rushes are within the range of graminoids and sedges. Likewise, although the unique phylogenetic position and physiology of *Equisetum* spp. relative to other vascular plants suggest it may have distinct carbon and nitrogen isotope compositions.

As discussed above, the strongest candidate for methodological error in our models, and Bayesian mixing models in general, are the trophic discrimination factors we used. We have no way of determining whether the SIDER-imputed TDFs reflect "real" caribou and muskox TDFs, although they are within the ranges of published TDFs for large herbivores (Sullivan and Krueger 1981; Krueger and Sullivan 1984; van der Merwe 1989; Koch 1998). In addition, model diagnostics suggest that, at the least, the Bayesian imputations used to obtain TDF estimates performed well. Finally, when generalized TDFs (Szpak et al. 2012) are applied, the estimated dietary proportions of forage source remain about the same (Appendix A, Supplemental Figures A1 and A2 and Supplemental Tables A1 and A2).

The diets of male and female, and adult and juvenile muskoxen on Banks Island differ somewhat (Oakes et al. 1992) and the same is probably true for caribou (Skogland 1989, 1990; Parker et al. 2005). Likewise, the $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ of actively-nursing caribou and muskoxen, as with most mammals, is influenced by the consumption of milk (Fogel et al. 1989; Jenkins et al. 2001; Polischuk et al. 2001; Fuller et al. 2003). A strong sex bias in the samples, or a mix of adult and juvenile bone collagen isotopic data could produce misleading mixing model results. Since the modern caribou and muskox bone collagen

samples include a mix of adult males and females, however, sex bias and ontogenetic differences in bone collagen isotopic composition are not a concern.

Although the proportional contributions of all dietary items can in theory be inferred from the $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ of herbivores, other metabolic processes unique to Arctic ruminants may affect the isotopic compositions of body tissues. These processes may offer alternative explanations for the unexpectedly large proportional estimates of yellow lichen consumption based on both caribou and muskox bone collagen isotopic compositions.

In a broad range of cervids, including caribou, metabolism and appetite decline in winter (Ryg and Jacobsen 1982; Larsen et al. 1985; Tyler and Blix 1990). The same declines apparently occur in muskoxen as well (Tener 1965; Hudson and Christopherson 1985; Tyler and Blix 1990). Variable metabolic rate probably does not directly affect tissue stable isotopic compositions (Carleton and Martínez del Rio 2005; Smith et al. 2010). If metabolism is lowered to the point where tissue growth or turnover ceases, however, winter dietary isotopic signals will be underrepresented in bone collagen. There is some evidence for winter growth cessation in wild caribou (McEwan 1968; Ryg and Jacobsen 1982) but it is based largely on plateau in body weight. Caribou and muskoxen both build up fat stores during summer and fall which they then use during winter to avoid catabolizing body protein (Larsen et al. 1985; Adamczewski et al. 1987; Tyler and Blix 1990; Adamczewski 1992; Adamczewski et al. 1997; Hofmann 2000). Because of their highly efficient digestive system and low basal metabolic rate (Hudson and Christopherson 1985; Tyler and Blix 1990), muskoxen are often able to maintain their fat stores through the winter (Thing et al. 1987; Adamczewski et al. 1994). Most of the weight loss during winter is accounted for by utilization of fat reserves, though some protein loss does occur in both species, even when fat stores or high-quality forage is available (Adamczewski et al. 1987, 1988, 1993; Tyler and Blix 1990). Dental eruption indices for caribou (Kelsall 1968; Miller 1974) and muskoxen (Tener 1965; Henrichsen and Grue 1980) demonstrate continuous eruption (and subsequently, developmental) rates in both species, suggesting continuous growth throughout the winter.

Whether seasonal fat or protein catabolism in caribou and muskoxen results in ^{15}N enrichment (Hobson et al. 1993; Fuller et al. 2005; Drucker et al. 2012) probably depends on the severity of range conditions in an individual winter. Kempster et al. (2007) suggest that metabolic stress may need to reach a certain threshold before ^{15}N enrichment is induced in tissues, and given their evolutionary history, this threshold is probably high in both caribou and muskoxen. As Tyler and Blix (1990:221) argue, many Arctic species experience weight loss during winter, and "survive perfectly well" and "slowed growth and even weight loss are not necessarily consequences of undernutrition."

Caribou and muskoxen both recycle urea to mitigate protein loss during winter (Tener 1965; Klein and Schønheyder 1970; Batzli et al. 1981; Barboza and Parker 2008). In caribou, the specific mechanism of nitrogen retention involves cycling urea-rich saliva to the rumen, which are used to sustain gut protein synthesis (Hungate 1966; Hove and Jacobsen 1975; Wales et al. 1975). This specific cycling pathway is probably the same in muskoxen, as it is present in sheep, which are also members of the subfamily Caprinae (Denton 1957; Lyttleton 1960; Hungate 1966). Batzli et al. (1981:362) state that urea conservation "requires…a readily fermentable supply of carbohydrate…to supply energy and carbon for microbial protein synthesis." Because lichens are glucose- and carbohydrate-rich, and *Cetraria tilesii* is highly digestible (Thomas and Kroeger 1980; Côté 1998; Storeheier et al. 2002), caribou and muskoxen may both consume significant quantities of yellow lichen during the winter to satisfy maintenance energy demands and maintain the normal function of gut microflora. Indeed, Mathiesen et al. (1999; 2000) found that energy provided by lichen promoted the digestion of other winter forage in caribou. Glucose is also important in lactating ruminants (Annison and Linzell 1964; Linzell 1967; Annison et al. 1968; White and Luick 1976). In addition, *Cetraria tilesii* tends to grow on ridges and hilltops (Larter and Nagy 2001a), which are blown free of snow during the winter (Larter and Nagy 2001d). This means that less digging, and consequently less energy, is required to obtain this significant carbohydrate source. Although caribou are probably not able to survive on lichen alone (McEwan and Whitehead 1970; Nieminen 1980), a winter diet of sedges and lichen could provide enough crude protein, essential amino acids, and fermentable carbohydrates to maintain microbial synthesis (Ørskov 1992; Storeheier et al. 2002).

Having established that there are dietary and metabolic advantages to the consumption of yellow lichen during the winter, we argue that a suite of ecological and physiological factors favors its strong representation in bone collagen. Kielland (1997) found that *Cetraria richardsonii* readily absorbs glycine, a non-essential but proteinogenic amino acid that is abundant in tundra soils (Stevenson 1982; Kielland 1995). Hare et al. (1991) demonstrate that glycine is enriched in ^{13}C relative to other amino acids, which may in part explain why the $\delta^{13}C$ of *Cetraria tilesii* is higher than all other forage sources in our sample.

Earlier work with isotopically-labeled glycine in ruminants (Wright and Hungate 1967) demonstrates that rumen microflora readily metabolize it to produce CO_2 and ammonia. Significantly, Wright and Hungate (1967) also found that glycine is not deaminated during fermentation by rumen microflora. Since glycine is routed almost directly into bone collagen (Hare et al. 1991), and accounts for about one third of its total amino acid content (Brown 1975; Krueger Sullivan 1984; Harrison and Katzenberg 2003), the $\delta^{13}C_{bc}$ in caribou and muskoxen consuming yellow lichen is potentially weighted towards the $\delta^{13}C$ of glycine routed almost directly from the lichen.

One other possibility is that rumen microflora themselves, not just their byproducts, constitute a significant protein source for caribou and muskoxen (Sillen et al. 1989; Bocherens et al. 1996; Atasoglu et al. 2004) and therefore represent a missing source in our mixing models. Sponheimer et al. (2003) point out that foregut fermenters like caribou and muskoxen can digest significant amounts of their rumen microflora due to the forward location of the rumen in the GI tract. Likewise, Dewhurst et al. (2000:1-2) note that "over half of the amino acids absorbed by ruminants, and often two-thirds to three-quarters, derive from microbial protein…[therefore] microbial protein must be considered as an important protein resource." Reindeer are known to digest nitrogen-rich rumen flora (Klein and Schønheyder 1970), and although there are fewer data on similar functions in muskoxen, similar abilities exist in sheep and other caprines like muskoxen (Blackburn and Hobson 1960). Research on the carbon isotope compositions of bacteria and protozoa is largely focused on freshwater detritus-based foodwebs (Hall and Meyer 1998; Nichols and Garling 2000) and is not an appropriate analog for the ruminant digestive system. The

isotopic analysis of rumen microflora constitutes an interesting avenue for further research, especially within the realm of herbivore isotope biochemistry.

If *Cetraria* does play a significant role in the annual diets of caribou and muskoxen on Banks Island, as we argue above, why is it consistently underrepresented in fecal and particularly rumen analyses? Although these studies represent important advances in our understanding of caribou and muskox ecology, Dearden et al. (1975) found that the microhistological approach to fecal and rumen content analyses can underestimate some forage types like lichen. Microhistological analysis of forage fragments by Parker (1978) recorded no lichen in rumen samples from High Arctic caribou, even though Thomas and Edmonds (1983) visually identified significant amounts of lichen in the same rumen samples. In addition, the proportional estimates of *Salix arctica* produced by Parker (1978) are also higher than those from Thomas and Edmonds (1983). As discussed above, *Cetraria* is also highly digestible, and its turnover time in the rumen is low (Thomas and Kroeger 1980; Côté 1998; Storeheier et al. 2002). Since the rumen microflora of caribou, and probably muskoxen, are uniquely adapted to neutralizing lichen secondary metabolites, it is conceivable that yellow lichen is rapidly digested in both animals and is therefore underrepresented in both rumen and fecal studies. It is usually obvious when caribou or muskoxen have foraged on vascular plants like shrubs or grasses because they leave behind stripped branches and root crowns (Wilkinson et al. 1976; Trudell and White 1981; Klein and Bay 1990). Unlike vascular plants, however, lichens have no roots, and Trudell and White (1981) found that caribou can pluck lichens from the moss layer using only the movement of their lips. Consequently, it may not be apparent in observational studies of forage plots that lichens were consumed or even present.

2.5.4 Muskox Seasonal Dietary Variation Inferred from Dentin $\delta^{13}C$ and $\delta^{15}N$

As discussed in Section 2.4.9, the pattern of dentinogenesis in hypsodont/selenodont teeth, in combination with the crown dentin sampling methodology we used, results in each sequential microbulk dentin sample cross-cutting multiple dentin appositional layers. As a result, integrated isotopic signals in crown dentin collagen are likely significantly attenuated (Balasse and Tresset 2002; Balasse 2003). Muskox molars and permanent

premolars are large enough that, despite this attenuation, isotopic variation is apparent in their dentin sequential samples. The M1s and M2s of both modern muskoxen we sampled also show the same general patterns in $\delta^{13}C_{dc}$ and $\delta^{15}N_{dc}$, which suggests that the variation reflects real phenomena and is not just heavily-attenuated isotopic "noise". Caribou teeth, however, are too small to obtain adequate sequences of isotopic compositions using this method. We therefore discuss the muskox dentin collagen isotopic data first, and then interpret the caribou dentin collagen isotopic data in light of it. Overall, we find that seasonal dietary changes inferred from the intra-tooth dentin collagen isotope data, after accounting for developmental history, correspond well with the tooth eruption indices.

Tooth eruption indices (Tener 1965; Henrichsen and Grue 1980) demonstrate that in muskoxen, M1s start developing *in utero*, longitudinally from the apex of the crown, and begin erupting from the gumline in the first month or two after birth, and continue erupting (and hence, developing) throughout at least the first year of life (Figure 2.20). The apical portions of M1 crowns that developed prenatally, and that would therefore reflect maternal isotopic compositions (Fogel et al. 1989; Katzenberg et al. 1996), and during the first several months of life, are obliterated by occlusal wear in adulthood (Figure 2.2), as is the case in both modern muskox tooth samples (Appendix A, Supplemental Figure A3). Accounting for occlusal wear, and based on forage sample $\delta^{13}C$ presented here, we associate the minor, gradual increases in $\delta^{13}C_{dc}$ along M1 crowns of both muskoxen with shifts from forage with lower $\delta^{13}C$ in the first fall of life, to forage with higher $\delta^{13}C$ during the first winter.

Although there is no published information regarding their development in muskoxen, tooth eruption data (Tener 1965; Henrichsen and Grue 1980) also demonstrate that M2s begin erupting during the second summer of life, and continue to develop and erupt through at least the third summer of life (Figure 2.20). The M2 crowns in both muskoxen reflect a general trend towards decreasing $\delta^{13}C_{dc}$ followed by a sharp +1‰ increase in the $\delta^{13}C$ of the last (BIBS14-169 M2 DC5) and last two (BIBS14-445 M2 DC5, DC6) dentin sequential samples (Figure 2.18, Table 2.4). As in the M1 crowns, low $\delta^{13}C_{dc}$ in the fourth sequential sample of both M2s (Figure 2.18) probably reflects diet during the second summer of life, while the highest $\delta^{13}C_{dc}$ in both M2 crowns represents dietary compositions

in the second winter. Occlusal wear on the M2 of BIBS14-445 was less severe than on the M2 of BIBS14-169 (Appendix A, Supplemental Figure A3), and in BIBS14-445, the $\delta^{13}C$ and $\delta^{15}N$ of the last two microbulk dentin samples from the M1 overlaps with those of the first two microbulk dentin samples from the M2 (Figures 2.17a and 2.17b, Table 2.4). This isotopic overlap between teeth supports the tooth eruption data (Tener 1965; Henrichsen and Grue 1980), which suggest that the crown of the M2 begins developing well before the first winter of life, overlapping with the development of the M1 (Figure 2.20).

Muskox M3s probably start developing during the second fall or winter of life, and continue growing and erupting through at least the third year of life (Tener 1965; Henrichsen and Grue 1980) (Figure 2.20). The development of muskox P4s presumably overlaps with that of the M3 (Figure 2.20; Tener 1965; Henrichsen and Grue 1980), though given its small size relative to the M3, its development probably starts later, perhaps during the third winter of life. We associate the gradual decline in $\delta^{13}C_{dc}$ across crown dentin microbulk samples in BIBS14-169 M3 with dietary signals across the second winter, third summer and winter, and fourth summer. The P4, which erupts with, and probably develops during the same time as the M3, reflects dietary variation across the third winter, fourth summer, and fourth fall and winter.

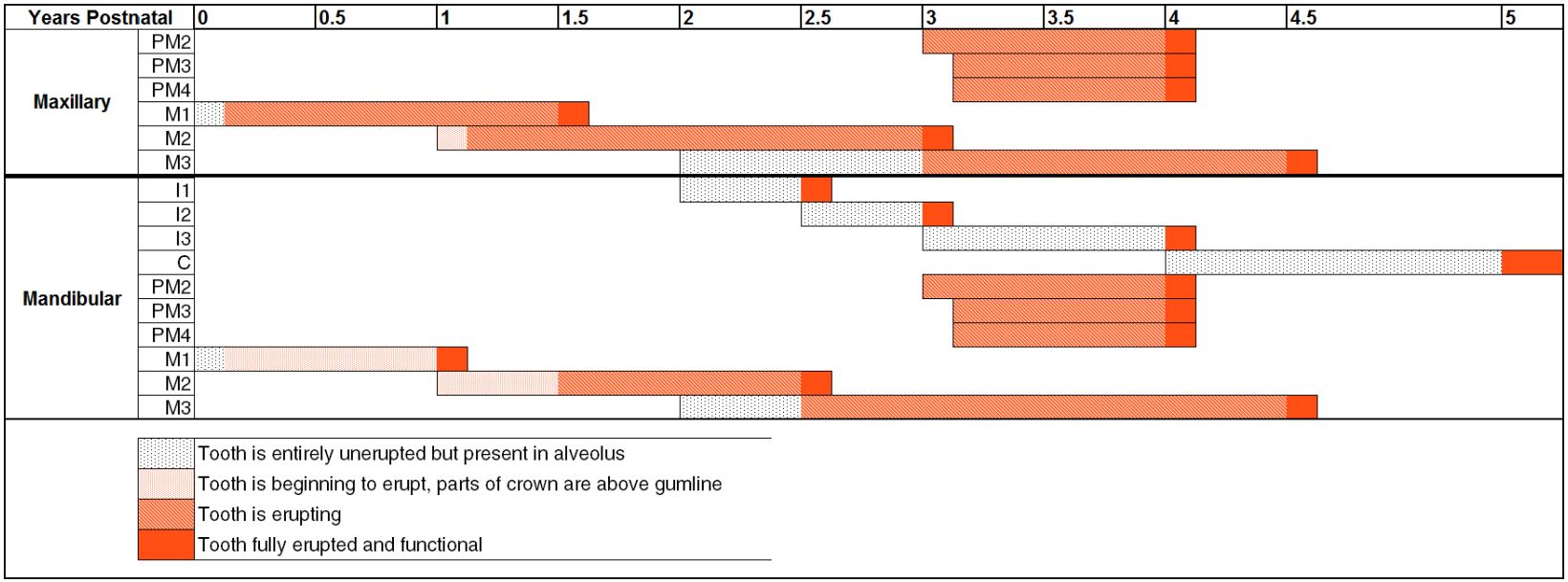


Figure 2.20. Eruption sequence of permanent dentition in muskoxen. “I” = incisor, “C” = canine, “PM” = premolar, and “M” = molar. Data are from Tener (1965) and Henrichsen and Grue (1980).

In the tooth crowns of both muskoxen, the inter-tooth pattern in tooth-averaged $\delta^{13}C_{dc}$ and $\delta^{15}N_{dc}$ is toward gradual depletion of both ^{13}C and ^{15}N (Tables 2.16 and 2.17). The most likely explanation for these patterns is the influence of milk proteins on dentin collagen isotopic compositions during the first two or three years of life. Similar patterns in $\delta^{13}C$ and $\delta^{15}N$ are observed in incrementally-growing tissues in many other mammalian species (Fogel et al. 1989; Bocherens et al. 1994, 1996; Hobson and Sease 1998; Balasse et al. 2001; Jenkins et al. 2001; Polischuk et al. 2001; Fuller et al. 2003), and no other processes readily account for these isotopic patterns while explaining the large offset in $\delta^{15}N$ between crown dentin and bulk bone collagen ($\Delta^{15}N_{dc\text{-}bc}$) (Table 2.17). For instance, seasonal catabolysis of body tissues could potentially enrich dentin collagen in ^{15}N, but if it occurs in multiple winters over the course of life, we should expect it to also influence the $\delta^{15}N$ of continuously-remodeled bone collagen. As a result, $\delta^{15}N_{bc}$ should to be equal to, or even higher than $\delta^{15}N_{dc}$, which only integrates isotopic variation during early life. Catabolic enrichment in ^{15}N would also not explain why tooth-averaged $\delta^{13}C_{dc}$ and $\delta^{15}N_{dc}$ decline across the teeth of both muskoxen. If catabolysis recurred each winter, we would expect $\Delta^{13}C_{dc\text{-}bc}$ and $\Delta^{15}N_{dc\text{-}bc}$ offsets to be nearly identical across teeth, or to vary randomly with the degree of catabolic activity in individual winters. The $\Delta^{15}N_{dc\text{-}bc}$ offsets in muskox teeth are also greater than in caribou teeth (Table 2.15). Based on differences in seasonal weight loss in caribou and muskoxen (Section 2.5.3), we might expect greater catabolic activity in caribou, resulting in greater $\Delta^{15}N_{dc\text{-}bc}$ offsets than in muskoxen. Finally, given that caribou and muskoxen have adapted to the tundra environment over millions of years, the threshold for catabolic enrichment in ^{15}N, if it occurs at all, should be very high in both species. We also considered seasonal assimilation of gut microflora (Section 2.5.3) as a potential explanation for the $\Delta^{15}N_{dc\text{-}bc}$ offsets in muskox teeth. It seems likely, however, that microfloral assimilation would result in $\Delta^{13}C_{dc\text{-}bc}$ offsets larger than those we observe in the teeth of both muskoxen. Finally, if microfloral assimilation occurs seasonally throughout life, we would again expect that bulk bone and microbulk dentin collagen $\delta^{13}C$ and $\delta^{15}N$ would be nearly identical.

Extended nursing also explains why: (1) there are large $\Delta^{15}N_{dc\text{-}bc}$ offsets in the tooth crowns of both muskoxen despite only limited *intra-tooth* variation in $\delta^{15}N_{dc}$, and, (2) why there is

more intra-tooth variation in dentin $\delta^{13}C$ than in $\delta^{15}N$. Since milk is synthesized out of the mother's protein pool (Minson et al. 1975; DeNiro and Epstein 1978; Boutton et al. 1988; Schurr 1998; Schoeller 1999), its $\delta^{13}C$ will ultimately reflect the $\delta^{13}C$ of assimilated forage. Conversely, the $\delta^{15}N$ of milk will largely reflect the mother's trophic position, plus some degree of trophic enrichment, and should not vary significantly with the $\delta^{15}N$ of the mother's diet (Fogel et al. 1989; Newsome et al. 2006). In ruminants, consumed milk is not fermented in the rumen and is instead shunted directly to the omasum for assimilation (Hungate 1975; Van Soest 1982). We assume that in a ruminant herbivore receiving a comparatively high-protein supplement like milk, any consumed forage will be used almost exclusively for energy while assimilated milk proteins will be routed directly to proteinaceous tissues like collagen. In other words, the carbon and nitrogen of ingested milk protein are routed, not "scrambled" (Ambrose and Norr 1993) in the tissues of nursing ruminants, and should therefore dominate tissue isotopic signals during the period of supplementation.

That intra-tooth $\delta^{13}C_{dc}$ is higher than bone collagen $\delta^{13}C$, but declines across teeth also suggests that milk lipids, which are depleted of ^{13}C (DeNiro and Epstein 1978), are used for energy or fat accumulation rather than tissue synthesis in muskoxen. The intra-tooth $\delta^{13}C_{dc}$ of teeth developing while a muskox nurses therefore reflects dietary $\delta^{13}C$ variation in its cow, plus a minor trophic level enrichment in ^{13}C. Conversely, the intra-tooth $\delta^{15}N_{dc}$ of the same teeth will uniformly reflect the nursling's temporarily-carnivorous trophic position as it consumes the cow's milk, and will all be significantly enriched in ^{15}N relative to bulk bone collagen $\delta^{15}N$. Since primary dentin in the tooth crown does not undergo extensive remodeling throughout life (Gage et al. 1989; Lowenstam and Weiner 1989; Balasse 2003), the influence of milk is preserved in crown dentin collagen isotopic signals, while in bone collagen, the milk signal is "overwritten" by continuous remodeling (Libby et al. 1964; Tieszen et al. 1983; Pate 1994).

The isotopic relationships between maternal diet and milk, and the $\delta^{13}C$ and $\delta^{15}N$ of a nursling's tissues have been established in ruminant and non-ruminant species in both observational and experimental studies. Minson et al. (1975), Boutton et al. (1988), Knobbe et al. (2006) and Hillal et al. (2015) all demonstrated that the $\delta^{13}C$ of continuously-sampled

milk in dairy cows reflects transitions from C_3- to C_4-based feed, while Knobbe et al. (2006) found no significant change in milk $\delta^{15}N$ between feed types. The same isotopic patterns have been observed in dentin collagen from steers (Balasse et al. 2001), humans (Fuller et al. 2003) and pinnipeds (Newsome et al. 2006), and in the blood of seal pups (Ducatez et al. 2008; Cherel et al. 2015).

In summary, intra-tooth $\delta^{13}C_{dc}$ largely reflects seasonal dietary variation not of the muskoxen themselves, but the cows that nursed them. Lower $\delta^{13}C_{dc}$ reflects greater proportions of the cows' forage with lower $\delta^{13}C$, such as forbs, during the summer. Higher $\delta^{13}C_{dc}$ reflects greater proportions of forage with higher $\delta^{13}C$ such as sedges and lichens during winter. We base this conclusion on forage $\delta^{13}C$ and the results of our dietary mixing models. Geographic variation in forage $\delta^{13}C$ (Section 2.4.3) can also amplify or attenuate oscillations in intra-tooth $\delta^{13}C_{dc}$. The gradual inter-tooth decline in $\delta^{13}C_{dc}$ and $\delta^{15}N_{dc}$ is the result of declining dietary supplementation with milk. In BIBS14-169, the near-absence of variation in intra-tooth $\delta^{15}N_{dc}$, coupled with the large $\Delta^{15}N_{dc\text{-}bc}$ offsets in each tooth suggests that nursing continued through the third winter of life. The $\Delta^{15}N_{dc\text{-}bc}$ offset declines slightly with the developmental order of the teeth. This suggests that the weaning process continued throughout the development of the M1, M2, M3, and P4. The abrupt ~ 1‰ decrease in $\delta^{15}N_{dc}$ between the last two sequential samples of the P4 indicates that milk supplementation stopped completely around the fourth summer of life.

Although prolonged nursing is not commonly observed in wild muskoxen (Tener 1965; Parker et al. 1990; Adamczewski et al. 1997), its cost in terms of maternal health, fecundity, and ultimately, demography is not clear. White et al. (1989) point out that the lactation curves (i.e. milk production intervals) of many ungulate species are relatively flexible. Their results, and those of White et al. (1997), also demonstrate that in muskoxen, lactation does not automatically trigger anestrum, so prolonged lactation is not necessarily an indicator of reduced fecundity. Still, milk production in muskoxen is costly in terms of maternal fat and protein stores (Adamczewski et al. 1997; Rombach et al. 2002). The captive muskox dams studied by White et al. (1989) received hay and protein supplements *ad libitum* and always exceeded the minimum body weight necessary for conception. It is unlikely that in the wild, a female muskox can afford to continue nursing a calf while

pregnant without significant metabolic costs to herself and the developing fetus. White et al. (1997) found that, of captive female muskoxen on a low-nutrition diet, only dams that could regain the body fat stores required to mate in the following autumn weaned their calf during the first winter of its life. Females that did not recover body fat stores by the spring following parturition did not mate in the following autumn, and instead continued to nurse the yearling through the next summer. Consequently, prolonged nursing in wild muskoxen, as indicated by the $\delta^{15}N_{dc}$ of crown dentin microbulk samples and accompanying $\Delta^{15}N_{dc\text{-}bc}$ offsets, potentially indicates reduced fecundity linked to decreased forage availability.

2.5.5 Caribou Seasonal Dietary Variation Inferred from Dentin $\delta^{13}C$ and $\delta^{15}N$

Although the small size of caribou tooth crowns (Appendix A, Supplemental Figure A4) limited our ability to obtain an adequate series of sequential microbulk dentin collagen samples, patterns of $\delta^{13}C_{dc}$ and $\delta^{15}N_{dc}$ across the teeth from BIBS16-19 resemble those from muskox teeth. Specifically, intra-tooth-averaged $\delta^{13}C_{dc}$ declines towards bulk bone $\delta^{13}C$ across teeth (Figure 2.16, Table 2.14), while intra-tooth-averaged $\delta^{15}N_{dc}$ remains nearly uniform (Figure 2.17, Table 2.15). In barren ground caribou, the M2 is fully erupted and in-wear by the end of the second summer of life (Figure 2.21; Kelsall 1968; Miller 1974), and the limited intra-and inter-tooth variation in $\delta^{15}N_{dc}$ from BIBS16-19 M1 and M2 suggests that this caribou continued nursing through at least the first winter of life. Conversely, the $\delta^{15}N$ of microbulk dentin collagen samples from BIBS15-57 M2 is ~ 2‰ lower, and their $\Delta^{15}N_{dc\text{-}bc}$ offsets are smaller (0.2‰) than those from BIBS16-19 M2, suggesting that this caribou was probably weaned during the first summer or fall of life. This weaning estimate agrees with published data for weaning times in caribou (Tener 1965; Kelsall 1968; Skoog 1968; White and Luick 1976; White 1983; Parker et al. 1990).

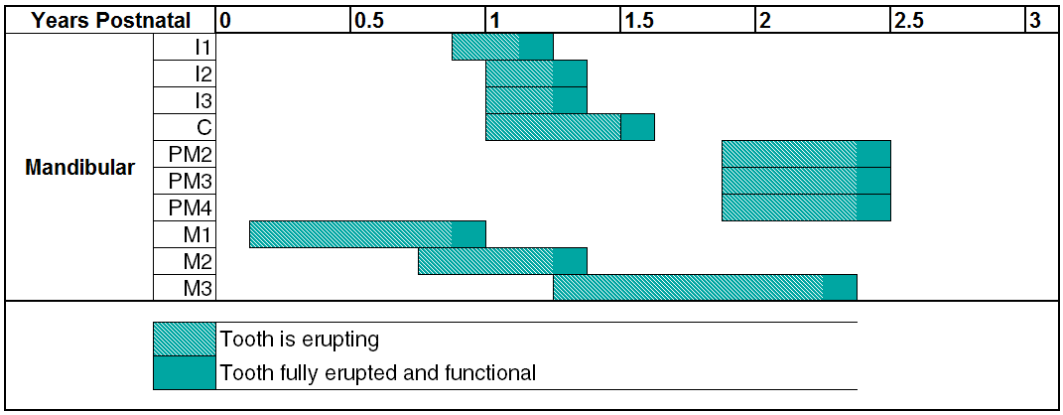


Figure 2.21. Eruption sequence of permanent dentition in barren ground caribou. "I" = incisor, "C" = canine, "PM" = premolar, and "M" = molar. Data are from Banfield (1954) and Miller (1974).

2.5.6 Implications of Modern Bone and Dentin Collagen for Modern Caribou and Muskox Ecology on Banks Island

The isotopic evidence presented here suggests that the inter-annual and possibly seasonal diets of caribou and muskoxen share a significant amount of overlap. Based on Bayesian dietary mixing models and our $\delta^{13}C_{dc}$ dataset, this overlap likely hinges on the consumption by both species of yellow lichen (*Cetraria tilesii*) and sedges (*Cyperaceae* spp.), particularly from the southern part of the island, throughout the winter. The isotopic data presented here may reflect dietary fluctuations related to reported declines in the muskox population, and increases in the caribou population on Banks Island during the last several years (Kelvin 2016). The evidence for prolonged nursing in the crown dentin collagen isotopic data hints at reduced fecundity in muskoxen, and it may be that when the muskox population begins to decline, caribou take advantage of areas or forage such as sedges normally utilized (or over-utilized) by muskoxen. Smith (1996) found that in summer ranges of muskoxen on Banks Island, heavy grazing increases the above-ground phytomass of *Eriophorum triste*. Likewise, fecal deposition by muskoxen appears to be positively correlated with above-ground phytomass and nutritional content (Smith 1996).

Again, although there is little existing evidence for outright forage competition between caribou and muskoxen, traditional knowledge and observation suggest that caribou avoid muskoxen when possible. A sudden decline in the muskox population might open well-fertilized sedge meadows not normally available to caribou. Similarly, caribou diet, like that of muskoxen (Oakes et al. 1992; Larter and Nagy 1997; 2004) may depend on population density. Consequently, large proportional contributions of sedges to caribou bone collagen may reflect the broadening of the caribou dietary niche to reduce inter-individual forage competition.

Even without outright forage competition, the large proportions of yellow lichen in the winter diets of both caribou and muskoxen are potentially unsustainable. Again, though yellow lichens are abundant, lichen phytomass is relatively low (Larter and Nagy 2001a) and lichens regrow much more slowly than vascular plants (Miller 1973; Henry and Gunn 1990; Klein 1987, 1992; Larter and Nagy 1997; Griller 2001; Joly et al. 2008). Lichen phytomass is also expected to decrease as the Arctic warms and shrub phytomass increases

(Chapin et al. 1995; Cornelissen et al. 2001; Walker et al. 2006; Tape et al. 2012; Tremblay et al. 2012; Thompson and Barboza 2014). Given that shrubs do not appear to account for significant proportions of annual diet in either caribou or muskoxen and are only digestible for very short periods, increased shrub phytomass may not make up for the decrease in lichen phytomass. This potentially places both species at increased risk for nutritional and metabolic stress during the winter, in addition to other factors such as increased disease and parasite load (Kutz et al. 2001, 2004, 2005, 2008; Hughes et al. 2009), ice-crusts caused by rapid thaw-freeze events (Klein 1999; Gunn et al. 2000; Larter and Nagy 2001d; Tyler 2010; Descamps et al. 2017), and in muskoxen, low genetic diversity (Holm et al. 1999; MacPhee et al. 2005; Rodrigues et al. forthcoming). Since the decline of fox-trapping in the 1970's (Usher 1965; Nagy 1999; Kelvin 2016) caribou and muskoxen have become important parts of the sport-hunting and craft industries on Banks Island (Joint Secretariat 2015; Kelvin 2016). Similarly, the Canadian government has emphasized the health benefits of traditional foods in the north as a means to combat rising rates of obesity and diabetes (Furgal and Seguin 2006; Northwest Territories Environment and Natural Resources 2008; Public Health Agency of Canada 2012). Muskoxen – and to a lesser extent caribou – are important dietary staples on Banks Island (Nagy 1999; Kelvin 2016). Consequently, a simultaneous decline in the caribou and muskox populations on Banks Island could negatively impact both the economy and food security for community members in Sachs Harbour.

2.6 Conclusion

The $\delta^{13}C$ and $\delta^{15}N$ of forage samples, and bulk bone collagen and sequentially sampled crown dentin collagen, sheds light on the dietary ecology of modern caribou and muskoxen on Banks Island. The results demonstrate that the isotopic compositions of hard tissues can be mined for information about multiple ecological and environmental phenomena.

Bayesian dietary mixing models suggest that yellow lichens (*Cetraria tilesii*) and sedges (*Cyperaceae* spp.), make significant contributions to $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ in both caribou and muskoxen. Forbs are also a significant forage item for caribou. Conversely, dwarf willow and other shrub species do not appear to make significant contributions to bone collagen in either caribou or muskoxen. The high proportions of yellow lichen, and the very low

proportions of dwarf willow inferred from the mixing models, run contrary to existing interpretations of caribou and muskox diet on Banks Island, and we acknowledge that our dietary mixing models may be flawed in some fundamental way. Still, we have attempted to account for obvious sources of error, and the putative contribution of yellow lichen to the bone collagen isotopic compositions of both species persists even when generalized TDF estimates are used. We suggest that the high digestibility of yellow lichen results in its underrepresentation in the rumen and in feces, while the higher lignin content of shrubs results in lower digestibility and higher representation in both the rumen and fecal matter. Additionally, although yellow lichen is not viewed as a significant forage item for caribou, and especially muskoxen, on Banks Island, its high carbohydrate content may play a vital role in providing energy and maintaining the urea cycling functions of rumen microflora during the long winters, when higher quality forage is not available. Previous research also demonstrates that the uptake of glycine by *Cetraria* is high, and that glycine is readily absorbed without deamination by rumen microflora. Glycine also makes up a significant proportion of the amino acids in bone collagen. Because of this, consumption of yellow lichen may significantly influence the $\delta^{13}C$ of bulk bone collagen, while $\delta^{15}N_{bc}$ is balanced by nitrogen from other forage sources.

Sequentially sampled crown dentin collagen $\delta^{13}C$ and $\delta^{15}N$ ($\delta^{13}C_{dc}$ and $\delta^{15}N_{dc}$) provides some insight into seasonal dietary variation in muskox. Conversely, $\delta^{13}C_{dc}$ and $\delta^{15}N_{dc}$ is less informative of seasonal dietary variability due to the small size of caribou teeth. Future research, however, may derive higher-resolution dentin collagen isotopic data from caribou teeth by employing other tooth microsampling techniques described in the literature (Wurster et al. 1999; Balasse and Tresset 2002; Zazzo et al. 2005, 2006). Muskox $\delta^{13}C_{dc}$ reflects maternal seasonal dietary variations between forage with lower $\delta^{13}C$ during summer and forage with higher $\delta^{13}C$ during winter. Based on the Bayesian mixing model results, we suggest that lower $\delta^{13}C_{dc}$ during the summer corresponds to higher consumption of forbs, while higher $\delta^{13}C_{dc}$ during the winter corresponds to higher consumption of lichens and sedges. Conversely, $\delta^{15}N_{dc}$ is nearly uniform within and between teeth, indicating that both muskoxen continued nursing well into the second year of life.

The influence of prolonged nursing in muskox dentin collagen isotopic compositions observed here also emphasizes the point that isotopic data from dentin, even in late-growing permanent dentition, are not necessarily accurate indicators of adult diet (Bocherens et al. 1994). Based on research linking prolonged lactation to poorer forage conditions and decreased fecundity in wild muskoxen, the prolonged nursing signal in the teeth of the muskoxen may explain recently reported declines in the muskox population on Banks Island. Although sedge phytomass on Banks Island is high enough to support both caribou and muskoxen, heavy grazing by both species may rapidly deplete yellow lichen phytomass. Lichens also grow more slowly than vascular plants, and are expected to be outcompeted by shrubs as the Arctic warms. Overgrazing of yellow lichens may have significant impacts on the ability of both species to meet their maintenance energy and nutritional demands during winter. If our results and their implications are accurate, the potential reduction in population size of both caribou and muskoxen could affect both the health and economy of people in Sachs Harbour.

2.7 References

Adamczewski JZ, Gates CC, Hudson RJ, Price MA. 1987. Seasonal Changes in Body Composition of Mature Female Caribou and Calves (*Rangifer tarandus groenlandicus*) on an Arctic Island with Limited Winter Resources. Canadian Journal of Zoology 65: 1149-1157.

Adamczewski JZ, Gates CC, Soutar BM, Hudson RJ. 1988. Limiting Effects of Snow on Seasonal Habitat Use and Diets of Caribou (*Rangifer tarandus groenlandicus*) on Coats Island, Northwest Territories, Canada. Canadian Journal of Zoology 66: 1986-1996.

Adamczewski JZ, Gunn A, Laarveld B, Flood PF. 1992. Seasonal Changes in Weight, Condition and Nutrition of Free-Ranging and Captive Muskox Females. Rangifer 12(3): 179-183.

Adamczewski JZ, Hudson RJ, gates CC. 1993. Winter Energy Balance and Activity of Female Caribou on Coats Island, Northwest Territories: The Relative Importance of Foraging and Body Reserves. Canadian Journal of Zoology 71: 1221-1229.

Adamczewski JZ, Kerr WM, Lammerding EF, Flood PF. 1994. Digestion of Low-Protein Grass Hay by Muskoxen and Cattle. The Journal of Wildlife Management 58(4): 679-685.

Adamczewski JZ, Fargey PJ, Laarveld B, Gunn A, Flood PF. 1997. The Influence of Fatness on the Likelihood of Early-Winter Pregnancy in Muskoxen (*Ovibos moschatus*). Theriogenology 50: 605-614.

Ambrose SH. 1990. Preparation and Characterization of Bone and Tooth Collagen for Isotopic Analysis. Journal of Archaeological Science 17: 431-451.

Ambrose SH, Norr L. 1993. Experimental Evidence for the Relationship of the Carbon Isotope Ratios of Whole Diet and Dietary Protein to Those of Bone Collagen and Carbonate. In: Lambert JB, Grupe G, editors. Prehistoric Human Bone: Archaeology at the Molecular Level. Berlin: Springer-Verlag. Pp. 1-38.

Annison EF, Linzell JL. 1964. The Oxidation and Utilization of Glucose and Acetate by the Mammary Gland of the Goat in Relation to Their Overall Metabolism and to Milk Formation. Journal of Physiology 175: 372-385.

Annison EF, Linzell JL, West CE. 1968. Mammary and Whole Animal Metabolism of Glucose and Fatty Acids in Fasting Lactating Goats. Journal of Physiology 197: 445-459.

Atasoglu C, Guliye AY, Wallace RJ. 2004. Use of Stable Isotopes to Measure *de novo* Synthesis and Turnover of Amino Acid-C and -N in Mixed Micro-Organisms from the Sheep rumen *in vitro*. British Journal of Nutrition 91: 253-261.

Balasse M, Bocherens H, Mariotti A, Ambrose SH. 2001. Detection of Dietary Changes by Intra-tooth Carbon and Nitrogen Isotopic Analysis: An Experimental Study of Dentine Collagen of Cattle (*Bos taurus*). Journal of Archaeological Science 28: 235-245.

Balasse M, Tresset A. 2002. Early Weaning of Neolithic Domestic Cattle (Bercy, France) Revealed by Intra-tooth Variation in Nitrogen Isotope Ratios. Journal of Archaeological Science 29: 853-859.

Balasse M. 2003. Potential Biases in Sampling Design and Interpretation of Intra-tooth Isotope Analysis. International Journal of Osteoarchaeology 13: 3-10.

Balée W. 1998. Historical Ecology: Premises and Postulates. In: Balée W, editor. Advances in Historical Ecology. New York: Columbia University Press. Pp. 13-29.

Balée W. 2006. The Research Program of Historical Ecology. Annual Review of Anthropology 35: 75-98.

Barbour MM, Farquhar GD. 2000. Relative Humidity- and ABA-Induced Variation in Carbon and Oxygen Isotope Ratios of Cotton Leaves. Plant, Cell and Environment 23: 473-485.

Barboza PS, Parker KL. 2008. Allocating Protein to Reproduction in Arctic Reindeer and Caribou. Physiological and Biochemical Zoology: Ecology and Evolutionary Approaches 81(6): 835-855.

Bartolomé J, Franch J, Gutman M, Seligman NAG. 1995. Technical Note: Physical Factors That Influence Fecal Analysis Estimates of Herbivore Diets. Journal of Range Management 48: 267-270.

Batzli GO, White RG, Bunnell FL. 1981. Herbivory: A Strategy of Tundra Consumers. In: Bliss LC, Heal OW, Moore JJ, editors. Tundra Ecosystems: A Comparative Analysis. Pp. 359-375.

Ben-David M, Hanley TA, Klein DR, Schell DM. 1997. Seasonal Changes in Diets of Coastal and Riverine Mink: The Role of Spawning Pacific Salmon. Canadian Journal of Zoology 75: 803-811.

Ben-David M, Bowyer RT, Duffy LK, Roby DD, Schell DM. 1998. Social Behavior and Ecosystem Processes: River Otter Latrines and Nutrient Dynamics of Terrestrial Vegetation. Ecology 79(7): 2567-2571.

Bjerke JW, Dahl T. 2002. Distribution Patterns of usnic Acid-Producing Lichens Along Local Radiation Gradients in West Greenland. Nova Hedwigia 75: 487-506.

Blackburn TH, Hobson PN. 1960. The Degradation of Protein in the Rumen of the Sheep and Redistribution of the Protein Nitrogen After Feeding. British Journal of Nutrition 14: 445-456.

Bocherens H, Fizet M, Mariotti A. 1994. Diet, Physiology and Ecology of Fossil Mammals as Inferred from Stable Carbon and Nitrogen Isotope Biogeochemistry: Implications for Pleistocene Bears. Palaeogeography, Palaeoclimatology, Palaeoecology 107: 213-225.

Bocherens H, Pacaud G, Lazarev PA, Mariotti A. 1996. Stable Isotope Abundances (^{13}C, ^{15}N) in Collagen and Soft Tissues from Pleistocene Mammals from Yakutia: Implications for the Palaeobiology of the Mammoth Steppe. Palaeogeography, Palaeoclimatology, Palaeoecology 126: 31-44.

Bond AL, Diamond AW. 2011. Recent Bayesian Stable-Isotope Mixing Models are Highly Sensitive to Variation in Discrimination Factors. Ecological Applications 21(4): 1017-1023.

Boutton TW, Tyrrell HF, Patterson BW, Varga GA, Klein PD. 1988. Carbon Kinetics of Milk Formation in Holstein Cows in Late Lactation. Journal of Animal Science 66: 2636-2645.

Brooks SP, Gelman A. 1998. General Methods for Monitoring Convergence of Iterative Simulations. Journal of Computational and Graphical Statistics 7(4): 434-455.

Brown CH. 1975. Structural Materials in Animals. New York: John Wiley and Sons.

Carleton SA, Martinez del Rio C. 2005. The Effect of Cold-Induced Increased Metabolic Rate on the Rate of ^{13}C and ^{15}N Incorporation in House Sparrows (*Passer domesticus*). Oecologia 144(2): 226-232.

Carlson SJ. 1990. Vertebrate Dental Structures. In: Carter JG, editor. Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends, Volume 1. New York: Van Nostrand Reinhold.

Caut S, Angulo E, Courchamp F. 2008. Caution on Isotopic Model Use for Analyses of Consumer Diet. Canadian Journal of Zoology 86: 438-445.

Caut S, Angulo E, Courchamp F. 2009. Variation in Discrimination Factors (Δ^{15}N and Δ^{13}C): The Effect of Diet Isotopic Values and Applications for Diet Reconstruction. Journal of Applied Ecology 46: 443-453.

Chapin FS III, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA. 1995. Responses of Arctic Tundra to Experimental and Observed Changes in Climate. Ecology 76(3): 694-711.

Cherel Y, Jaquemet S, Maglio A, Jaeger A. 2014. Differences in δ^{13}C and δ^{15}N Values Between Feathers and Blood of Seabird Chicks: Implications for Non-Invasive Isotopic Investigations. Marine Biology 161: 229-237.

Cherel Y, Hobson KA, Guinet C. 2015. Milk Isotopic Values Demonstrate That Nursing Fur Seal Pups are a Full Trophic Level Higher Than Their Mothers. Rapid Communications in Mass Spectrometry 29: 1485-1490.

Cornelissen JHC, Callaghan TV, Alatalo JM, Michelsen A, Graglia E, Hartley AE, Hik DS, Hobbie SE, Press MC, Robinson CH, Henry GHR, Shaver GR, Phoenix GK, Gwynn Jones D, Jonasson S, and 7 Others. 2001. Global Change and Arctic Ecosystems: Is Lichen Decline a Function of Increases in Vascular Plant Biomass? Journal of Ecology 89: 984-994.

Côté SD. 1998. In Vitro Digestibilities of Summer Forages Utilized by the Rivière George Caribou Herd. Arctic 51(1): 48-54.

Cox G, Sealy J. 1997. Investigating Identity and Life Histories: Isotopic Analysis and Historical Documentation of Slave Skeletons Found on the Cape Town Foreshore, South Africa. International Journal of Historical Archaeology 1(3): 207-224.

Crumley CL. 2007. Historical Ecology: Integrated Thinking at Multiple Temporal and Spatial Scales. In: Hornborg A, Crumley C, editors. The World System and The Earth System: Global Socio-Environmental Change and Sustainability Since the Neolithic. California: Left Coast Press. Pp. 15-28.

Culberson C. 1977. Chemical and Botanical Quick Guide to Lichen Products. Bryologist S1(73): 77-377.

Dearden BL, Pegau RE, Hansen RM. 1975. Precision of Microhistological Estimates of Ruminant Food Habits. The Journal of Wildlife Management 39(2): 402-407.

DeNiro MJ, Epstein S. 1978. Influence of Diet on the Distribution of Carbon Isotopes in Animals. Geochimica et Cosmochimica Acta 42: 495-506.

DeNiro MJ, Epstein S. 1981. Influence of Diet on the Distribution of Nitrogen Isotopes in Animals. Geochimica et Cosmochimica Acta 45: 341-351.

DeNiro MJ. 1985. Postmortem Preservation and Alteration of *In Vivo* Bone Collagen Isotope Ratios in Relation to Palaeodietary Reconstruction. Nature 317: 806-809.

Denton DA. 1957. The Study of Sheep with Permanent Unilateral Parotid Fistulae. Quarterly Journal of Experimental Physiology 42: 72-95.

Descamps S, Aars J, Fuglei E, Kovacs KM, Lydersen C, Pavlova O, Pedersen ÅØ, Ravolainen V, Strøm H. 2017. Climate Change Impacts on Wildlife in a High Arctic Archipelago – Svalbard, Norway. Global Change Biology 23: 490-502.

DeVries MS, Stock BC, Christy JH, Goldsmith GR, Dawson TE. 2016. Specialized Morphology Corresponds to a Generalist Diet: Linking Form and Function in Smashing Mantis Shrimp Crustaceans. Oecologia 182: 429-442.

Dewhurst RJ, Davies DR, Merry RJ. 2000. Microbial Protein Supply from the Rumen. Animal Feed Science and Technology 85: 1-21.

Drever MC, Blight LK, Hobson KA, Bertram DF. 2000. Predation on Seabird Eggs by Keen's Mice (*Peromyscus keeni*): Using Stable Isotopes to Decipher the Diet of a Terrestrial Omnivore on a Remote Offshore Island. Canadian Journal of Zoology 78: 2010-2018.

Drucker DG, Hobson KA, Münzel SC, Pike-Tay A. 2012. Intra-Individual Variation in Stable Carbon (δ13C) and Nitrogen (δ15N) Isotopes in Mandibles of Modern Caribou of Qamanirjuaq (*Rangifer tarandus groenlandicus*) and Banks Island (*Rangifer tarandus pearyi*): Implications for Tracing Seasonal and Temporal Changes in Diet. International Journal of Osteoarchaeology 22: 494-504.

Ducatez S, Dalloyau S, Richard P, Guinet C, Cherel Y. 2008. Stable Isotopes Document Winter Trophic Ecology and Maternal Investment of Adult Female Southern Elephant Seals (*Mirounga leonina*) Breeding at the Kerguelen Islands. Marine Biology 155: 413-420.

Eldsen SR, Phillipson AT. 1948. Ruminant Digestion. Annual Review of Biochemistry 17(1): 705-726.

Fantle MS, Dittel AI, Schwalm SM, Epifanio CE, Fogel ML. 1999. A Food Web Analysis of the Juvenile Blue Crab, *Callinectes sapidus*, Using Stable Isotopes in Whole Animals and Individual Amino Acids. Oecologia 120: 416-426.

Farquhar GD, O'Leary MH, Berry JA. 1982. On the Discrimination Between Carbon Isotope Discrimination and the Intercellular Carbon Dioxide Concentration in Leaves. Australian Journal of Plant Physiology 9: 121-137.

Farquhar GD, Ehleringer JR, Hubick KT. 1989. Carbon Isotope Discrimination and Photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology 40: 503-537.

Fogel ML, Tuross N, Owsley DW. 1989. Nitrogen Isotope Tracers of Human Lactation in Modern and Archaeological Populations. Annual Report of the Director Geophysical Laboratory, Carnegie Institution, Washington, 1988-1989. Pp. 111-117.

Forchhammer MC, Post E, Stenseth NC, Boertmann DM. 2002. Long-term Responses in Arctic Ungulate Dynamics to Changes in Climatic and Trophic Processes. Population Ecology 44: 113-120.

Fuller BT, Richards MP, Mays SS. 2003. Stable Carbon and Nitrogen Isotope Variations in Tooth Dentine Serial Sections from Wharram Percy. Journal of Archaeological Science 30: 1673-1684.

Furgal C, Seguin J. 2006. Climate Change, Health, and Vulnerability in Canadian Northern Aboriginal Communities. Environmental Health Perspectives 114(12): 1964-1970.

Gaare R, Skogland T. 1975. Wild Reindeer Food Habits and Range Use at Hardangervidda. In: Wielgolaski FE, editor. Ecological Studies, Analysis and Synthesis. Fennoscandian Tundra Ecosystem. Berlin: Springer Verlag. Pp. 195-205.

Gage JP, Francis MJO, Triffitt JT. 1989. Collagen and Dental Matrices. London: Wright Press.

Gannes LZ, Martinez del Rio C, Koch P. 1998. Natural Abundance Variations in Stable Isotopes and Their Potential Uses in Animal Physiological Ecology. Comparative Biochemistry and Physiology 119A(3): 725-737.

Geange SW, Pledger S, Burns KC, Shima JS. 2011. A Unified Analysis of Niche Overlap Incorporating Data of Different Types. Methods in Ecology and Evolution 2: 175-184.

Gelman A, Rubin D. 1992a. Inference from Iterative Simulation Using Multiple Sequences. Statistical Science 7: 457-511.

Gelman A, Rubin D. 1992b. A Single Series from the Gibbs Sampler Provides a False Sense of Security. In: Bernardo JM, Berger JO, Dawid AP, Smith AFM, editors. Bayesian Statistics 4. New York: Oxford University Press. Pp. 625-631.

Gelman A, Shirley K. 2011. Inference from Simulations and Monitoring Convergence. In: Brooks S, Gelman A, Jones G, Meng X-L. Handbook of Markov Chain Monte Carlo. Boca Raton: Chapman & Hall/CRC. Pp. 163-174.

Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin DB. 2013. Bayesian Data Analysis, Third Edition. Boca Raton: CRC Press.

Geweke J. 1992. Evaluating the Accuracy of Sampling-Based Approaches to the Calculation of Posterior Moments. In: In: Bernardo JM, Berger JO, Dawid AP, Smith AFM, editors. Bayesian Statistics 4. New York: Oxford University Press. Pp. 169-193.

Geyer CJ. 1992. Practical Markov Chain Monte Carlo. Statistical Science 7: 473-483.

Geyer CJ. 2011. Introduction to Markov Chain Monte Carlo. In: Brooks S, Gelman A, Jones G, Meng X-L. Handbook of Markov Chain Monte Carlo. Boca Raton: Chapman & Hall/CRC. Pp. 3-48.

Gill RB, Carpenter LH, Bartmann RM, Baker DL, Schoonveld GG. 1983. Fecal Analysis to Estimate Mule Deer Diets. The Journal of Wildlife Management 47: 902-915.

Glad T, Barboza P, Mackie RI, Wright A-DG, Brusetti L, Mathiesen SD, Sundset MA. 2014. Dietary Supplementation of Usnic Acids, An Antimicrobial Compound in Lichens, Does Not Affect Rumen Bacterial Diversity or Density in Reindeer. Current Microbiology 68: 724-728.

Gordon IJ, Illius AW. 1994. The Functional Significance of the Browser-Grazer Dichotomy in African Ruminants. Oecologia 98: 167-175.

Gray DR. 1973. Social Organization and Behaviour of Muskoxen (Ovibos moschatus) on Bathurst Island, N.W.T. [Dissertation]. [Edmonton (AB)]: University of Alberta.

Grayhound Information Services. 1997. The Natural and Cultural Resources of Aulavik National Park. Report on file at Parks Canada Western Service Centre, Winnipeg, Manitoba.

Greer AL, Horton TW, Nelson XJ. 2015. Simple Ways to Calculate Stable Isotope Discrimination Factors and Convert Between Tissues. Methods in Ecology and Evolution 6: 1341-1348.

Griller N. 2001. Short and Long term Recovery of Plant Communities Following Intensive Grazing by Caribou (*Rangifer tarandus*) and Muskoxen (*Ovibos moschatus*) in the Low Arctic of Nunavut, Canada. [Dissertation]. [Vancouver (BC)]: University of British Columbia.

Gunn A, Shank C, McLean B. 1991. The History and Management of Muskoxen on Banks Island. Arctic 44(3): 188-195.

Gunn A, Miller FL, Nishi J. 2000. Status of Endangered and Threatened Caribou on Canada's Arctic Islands. Rangifer Special Issue 12: 39-50.

Gustine DD, Barboza PS, Lawler JP, Arthur SM, Shults BS, Persons K, Adams LG. 2011. Characteristics of Foraging Sites and Protein Status in Wintering Muskoxen: Insights from Isotopes of Nitrogen. Oikos 120: 1546-1556.

Hall RO, Meyer JL. 1998. The Trophic Significance of Bacteria in a Detritus-Based Stream Food Web. Ecology 79(6): 1995-2012.

Handley LL, Raven JA. 1992. The Use of Natural Abundance of Nitrogen Isotopes in Plant Physiology and Ecology. Plant, Cell and Environment 15: 965-985.

Handley LL, Austin AT, Robinson D, Scrimgeour CM, Raven JA, Heaton THE, Schmidt S, Stewart GR. 1999. The ^{15}N Abundance ($\delta^{15}N$) of Ecosystem Samples Reflects Measures of Water Availability. Australian Journal of Plant Physiology 26: 185-199.

Hare PE, Fogel ML, Stafford TW Jr., Mitchell AD, Hoering TC. 1991. The Isotopic Composition of Carbon and Nitrogen in Individual Amino Acids Isolated from Modern and Fossil Proteins. Journal of Archaeological Science 18: 277-292.

Harrison RG, Katzenberg MA. 2003. Paleodiet Studies Using Stable Carbon Isotopes from Bone Apatite and Collagen: Examples from Southern Ontario and San Nicolas Island, California. Journal of Anthropological Archaeology 22: 227-244.

Healy K, Kelly SBA, Guillerme T, Inger R, Bearhop S, Jackson AL. 2016. Predicting Trophic Discrimination Factor Using Bayesian Inference and Phylogenetic, Ecological and Physiological Data. DEsIR: Discrimination Estimation in R. PeerJ Preprints 4: e1950v1.

Hedges REM, van Klinken GJ. 2000. "Consider a Spherical Cow…"—on Modeling and Diet. In: Ambrose SH, Katzenberg MA, editors. Biogeochemical Approaches to Paleodietary Analysis. New York: Kluwer Academic Publishers. Pp. 211-242.

Hedges REM, Clement JG, Thomas CDL, O'Connell TC. 2007. Collagen Turnover in the Adult Femoral Mid-Shaft: Modeled from Anthropogenic Radiocarbon Tracer Measurements. American Journal of Physical Anthropology 133: 808-816.

Henrichsen P, Grue H. 1980. Age Criteria in the Muskox (*Ovibos moschatus*) from Greenland. Danish Review of Game Biology 11(4): 1-18.

Henry GHR, Gunn A. 1990. Recovery of Tundra Vegetation After Overgrazing by Caribou in Arctic Canada. Arctic 44(1): 38-42.

Hickey CG. 1982. Archaeological and Historical Investigations of Nineteenth Century Copper Inuit Culture. Preliminary report on file at the Canadian Museum of Civilization, Ottawa, Ontario.

Hidalgo ME, Bascuñan L, Quilhot W, Fernández E, Rubio C. 2005. Spectroscopic and Photochemical Properties of the Lichen Compound Lobaric Acid. Photochemistry and Photobiology 81: 1447-1449.

Hill PA, Orth M. 1998. Bone Remodelling. British Journal of Orthodontics 25: 101-107.

Hillal H, Voight J, Metges CC, Hammon HM. 2015. Milk Production and Nutrient Partitioning as Measured by ^{13}C Enrichment of Milk Components During C_3 and C_4 Plant Feeding in Purebred Holstein and in Charolais x Holstein F_2 Crossbred Cows. Isotopes in Environmental and Health Studies 51(1): 46-57.

Hillson S. 2000. Teeth. Cambridge: Cambridge University Press.

Hobson KA, Alisauskas RT, Clark RG. 1993. Stable-Nitrogen Isotope Enrichment in Avian Tissues Due to Fasting and Nutritional Stress: Implications for Isotopic Analyses of Diet. The Condor 95(2): 388-394.

Hobson KA, Sease J. 1998. Stable Isotope Analyses of Tooth Annuli Reveal Temporal Dietary Records: An Example Using Steller Sea Lions. Marine Mammal Science 14(1): 116-129.

Hofmann RR, Stewart DRM. 1972. Grazer or Browser: A Classification Based on the Stomach-Structure and Feeding Habits of East African Ruminants. Mammalia 36(2): 226-240.

Hofmann RR. 1989. Evolutionary Steps of Ecophysiological Adaptation and Diversification of Ruminants: A Comparative View of Their Digestive System. Oecologia 78(4): 443-457.

Hofmann RR. 2000. Functional and Comparative Digestive System Anatomy of Arctic Ungulates. Rangifer 20(2-3): 71-81.

Holechek JL, Valdez R. 1985. Magnification and Shrub Stemmy Material Influences on Fecal Analysis Accuracy. Journal of Range Management 38(4): 350-352.

Holm L-E, Forchhammer MC, Boomsma JJ. 1999. Low Genetic Variation in Muskoxen (*Ovibos moschatus*) from Western Greenland Using Microsatellites. Molecular Ecology 8: 675-679.

Hörnicke H, Björnhag G. 1980. Coprophagy and Related Strategies for Digesta Utilization. In: Ruckebusch Y, Thivend P, editors. Digestive Physiology and Metabolism in Ruminants. Proceedings of the 5th International Symposium on Ruminant Physiology Held at Clermont-Ferrand on 3rd-7th September, 1979. Lancaster: MTP Press.

Hove K, Jacobsen E. 1975. Renal Excretion of Urea in Reindeer. Acta Veterinaria Scandinavica 16: 513-519.

Hudson RJ, Christopherson RJ. 1985. Maintenance Metabolism. In: Hudson RJ, White RG, editors. Bioenergetics of Wild Herbivores. Boca Raton: CRC Press. Pp. 121-142.

Hughes J, Albon SD, Irvine RJ, Woodin S. 2009. Is There a Cost of Parasites to Caribou? Parasitology 136: 253-265.

Hungate RE. 1966. The Rumen and Its Microbes. New York: Academic Press.

Hungate RE. 1975. The Rumen Microbial Ecosystem. Annual Review of Ecology and Systematics 6: 39-66.

Hut G. 1987. Consultants' Group Meeting on Stable Isotope Reference Samples for Geochemical and Hydrological Investigations, IAEA, Vienna, 16-18 September 1985. Vienna: Report to the Director General.

Ihl C, Klein DR. 2001. Habitat and Diet Selection by Muskoxen and Reindeer in Western Alaska. The Journal of Wildlife Management 65(4): 964-972.

Inger R, Jackson A, Parnell A, Bearhop S. No Date. SIAR V4 (Stable Isotope Analysis in R): An Ecologist's Guide. Available from: https://www.tcd.ie/Zoology/research/research/theoretical/siar/SIAR_For_Ecologists.pdf.

Jackson AL, Inger R, Bearhop S, Parnell A. 2009. Erroneous Behaviour of MixSIR, A Recently Published Bayesian Isotope Mixing Model: A Discussion of Moore & Semmens (2008). Ecology Letters 12: E1-E5.

Jenkins SG, Partridge ST, Stephenson TR, Farley SD, Robbins CT. 2001. Nitrogen and Carbon Isotope Fractionation Between Mothers, Neonates, and Nursing Offspring. Oecologia 129: 336-341.

Jenkins DA, Campbell M, Hope G, Goorts J, McLoughlin P. 2011. Recent Trends in Abundance of Peary Caribou (*Rangifer tarandus Pearyi*) and Muskoxen (*Ovibos moschatus*) in the Canadian Arctic Archipelago, Nunavut. Department of Environment, Government of Nunavut, Wildlife Report Number 1. Nunavut: Pond Inlet.

Joint Secretariat. 2015. Inuvialuit and Nanuq: A Polar Bear Traditional Knowledge Study. Joint Secretariat, Inuvialuit Settlement Region. Available from: http://www.wmacns.ca/current/projects/37/.

Joly K, Cole MJ, Jandt RR. 2008. Diets of Overwintering Caribou, Rangifer tarandus, Track Decadal Changes in Arctic Tundra Vegetation. Canadian Field Naturalist 121(4): 379-383.

Jørkov MLS, Heinemeier J, Lynnerup N. 2007. Evaluating Bone Collagen Extraction Methods for Stable Isotope Analysis in Dietary Studies. Journal of Archaeological Science 34: 1824-1829.

Kadye WT, Booth AJ. 2012. Integrating Stomach Content and Stable Isotope Analyses to Elucidate the Feeding Habits of Non-Native Sharptooth Catfish *Clarias gariepinus*. Biological Invasions 14: 779-795.

Katzenberg MA, Herring DA, Saunders SR. 1996. Weaning and Infant Mortality: Evaluating the Skeletal Evidence. Yearbook of Physical Anthropology 39: 177-199.

Kelsall JP. 1968. The Migratory Barren-Ground Caribou of Canada. Ottawa: Canadian Wildlife Service, Department of Northern Affairs and National Resources, Natural and Historic Resources Branch.

Kelvin LE. 2016. There Is More Than One Way to Do Something Right: Applying Community-Based Approaches to an Archaeology of Banks Island, NWT. [Dissertation]. [London (ON)]: University of Western Ontario.

Kempster B, Zanette L, Longstaffe FJ, MacDougall-Shackleton SA, Wingfield JC, Clinchy M. 2007. Do Stable Isotopes Reflect Nutritional Stress? Results from a Laboratory Experiment on Song Sparrows. Oecologia 151: 365-371.

Kielland K. 1995. Landscape Patterns of Free Amino Acids in Arctic Tundra Soils. Biogeochemistry 31: 85-98.

Kielland K. 1997. Role of Free Amino Acids in the Nitrogen Economy of Arctic Cryptograms. Ecoscience 4(1): 75-79.

Klein DR, Schønheyder F. 1970. Variation in Ruminal Nitrogen Levels Among Some Cervidae. Canadian Journal of Zoology 48: 1437-1442.

Klein DR. 1987. Vegetation Recovery Patterns Following Overgrazing by Reindeer on St. Matthews Island. Journal of Range Management 40: 336-338.

Klein DR, Bay C. 1990. Foraging Dynamics of Muskoxen in Peary Land, Northern Greenland. Holarctic Ecology 13(4): 269-280.

Klein DR. 1991. Limiting Factors in Caribou Population Ecology. Rangifer Special Issue 7: 30-35.

Klein DR. 1992. Comparative Ecological and Behavioral Adaptation of *Ovibos moschatus* and *Rangifer tarandus*. Rangifer 12(2): 47-55.

Klein DR. 1999. The Roles of Climate and Insularity in Establishment and Persistence of *Rangifer tarandus* Populations in the High Arctic. Ecological Bulletins 47: 96-104.

Knobbe N, Vogl J, Pritzkow W, Panne U, Fry H, Lochotzke HM, Preiss-Weigert A. 2006. C and N Stable Isotope Variation in Urine and Milk of Cattle Depending on the Diet. Analytical and Bioanalytical Chemistry 386: 104-108.

Koch PL. 1998. Isotopic Reconstruction of Past Continental Environments. Annual Review of Earth and Planetary Sciences 26: 573-613.

Koch PL. 2007. Isotopic Study of the Biology of Modern and Fossil Vertebrates. In: Michener R, Lajtha K, editors. Stable Isotopes in Ecology and Environmental Science. Malden: Blackwell. Pp. 99-154.

Kong A. 1992. A Note on Importance Sampling Using Standardized Weights. Technical Report Number 348, Department of Statistics. Chicago: The University of Chicago.

Krueger HW, Sullivan CH. 1984. Models for Carbon Isotope Fractionation Between Diet and Bone. In: Turnlund JR, Johnson PE, editors. ACS Symposium Series Number 258 Stable Isotopes in Nutrition. Pp. 205-220.

Kutz SJ, Hoberg EP, Polley L. 2001. A New Lungworm in Muskoxen: An Exploration in Arctic Parasitology. TRENDS in Parasitology 17(6): 276-280.

Kutz SJ, Hoberg EP, Nagy J, Polley L, Elkin B. 2004. "Emerging" Parasitic Infections in Arctic Ungulates. Integrative and Comparative Biology 44: 109-118.

Kutz SJ, Hoberg EP, Polley L, Jenkins EJ. 2005. Global Warming is Changing the Dynamics of Arctic Host-Parasite Systems. Proceedings of the Royal Society B 272: 2571-2576.

Kutz SJ, Thompson RCA, Polley L, Kandola K, Nagy J, Wielinga CM, Elkin BT. 2008. *Giardia* Assemblage A: Human Genotype in Muskoxen in the Canadian Arctic. Parasites and Vectors 1(32).

Lanfear R, Hua X, Warren DL. 2016. Estimating the Effective Sample Size of Tree Topologies from Bayesian Phylogenetic Analyses. Genome Biology and Evolution 8(8): 2319-2332.

Larsen TS, Nilsson NØ, Blix AS. 1985. Seasonal Changes in Lipogenesis and Lipolysis in Isolated Adipocytes from Svalbard and Norwegian Reindeer. Acta Physiologica Scandinavica 123: 97-104.

Larter NC, Nagy JA. 1997. Peary Caribou and Banks Island Forage: Assessing Seasonal Diet Similarities. Rangifer 17(1): 9-16.

Larter NC, Nagy JA. 2001a. The Distribution of Forage Types Among Four Terrestrial Habitats on Southern Banks Island. Department of Resources, Wildlife & Economic Development, Government of the Northwest Territories, Manuscript Report Number 142. Northwest Territories: Inuvik.

Larter NC, Nagy JA. 2001b. Seasonal and Annual Variability in the Quality of Important Forage Plants on Banks Island, Canadian High Arctic. Applied Vegetation Science 4: 115-128.

Larter NC, Nagy JA. 2001c. Calf Production, Calf Survival, and Recruitment of Muskoxen on Banks Island During a Period of Changing Population Density from 1986-99. Arctic 54(4): 394-406.

Larter NC, Nagy JA. 2001d. Variation Between Snow Conditions at Peary Caribou and Muskox Feeding Sites and Elsewhere in Foraging Habitats on Banks Island in the Canadian High Arctic. Arctic, Antarctic, and Alpine Research 33(2): 123-130.

Larter NC, Nagy JA. 2002. Does Seasonal Variation in Forage Quality Influence the Potential for Resource Competition Between Muskoxen and Peary Caribou on Banks Island? Rangifer 22(2): 143-153.

Larter NC, Nagy JA. 2004. Seasonal Changes in the Composition of the Diets of Peary Caribou and Muskoxen on Banks Island. Polar Research 23(2): 131-140.

Latour PB. 1987. Observations on Demography, Reproductions, and Morphology of Muskoxen (*Ovibos moschatus*) on Banks Island, Northwest Territories. Canadian Journal of Zoology 65: 265-269.

Lee-Thorp JA, Sealy JC, van der Merwe N. 1989. Stable Carbon Isotope Ratio Differences Between Bone Collagen and Bone Apatite, and Their Relationship to Diet. Journal of Archaeological Science 16: 585-599.

Libby WF, Berger R, Mead J, Alexander G, Ross J. 1964. Replacement Rates for Human Tissue from Atmospheric Radiocarbon. Science 146: 1170-1172.

Link WA, Eaton MJ. 2012. On Thinning of Chains in MCMC. Methods in Ecology and Evolution 3: 112-115.

Linzell JL. 1967. The Effect of Infusions of Glucose, Acetate and Amino Acids on Hourly Milk Yield in Fed, Fasted and Insulin-Treated Goats. Journal of Physiology 190: 347-357.

Liu JS. 1996. Metropolized Independent Sampling with Comparisons to Rejection Sampling and Importance Sampling. Statistics and Computing 6: 113-119.

Longin R. 1971. New Method of Collagen Extraction for Radiocarbon Dating. Nature 230: 241-242.

Lowenstam HA, Weiner S. 1989. On Biomineralization. New York: Oxford University Press.

Lubetkin SC, Simenstad CA. 2004. Multi-Source Mixing Models to Quantify Food Web Sources and Pathways. Journal of Applied Ecology 41: 996-1008.

Lyttleton JW. 1960. Bloat in Cattle. New Zealand Journal of Agricultural Research 3(1): 63-68.

MacEachern SN, Berliner LM. 1994. Subsampling the Gibbs Sampler. The American Statistician 48: 188-190.

MacPhee RDE, Tikhonov AN, Mol D, Greenwood AD. 2005. Later Quaternary Loss of Genetic Diversity in Muskox (*Ovibos*). BMC Evolutionary Biology 5(49).

Manning TH, MacPherson AH. 1958. The Mammals of Banks Island. Arctic Institute of North America Technical Papers 2: 5-74.

Manning TH. 1960. The Relationship of the Peary and Barren Ground Caribou. Arctic Institute of North America Technical Papers 4: 5-52.

Martino L, Elvira V, Louzada F. 2017. Effective Sample Size for Importance Sampling Based on Discrepancy Measures. Signal Processing 131: 386-401.

Mathiesen SD, Sørmo W, Aagnes Utsi TH. 1999. Forage Chemistry and the Digestive System in Reindeer (*Rangifer tarandus tarandus*) in Northern Norway and on South Georgia. Rangifer 19: 91-101.

Mathiesen SD, Sørmo W, Aagnes Utsi TH. 2000. Comparative Aspects of Volatile Fatty Acid Production in Reindeer (Rangifer tarandus tarandus) in Northern Norway and on South Georgia. Rangifer 20(4): 201-210.

Matsubayashi J, Morimoto J, Mano T, Aryal A, Nakamura F. Using Stable Isotopes to Understand the Feeding Ecology of the Hokkaido Brown Bear (*Ursus arctos*) in Japan. Ursus 25(2): 87-97.

McEwan EH. 1968. Hematological Studies of Barren-Ground Caribou. Canadian Journal of Zoology 46: 1031-1036.

McEwan EH, Whitehead PE. 1970. Seasonal Changes in the Energy and Nitrogen Intake in Reindeer and Caribou. Canadian Journal of Zoology 48(5): 905-913.

McGhee R. 1996. Ancient People of the Arctic. Gatineau: Canadian Museum of Civilization.

Miller GH. 1973. Variations in Lichen Growth from Direct Measurements: Preliminary Curves for *Alectoria miniscula* from Eastern Baffin Island, N. W. T., Canada. Arctic and Alpine Research 5(4): 333-339.

Miller FL. 1974. Biology of the Kaminuriak Population of Barren-ground Caribou. Park 2: Dentition as an Indicator of Age and Sex; Composition and Socialisation of the Population. Canadian Wildlife Service Report Series 31.

Miller FL, Gunn A. 2003. Status, Population Fluctuations and Ecological Relationships of Peary Caribou on the Queen Elizabeth Islands: Implications for Their Survival. Rangifer Special Issue Number 14: 213:226.

Minigawa M, Wada E. 1984. Stepwise Enrichment of ^{15}N Along Food Chains: Further Evidence and the Relation Between $\delta^{15}N$ and Animal Age. Geochimica et Cosmochimica Acta 48: 1135-1140.

Minson DJ, Ludlow MM, Troughton JH. 1975. Differences in Natural Carbon Isotope Ratios of Milk and Hair from Cattle Grazing Tropical and Temperate Pastures. Nature 26: 602.

Moore JW, Semmens BX. 2008. Incorporating Uncertainty and Prior Information into Stable Isotope Mixing Models. Ecology Letters 11: 470-480.

Nagy M. 1999. Aulavik Oral History Project on Banks Island, NWT: Final Report. Inuvik: Inuvialuit Social Development Program.

Newsome SD, Koch PL, Etnier MA, Aurioles-Gamboa D. 2006. Using Carbon and Nitrogen Isotope Values to Investigate Maternal Strategies in Northeast Pacific Otariids. Marine Mammal Science 22(3): 556-572.

Nichols SJ, Garling D. 2000. Food-Web Dynamics and Trophic-Level Interactions in a Multispecies Community of Freshwater Unionids. Canadian Journal of Zoology 78: 871-882.

Nieminen M. 1980. Nutritional and Seasonal Effects on the Haematology and Blood Chemistry in Reindeer (*Rangifer Tarandus Tarandus* L.). Comparative Biochemistry and Physiology 66A: 399-413.

Northwest Territories Environment and Natural Resources. 2008. NWT Climate Change Impacts and Adaptation Report. Available from: http://www.enr.gov.nt.ca/sites/default/files/reports/nwt_climate_change_impacts_and_adaptation_report.pdf.

Oakes EJ, Harmsen R. 1992. Sex, Age, and Seasonal Differences in the Diets and Activity Budgets of Muskoxen (*Ovibos moschatus*). Canadian Journal of Zoology 70: 605-616.

Oelbermann K, Scheu S. 2002. Stable Isotope Enrichment (δ^{15}N and δ^{13}C) in a Generalist Predator (*Pardosa lugubris*, Araneae; Lycosidae): Effects of Prey Quality. Oecologia 130: 337-344.

Ørskov ER. 1992. Protein Nutrition in Ruminants, Second Edition. London: Academic Press.

Palmer LJ. 1944. Food Requirements of some Alaskan Game Mammals. Journal of Mammalogy 25(1): 49-54.

Palo RT. 1993. Usnic Acid, A Secondary Metabolite of Lichens and Its Effect on *in vitro* Digestibility in Reindeer. Rangifer 13(1): 39-43.

Parker GR. 1978. The Diets of Muskoxen and Peary Caribou on Some Islands in the Canadian High Arctic. Canadian Wildlife Service Occasional Papers 35.

Parker KL, Barboza PS, Stephenson TR. 2005. Protein Conservation in Female Caribou (Rangifer tarandus): Effects of Decreasing Diet Quality During Winter. Journal of Mammalogy 86(3): 610-622.

Parnell AC, Inger R, Bearhop S, Jackson AL. 2010. Source Partitioning Using Stable Isotopes: Coping with Too Much Variation. PLoS ONE 5(3): e9672.

Pate FD. 1994. Bone Chemistry and Paleodiet. Journal of Archaeological Method and Theory 1(2): 161-209.

Peterson J, Wunder BA. 1997. Food Sorting by Collared Lemmings (*Dicrostonyx groenlandicus*) and Prairie Voles (*Microtus ochrogaster*): A Cautionary Note for Digestibility Studies. Comparative Biochemistry and Physiology 116A(2): 119-124.

Phillips DL, Inger R, Bearhop S, Jackson AL, Moore JW, Parnell AC, Semmens BX, Ward EJ. 2014. Best Practices for Use of Stable Isotope Mixing Models in Food-Web Studies. Canadian Journal of Zoology 92: 823-835.

Polischuk SC, Hobson KA, Ramsay MA. 2001. Use of Stable-Carbon and -Nitrogen Isotopes to Assess Weaning and Fasting in Female Polar Bears and Their Cubs. Canadian Journal of Zoology 79(3): 499-511.

Polunin N. 1959. Circumpolar Arctic Flora. Oxford: Clarendon Press.

Porsild AE. 1957. Illustrated Flora of the Canadian Arctic Archipelago. National Museum of Canada Bulletin Number 146. Ottawa, Canada: Department of Northern Affairs and National Resources.

Public Health Agency of Canada. 2012. Nunavut/Northwest Territories: Healthy Foods North – A Culturally Appropriate and Community-Based Program to Promote Healthy Eating and Lifestyle. Available from: http://www.phac-aspc.gc.ca/publicat/2009/be-eb/nunavut-eng.php.

Qi H, Coplen TB, Geilmann H, Brand WA, Böhlke JK. 2004. Two New Organic Reference Materials for δ^{13}C and δ^{15}N Measurements and a New Value for the δ^{13}C of NBS 22 Oil. Rapid Communications in Mass Spectrometry 17: 2483-2487.

R Development Core Team. 2009. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. Available from: http://www.R-project.org.

Robbins CT, Felicetti LA, Sponheimer M. 2005. The Effect of Dietary Protein Quality on Nitrogen Isotope Discrimination in Mammals and Birds. Oecologia 144(4): 534-540.

Robbins CT, Felicetti LA, Florin ST. 2010. The Impact of Protein Quality on Stable Nitrogen Isotope Ratio Discrimination and Assimilated Diet Estimation. Oecologia 162(3): 571-579.

Rombach EP, Barboza PS, Blake JE. 2002. Utilization of Copper During Lactation and Neonatal Development in Muskoxen. Canadian Journal of Zoology 80: 1460-1469.

Rosing MN, Ben-David M, Barry RP. 1998. Analysis of Stable Isotope Data: A K Nearest-Neighbors Randomization Test. The Journal of Wildlife Management 62(1): 380-388.

Rundel PW. 1978. The Ecological Role of Secondary Lichen Substances. Biochemical Systematics and Ecology 6: 157-170.

Ryg M, Jacobsen E. 1982. Effects of Castration on Growth and Food Intake Cycles in Young Male Reindeer (*Rangifer tarandus tarandus*). Canadian Journal of Zoology 60: 942-945.

Salgado-Flores A, Bockwoldt M, Hagen LH, Pope PB, Sundset MA. 2016. First Insight into the Faecal Microbiota of the High Arctic Muskoxen (*Ovibos moschatus*). Microbial Genomics 2(7): e000066.

SAS Institute Inc. 2011. Introduction to Bayesian Analysis Procedures. In: SAS/STAT® 9.3 User's Guide. Cary, NC: SAS Institute Inc. Pp. 129-165.

Schoeller DA. 1999. Isotope Fractionation: Why Aren't We What We Eat? Journal of Archaeological Science 26: 667-673.

Schoeninger MJ, Moore KM, Murray ML, Kingston JD. 1989. Detection of Bone Preservation in Archaeological and Fossil Samples. Applied Geochemistry 4: 281-292.

Schurr MR. 1998. Using Stable Nitrogen-Isotopes to Study Weaning Behavior in Past Populations. World Archaeology 30(2): 327-342.

Scotter GW. 1972. Chemical Composition of Forage Plants from the Reindeer Preserve, Northwest Territories. Arctic 25: 21-27.

Semmens BX, Moore JW, Ward EJ. 2009. Improving Bayesian Isotope Mixing Models: A Response to Jackson *et al.* (2009). Ecology Letters 12: E6-E8.

Semmens B, Stock B, Ward E, Moore J, Parnell A, Jackson A, Phillips D, Bearhop S, Inger R. 2013. MixSIAR: A Bayesian Stable Isotope Mixing Model for Characterizing Intrapopulation Niche Variation. Presented at Ecological Society of America, Minneapolis, MN, August 04-09.

Shank CC, Wilkinson PF, Penner DF. 1978. Diet of Peary Caribou, Banks Island, N.W.T. Arctic 31(2): 125-132.

Sillen A, Sealy JC, van der Merwe NJ. 1989. Chemistry and Paleodietary Research: No More Easy Answers. American Antiquity 54(3): 504-512.

Skogland T. 1989. Comparative Social Organization of Wild Reindeer in Relation to Food, Mates, and Predator Avoidance. Advances in Ethology 29. Berlin: Paul Perey Verlag. Pp. 1-74.

Skogland T. 1990. Density Dependence in a Fluctuating Wild Reindeer Herd; Maternal vs. Offspring Effects. Oecologia 84(4): 442-450.

Skoog RO. 1968. Ecology of the Caribou (*Rangifer tarandus granti*) in Alaska. [Dissertation]. [Berkeley (CA)]: University of California Berkeley.

Smith DL. 1996. Muskoxen/Sedge Meadow Interactions, North-Central Banks Island, Northwest Territories, Canada. [Dissertation]. [Saskatoon (SK)]: University of Saskatchewan.

Smith JJ, Millar JS, Longstaffe FJ, Boonstra R. 2010. The Effect of Metabolic Rate on Stable Carbon and Nitrogen Isotope Compositions in Deer Mice, *Peromyscus maniculatus*. Canadian Journal of Zoology 88: 36-42.

Sørmo W, Hagra ØE, White RG, Mathiesen SD. 1997. Comparative Aspects of Volatile Fatty Acid Production in the Rumen and Distal Fermentation Chamber in Svalbard Reindeer. Rangifer 17(2): 81-95.

Sponheimer M, Robinson T, Ayliffe L, Roeder B, Hammer J, Passey B, West A, Cerling T, Dearing D, Ehleringer J. 2003. Nitrogen Isotopes in Mammalian Herbivores: Hair δ^{15}N Values from a Controlled Feeding Study. International Journal of Osteoarchaeology 13: 80-87.

Spencer GC, Krumboltz OF. 1929. Chemical Composition of Alaska Lichens. Journal of the Association of Official Agricultural Chemists 12: 317-319.

Staaland H, Sæbø S. 1987. Seasonal Variation in Mineral Status of Reindeer Calves from Elgaa Reindeer Herding District, Norway. Rangifer 7: 22-28.

Stevenson FJ. 1982. Nitrogen in Agricultural Soils, Agronomy Monograph 22. Madison: American Society of Agronomy.

Stock BC, Semmens BX. 2013. MixSIAR GUI User Manual. Version 3.1. Available from: https://github.com/brianstock/MixSIAR.

Stock BC, Semmens BX. 2016. Unifying Error Structures in Commonly Used Biotracer Mixing Models. Ecology 97(10): 2562-2569.

Storeheier PV, Mathiesen SD, Tyler NJC, Olsen MA. 2002. Nutritive Value of Terricolous Lichens for Reindeer in Winter. Lichenologist 34(4): 247-257.

Sullivan CH, Krueger HW. 1981. Carbon Isotope Analysis of Separate Chemical Phases in Modern and Fossil Bone. Nature 292: 333-335.

Sundset MA, Kohn A, Mathiesen SD, Præsteng KE. 2008. Naturwissenschaften 95: 741-749.

Sundset MA, Barboza PS, Green TK, Folkow LP, Schytte Blix A, Mathiesen SD. 2010. Microbial Degradation of Usnic Acid in the Reindeer Rumen. Naturwissenschaften 97: 273-278.

Svihus B, Holand Ø. 2000. Lichen Polysaccharides and Their Relation to Reindeer/Caribou Nutrition. Journal of Range Management 53(6): 642-648.

Szpak P, Orchard TJ, McKechnie I, Gröcke DR. 2012. Historical Ecology of late Holocene Sea Otters (*Enhydra lutris*) from Northern British Columbia: Isotopic and Zooarchaeological Perspectives. Journal of Archaeological Science 39: 1553-1571.

Szpak P, White CD, Longstaffe FJ, Millaire J-F, Vásquez Sánchez VF. 2013. Carbon and Nitrogen Isotopic Survey of Northern Peruvian Plants: Baselines for Paleodietary and Paleoecological Studies. PLoS ONE 8(1): e53763.

Tahmasebi F. 2015. Carbon and Nitrogen Isotopic Investigations of the Late Pleistocene Paleoecology of Eastern Beringia, Yukon Territory, Using Soils, Plants, and Rodent Bones. [Dissertation]. [London (ON)]: University of Western Ontario.

Tape KD, Hallinger M, Welker JM, Ruess RW. 2012. Landscape Heterogeneity of Shrub Expansion in Arctic Alaska. Ecosystems 15: 711-724.

Tener JS. 1965. Muskoxen in Canada: A Biological and Taxonomic Review. Ottawa: Canadian Wildlife Service, Department of Northern Affairs and National Resources, Natural and Historic Resources Branch.

Thing H, Klein DR, Jingfors K, Holt S. 1987. Ecology of Muskoxen in Jameson Land, Northeast Greenland. Holarctic Ecology 10(2): 95-103.

Thomas DC, Kroeger P. 1980. *In Vitro* Digestibilities of Plants in Rumen Fluids of Peary Caribou. Arctic 33(4): 757-767.

Thomas DC, Edmonds EJ. 1983. Rumen Contents and Habitat Selection of Peary Caribou in Winter, Canadian Arctic Archipelago. Arctic and Alpine Research 15(1): 97-105.

Thomas DC, Edmonds EJ, Armbruster HJ. 1999. Range Types and Their Relative Use by Peary Caribou and Muskoxen on Melville Island, NWT. Canadian Wildlife Service Technical Report Series Number 343.

Thompson DP, Barboza PS. 2014. Nutritional Implications of Increased Shrub Cover for Caribou (*Rangifer tarandus*) in the Arctic. Canadian Journal of Zoology 92: 339-351.

Tieszen LL, Boutton TW, Tesdahl KG, Slade NA. 1983. Fractionation and Turnover of Stable Carbon Isotopes in Animal Tissues: Implications for $\delta^{13}C$ Analysis of Diet. Oecologia 57: 32-37.

Tieszen LL, Fagre T. 1993. Effect of Diet Quality and Composition on the Isotopic of Respiratory CO_2, Bone Collagen, Bioapatite, and Soft Tissues. In: Lambert JB, Grupe G, editors. Prehistoric Human Bone: Archaeology at the Molecular Level. Berlin: Springer-Verlag. Pp. 121-156.

Tremblay B, Lévesque E, Boudreau S. 2012. Recent Expansion of Erect Shrubs in the Low Arctic: Evidence from Eastern Nunavik. Environmental Research Letters 7.

Trudell J, White RG. 1981. The Effect of Forage Structure and Availability on Food Intake, Biting Rate, Bite Size and Daily Eating Time of Reindeer. Journal of Applied Ecology 18(1): 63-81.

Tyler NJC, Blix AS. 1990. Survival Strategies in Arctic Ungulates. Rangifer Special Issue Number 3: 211-230.

Tyler NJC. 2010. Climate, Snow, Ice, Crashes, and Declines in Populations of Reindeer and Caribou (*Rangifer tarandus L.*). Ecological Monographs 80(2): 197-219.

Usher PJ. 1965. Banks Island: An Area Economic Survey. Report on file at Industrial Division, Department of Northern Affairs and National Resources, Ottawa, Ontario.

van der Merwe NJ. 1989. Natural Variation in ^{13}C Concentration and Its Effect on Environmental Reconstruction Using $^{13}C/^{12}C$ Ratios in Animal Bones. In: Price TD, editor. The Chemistry of Prehistoric Human Bone. Cambridge: Cambridge University Press. Pp. 105-125.

van Geel B, Guthrie RD, Altmann JG, Broekens P, Bull ID, Gill FL, Jansen B, Nieman AM, Gravendeel B. 2011. Mycological Evidence of Coprophagy from the Feces of an Alaskan Late Glacial Mammoth. Quaternary Science Reviews 30: 2289-2303.

van Klinken GJ. 1999. Bone Collagen Quality Indicators for Palaeodietary and Radiocarbon Measurements. Journal of Archaeological Science 26: 687-695.

Van Soest PJ. 1982. Nutritional Ecology of the Ruminant. Ithaca: Cornell University Press.

Vanderklift MA, Ponsard S. 2003. Sources of Variation in Consumer-Diet δ^{15}N Enrichment: A Meta-Analysis. Oecologia 136: 169-182.

Verburg P. 2007. The Need to Correct for the Suess Effect in the Application of δ^{13}C in Sediment of Autotrophic Lake Tanganyika, as a Productivity Proxy in the Anthropocene. Journal of Paleolimnology 37: 591-602.

Vincent D, Gunn A. 1981. Population Increase of Muskoxen on Banks Island and Implications for Competition with Peary Caribou. Arctic 34(2): 175-179.

Wales RA, Milligan LP, McEwan EH. 1975. Urea Recycling in Caribou, Cattle and Sheep. In: Luick JR, Lent PC, Klein DR, White RG, editors. Proceedings of the First International Reindeer and Caribou Symposium. Fairbanks: University of Alaska. Pp. 297-307.

Walker MD, Wahren CH, Hollister RD, Henry GHR, Ahlquist LE, Alatalo JM, Bret-Harte MS, Calef MP, Callaghan TV, Carroll AB, Epstein HE, Jonsdottir IS, Klein JA, Magnusson B, Molau U, and 12 others. 2006. Plant Community Responses to Experimental Warming Across the Tundra Biome. Proceedings of the National Academy of Sciences 103(5): 1342-1346.

White RG, Luick JR. 1976. Glucose Metabolism in Lactating Reindeer. Canadian Journal of Zoology 54: 55-64.

White RG. 1983. Foraging Patterns and Their Multiplier Effects on Productivity of Northern Ungulates. Oikos 40(3): 377-384.

White RG, Holleman DF, Tiplady BA. 1989. Seasonal Body Weight, Body Condition, and Lactational Trends in Muskoxen. Canadian Journal of Zoology 67: 1125-1133.

White RG, Rowell JE, Hauer WE. 1997. The Role of Nutrition, Body Condition and Lactation on Calving Success in Muskoxen. Journal of the Zoological Society of London 243: 13-20.

Wilkinson PF, Shank CC, Penner DF. 1976. Muskox-Caribou Summer Range Relations on Banks Island, N.W.T. The Journal of Wildlife Management 40(1): 151-162.

Wishart RP. 2004. A Story About a Muskox: Some Implications of Tetlit Gwich'in Human-Animal Relationships. In: Anderson DG, Nuttall M, editors. Cultivating Arctic Landscapes: Knowing and Managing Animals in the Circumpolar North. New York: Berghahn Books. Pp. 79-92.

Wright DE, Hungate RE. 1967. Metabolism of Glycine by Rumen Microorganisms. Applied Microbiology 15(1): 152-157.

Wurster CM, Patterson WP, Cheatham MM. 1999. Advances in Micromilling Techniques: A New Apparatus for Acquiring High-resolution Oxygen and Carbon Stable Isotope Values and Major/Minor Elemental Ratios from Accretionary Carbonate. Computers and Geosciences 25: 1159-1166.

Zazzo A, Balasse M, Patterson WP. 2005. High-resolution δ^{13}C Intratooth Profiles in Bovine Enamel: Implications for Mineralization Pattern and Isotopic Attenuation. Geochimica et Cosmochimica Acta 69(14): 3631-3642.

Zazzo A, Balasse M, Patterson WP. 2006. The Reconstruction of Mammal Individual History: Refining High-resolution Isotope Record in Bovine Tooth Dentine. Journal of Archaeological Science 33: 1177-1187.

Chapter 3

3 Isotopic Evidence from Bone and Dentin Collagen for Variation in the Ecological Niches of Caribou (*Rangifer tarandus* spp.) and Muskoxen (*Ovibos moschatus*) on Banks Island, NWT, Canada Over the Last 4000 Years and Its Implications for Ancient Hunters

Researchers have suggested that large gaps in the archaeological record of Banks Island, located in the Northwest Territories of Canada, reflect caribou or muskox population crashes resulting from ecological variation and/or human overexploitation. Here, we use shaped-based metrics derived from stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope compositions of archaeological bulk bone collagen to investigate caribou and muskox ecology on Banks Island over the last 4000 years. Results indicate that, following the competitive exclusion principle, the isotopic niches of caribou and muskoxen are typically distinct, but that during some cultural periods isotopic niche areas and isotopic niche overlap increase significantly. When the differential carbon and nitrogen trophic discrimination factors (TDFs) of caribou and muskoxen are taken into account, the isotopic data indicate that caribou and muskox ecological niches are highly dynamic. Transposed isotopic niches prior to the Classic Thule period (~ 650-500 cal. BP) follow the expectations of the Ecological Displacement model, but appear to come under the control of competitive specialization afterwards. This change in niche dynamics probably relates to the ability of muskoxen to exploit increased graminoid availability. We also analyze the $\delta^{13}C$ and $\delta^{15}N$ of sequentially sampled crown dentin collagen samples from archaeological caribou and muskox teeth to investigate seasonal partitioning of forage across time. Dentin collagen isotopic data support the hypothesis that competitive specialization after ~ 500 cal. BP negatively affected caribou productivity. We then discuss the implications of these findings on the potential relationships between human hunters and caribou and muskoxen on Banks Island over the last 4000 years.

3.1 Introduction

3.1.1 Rationale

Banks Island is the westernmost island in the Canadian Arctic Archipelago (Figure 3.1), and is archaeologically significant in that it is the probable entry point into the Eastern Arctic (i.e. the North American Arctic and Greenland) for both people of the Arctic Small Tool Tradition (ASTt) some 4000 years ago (Arundale 1981; McGhee 1982; Helmer 1994), and again for Thule Inuit groups approximately 1000 years ago (Friesen and Arnold 2008; Raghavan et al. 2014). The island is inhabited by major portions of both the global muskox (*Ovibos moschatus*) and Peary caribou (*Rangifer tarandus Pearyi*) populations (COSEWIC 2004), and as discussed below, its archaeological record indicates a long history of interactions between humans and these two large-bodied herbivores. The geographical proximity to the parent cultures of both the ASTt and Thule Inuit groups in Alaska and the Bering Strait region (Collins 1953, Giddings 1964, Arnold 1986; Bielawski 1988), and the general – but at times variable – abundance of caribou and muskoxen placed Banks Island on a unique archaeological trajectory relative to areas farther east (Figure 3.2a).

In this chapter, we: (1) use bulk bone collagen carbon and nitrogen isotope compositions to investigate changes in the ecological niches and niche relationships of caribou and muskoxen over the last 4000 years on Banks Island; and (2) use sequential dentin collagen carbon and nitrogen isotope compositions to investigate both seasonal dietary variation over time and potential relationships between the length of weaning and reduced fecundity in both species.

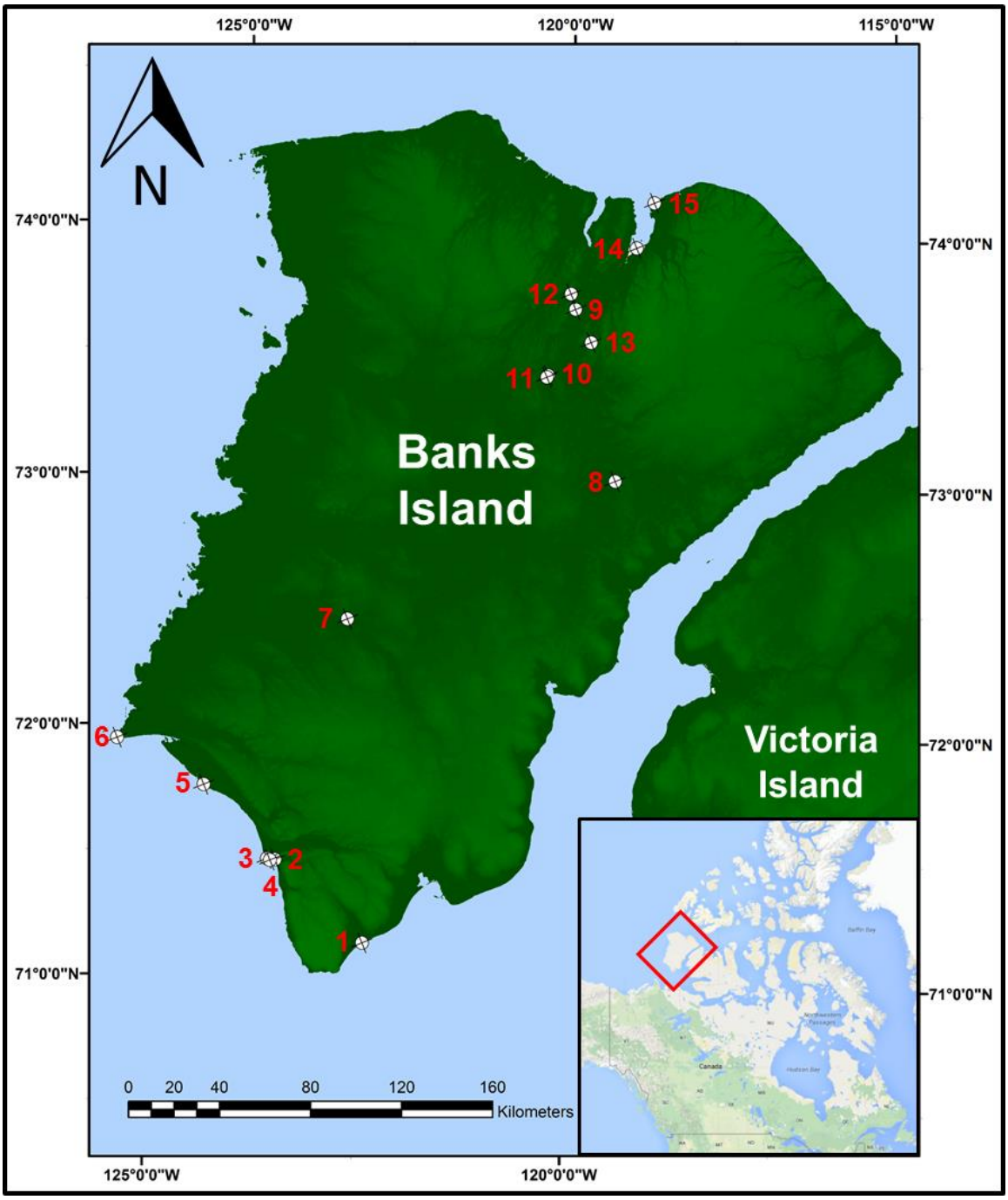


Figure 3.1. Locations of archaeological sites from which we collected caribou and muskox bones and teeth, and the location of Banks Island within North America (inset). **(1)** Nelson River (OhRh-1); **(2)** OjRk-1; **(3)** OjRl-2; **(4)** Lagoon (OjRl-3); **(5)** Agvik (OkRn-1); **(6)** Cape Kellett (OlRr-1); **(7)** Sunnguqpaaluk (PdRi-1); **(8)** Nasogaluak (PgPw-3)*; **(9)** Twin Lakes (PjPx-10**)**; **(10)** Shoran Lake (PjRa-1); **(11)** Umingmak (PjRa-2); **(12)** PkPx-18; **(13)** Head Hill (PlPx-1); **(14)** Arviq (QaPv-5); **(15)** Back Point (QbPu-3).

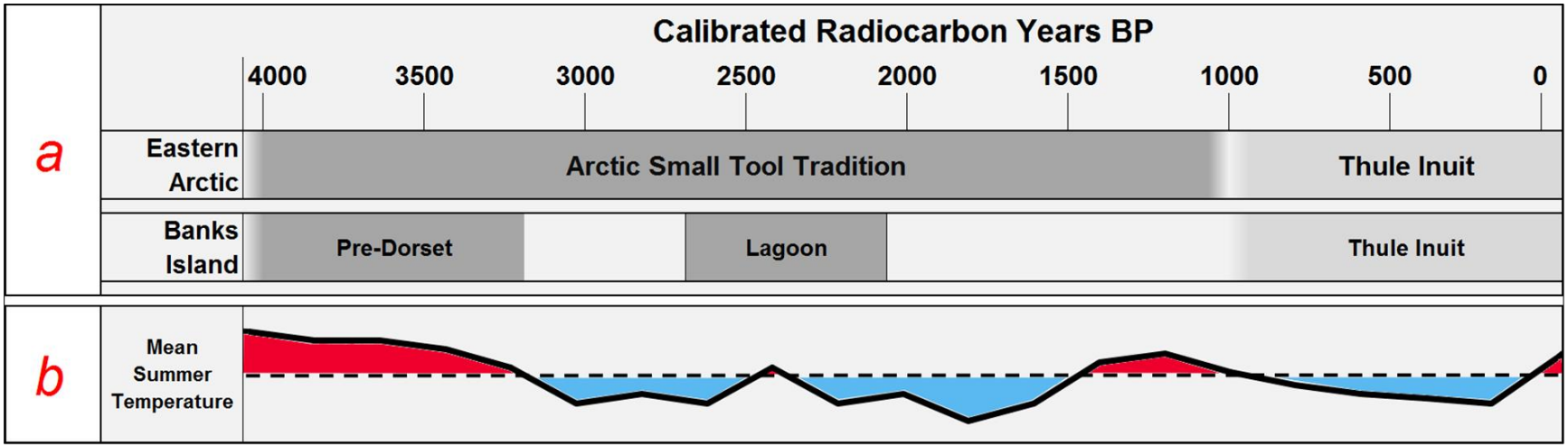


Figure 3.2. (*a*) Timeline of archaeological human occupations in the Eastern Arctic overall, and on Banks Island. **(*b*)** Generalized illustration of variation in mean summer temperature on Banks Island over the last 4000 years cal. BP, relative to mean summer temperature at 0 cal. BP (1950 AD) (dashed line). The figure is produced using data from Bradley (2000), Peros and Gajewski (2009), and Gajewski (2015b).

3.1.2 The Archaeology and Zooarchaeology of Banks Island

The archaeological record of Banks Island (reviewed in Chapter 1; see also Toews 1998; Hodgetts 2013; Hodgetts et al. 2015) reflects changing patterns of human interaction with animals over time. In the Canadian Arctic, the early phase of the ASTt occupation is classically referred to as the "Pre-Dorset" period to distinguish it from both the later, widespread "Dorset" period, and from other regional variants of the early ASTt period like the Saqqaq and Independence I cultures of Greenland (Knuth 1965; McGhee 1976; Maxwell 1985; Møbjerg 1999). During the Pre-Dorset period, most archaeological sites in the Canadian Arctic reveal a subsistence focus on terrestrial faunal resources (Knuth 1967; Maxwell 1984, 1985). Groups immediately east and farther south specialized in caribou hunting during this time (Harp 1958; Wilmeth 1979; Arnold 1983), whereas Pre-Dorset sites concentrated in the interior of Banks Island indicate heavy reliance on muskoxen (Taylor 1967; Müller-Beck 1977; Münzel 1987). After ~ 3400 cal. BP, however (Figure 3.2a, Figure 3.3, Table 3.1), Pre-Dorset groups apparently abandoned Banks Island.

Current archaeological evidence suggests there was never a major Dorset cultural presence on Banks Island. Caribou and muskox bones from the Lagoon site (OjRl-3), located on the southern coast, however, produce dates between ~ 2700 and 2100 cal. BP (Figure 3.3, Table 3.1), overlapping in time with the Early Dorset period farther east. Artifacts from the Lagoon site also exhibit a unique blend of influences from both ASTt groups farther east and people of the Norton Tradition (~ 3000-1150 cal. BP) in Alaska, who are generally thought to have had little or no contact with the Eastern Arctic (Giddings 1964; Arnold 1980; Maxwell 1985). In contrast to Pre-Dorset sites, the Lagoon site faunal assemblage is smaller and is characterized by juvenile ringed seal (*Phoca hispida*), goose (*Chen* spp. and *Branta* spp.), ptarmigan (*Lagopus* spp.), and muskoxen, with very few caribou skeletal elements (Arnold 1980). Recent radiocarbon dates from the Arviq (QaPv-5) site, located on the northeast coast of Banks Island, and PkPx-18, a small camp site in the northern interior of the island (Figure 3.1), also coincide with those from the Lagoon site (Figure 3.3, Table 3.1; Hodgetts and Eastaugh 2010; Hodgetts et al. 2013).

Radiocarbon dates from the Nelson River site (Figure 3.1) indicate that the Thule Inuit re-occupied Banks Island following the Lagoon phase around 950 cal. BP (Figure 3.3) (Arnold 1986; Friesen and Arnold 2008). Radiocarbon dates from another site on the south coast of Banks Island, Cape Kellett (OlRr-1) indicate that it was occupied around the same time (Hodgetts, unpublished data). Nelson River is the earliest-known Thule Inuit site in the Eastern Arctic (Friesen and Arnold 2008), and reveals close material ties with the concurrent Birnirk culture of Alaska (McGhee 1984), such as harpoon head types and the use of driftwood for the structure of winter houses (Arnold 1986). Faunal remains from excavations at Nelson River indicate that ringed seals and bowhead whales (*Balaena mysticetus*) were probably the most important food resources, followed by ptarmigan and arctic hare (*Lepus arcticus*). As at the Lagoon site, faunal skeletal evidence from Early Thule sites indicates limited caribou hunting.

Radiocarbon dates (Figure 3.3, Table 3.1) also suggest that the Thule Inuit have probably inhabited Banks Island continuously since their arrival at Nelson River. Although most of the known Middle or "Classic" (Friesen and Arnold 2008) Thule sites on Banks Island are located along the southern coast, radiocarbon dates from a small campsite at the mouth of Mercy Bay (QbPu-3, Figure 3.1), and qarmats (i.e. a skin-roofed sod structures) at PjRa-2, and PkPx-18 demonstrate that the Thule were also active in the northern part of the island, often reusing Pre-Dorset camp and hunting sites (Hickey 1982; Hodgetts et al. 2009; Hodgetts and Eastaugh 2010; Hodgetts 2013; Hodgetts and Munizzi 2015). Throughout the Early and Classic Thule periods on Banks Island, faunal usage continued to revolve around marine and coastal resources, with few caribou, then muskox, remains appearing at archaeological sites.

Around 450 cal. BP, however, Inuit campsites, meat processing stations, and caches also begin to appear further inland in greater frequencies, and these sites contain greater quantities of caribou and muskox remains. Although this period is sometimes referred to as the Copper Inuit (Jenness 1917, 1923; Hickey 1982; Will 1985) or Inuinnait (Collignon and Weber Müller-Wille 2006) period, we refer to it simply as the Inuit period. During this time, family-based groups exploited both marine and terrestrial resources in a yearly round (Hickey 1982; Hodgetts 2013). Throughout the summer, muskoxen, caribou, and other

inland fauna were hunted in the northern interior of the island, often at existing Pre-Dorset sites (Hickey 1982; Hodgetts et al. 2009), while during the winter seals and polar bears were hunted on the sea ice. This seasonal pattern continued into the 19th century, when oral histories (Nagy 1999) record that significant numbers of the caribou and muskoxen perished after freezing spring rains. After this, economic attention turned to fox trapping and fur trading (Nagy 1999; Kelvin 2016).

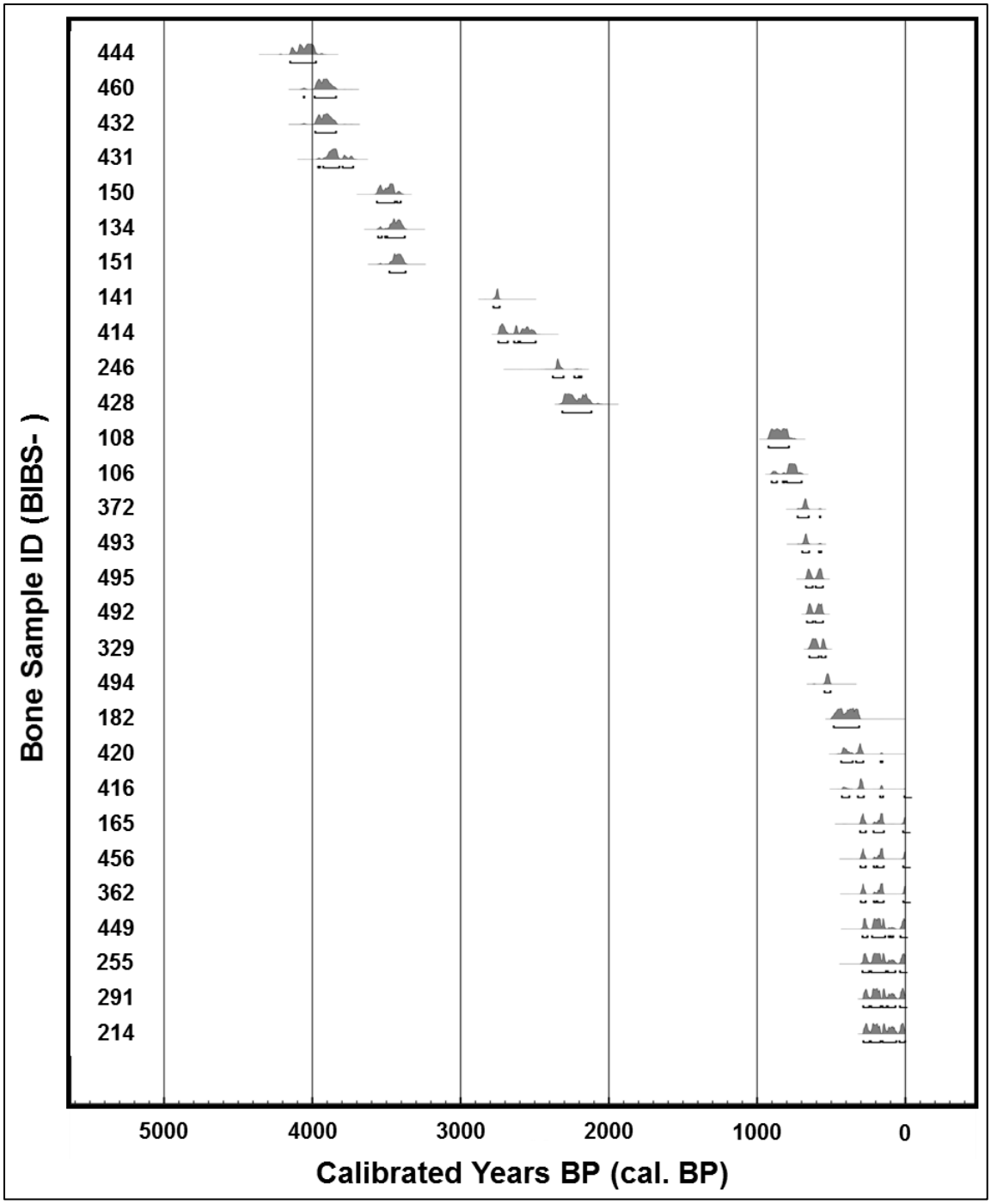


Figure 3.3. Calibrated radiocarbon ranges for bone samples listed in Table 3.1, obtained using the IntCal13 calibration curve (Reimer et al. 2013) in the CALIB software program (version 7.0.4) (Stuiver et al. 2017).

Table 3.1. Radiocarbon dates from archaeological sites on Banks Island. We used the IntCal13 calibration curve (Reimer et al. 2013) in the CALIB software program (version 7.0.4) (Stuiver et al. 2017) to perform the calibrations.

Sample ID	Site Name	Borden	Taxon	Element	Lab ID	^{14}C BP (1σ error)	Calibrated ^{14}C BP (2σ error)		
							Range 1	Range 2	Range 3
Pre-Dorset									
BIBS-444	Shoran Lake	PjRa-1	Muskox	Femur	D-AMS 012664	3711 ± 29	4102 – 3976	4148 – 4109	
BIBS-460	Shoran Lake	PjRa-1	Muskox	Radioulna	D-AMS 012667	3613 ± 28	3984 – 3842		
BIBS-432	Twin Lakes	PjPx-10	Muskox	Long bone	D-AMS 012663	3605 ± 29	3979 – 3840		
BIBS-431	Twin Lakes	PjPx-10	Muskox	Humerus	D-AMS 012662	3556 ± 29	3797 – 3724	3926 – 3817	3960 – 3950
BIBS-150	Umingmak	PjRa-2	Muskox	Femur	D-AMS 012646	3259 ± 28	3428 – 3404	3564 – 3443	
BIBS-134	Twin Lakes	PjPx-10	Muskox	Femur	D-AMS 012644	3224 ± 29	3495 – 3377	3508 – 3506	3554 – 3532
BIBS-151	Umingmak	PjRa-2	Caribou	Metatarsus	D-AMS 012647	3211 ± 28	3479 – 3373		
Lagoon									
BIBS-141	Lagoon	OjRl-3	Muskox	Cranium	D-AMS 012645	2628 ± 25	2777 – 2738		
BIBS-414	Lagoon	OjRl-3	Muskox	Cranium	D-AMS 012658	2530 ± 28	2598 – 2495	2639 – 2610	2744 – 2682
	Lagoon	OjRl-3	Muskox	Scapula	RL-767†	2390 ± 110	2260 – 2158	2743 – 2298	
	Lagoon	OjRl-3	Muskox	Scapula	RL-766†	2290 ± 120	2024 – 2007	2622 – 2038	2707 – 2627
	Lagoon	OjRl-3	Muskox	Scapula	RL-765†	2320 ± 120	2091 – 2061	2724 – 2098	
BIBS-246		PkPx-18	Caribou	Radioulna	D-AMS 012652	2321 ± 29	2192 – 2187	2231 – 2203	2367 – 2306
BIBS-428		PkPx-18	Muskox	Horn core	D-AMS 012661	2186 ± 33	2313 – 2118		

Early Thule									
BIBS-108		PkPx-18	Muskox	Innominate	D-AMS 012643	927 ± 28	921 – 786		
BIBS-106	Umingmak	PjRa-2	Muskox	Mandible	D-AMS 012642	864 ± 28	800 – 699	826 – 813	901 – 865
BIBS-372	Cape Kellett	OlRr-1	Caribou	Mandible	D-AMS 012657	729 ± 30	711 – 652	725 – 714	
Classic Thule									
BIBS-493	Agvik	OkRn-1	Caribou	Mandible	D-AMS 012669	718 ± 28	582 – 569	696 – 650	
BIBS-495	Agvik	OkRn-1	Caribou	Metatarsus	D-AMS 012671	651 ± 27	604 – 557	669 – 627	
BIBS-492	Agvik	OkRn-1	Caribou	Humerus	D-AMS 012668	635 ± 23	607 – 555	662 – 624	
BIBS-329	Cape Kellett	OlRr-1	Caribou	Radioulna	D-AMS 012655	586 ± 25	568 – 538	648 – 584	
BIBS-494	Agvik	OkRn-1	Caribou	Mandible	D-AMS 012670	499 ± 25	543 – 506		
Inuit									
BIBS-182		OjRk-1	Caribou	Tibia	D-AMS 012649	343 ± 29	481 – 313		
BIBS-420	Sunnguqpaaluk	PdRi-1	Caribou	Radioulna	D-AMS 012660	276 ± 27	164 – 156	332 – 285	433 – 355
BIBS-416		OjRl-2	Muskox	Cranium	D-AMS 012659	257 ± 25	170 – 153	321 – 280	427 – 389
BIBS-165	Head Hill	PlPx-1	Muskox	Mandible	D-AMS 012648	214 ± 26	191 – 146	213 – 194	304 – 269
BIBS-456	Head Hill	PlPx-1	Muskox	Mandible	D-AMS 012666	210 ± 23	190 – 147	213 – 196	302 – 270
BIBS-362	Head Hill	PlPx-1	Muskox	Mandible	D-AMS 012656	207 ± 21	189 – 147	212 – 196	300 – 270
BIBS-449	Head Hill	PlPx-1	Muskox	Mandible	D-AMS 012665	173 ± 25	99 – 83	224 – 136	289 – 255
BIBS-255	Twin Lakes	PjPx-10	Caribou	Tibia	D-AMS 012653	167 ± 32	117 – 69	230 – 129	290 – 247
BIBS-291	Head Hill	PlPx-1	Muskox	Mandible	D-AMS 012654	152 ± 25	118 – 66	231 – 166	283 – 245
BIBS-214	Sunnguqpaaluk	PdRi-1	Caribou	Maxilla	D-AMS 012651	147 ± 27	122 – 62	233 – 168	281 – 242

† From Arnold (1980); not shown in Figure 3.3.

3.1.3 Archaeological Settlement-Subsistence Patterns on Banks Island

Researchers have suggested that the long occupational hiatuses on Banks Island following the Pre-Dorset period and Lagoon period, and the limited representation of caribou or muskoxen at archaeological sites between ~ 3400 and 400 cal. BP are the results of periods of decreased availability or caribou or muskoxen over the last 4000 years. These putative population crashes are attributed to overhunting by humans, climatic variation, forage competition, or a combination of these factors (Stefansson 1921; Barr 1991; Reynolds 1998; Klein 1999; Dyke and Savelle 2009; Savelle and Dyke 2002, 2009; Tyler 2010; Dyke et al. 2011). These ideas all represent hypotheses that are potentially testable using zooarchaeological material. Several researchers (Grayson 1981; Ervynck 1999; Lyman 2008; Humphries and Winemiller 2009), however, have raised concerns about the use of zooarchaeological data for ecological reconstructions because species representations at archaeological sites reflect selection by human hunters, not natural abundances. In this regard, the application of stable isotope analysis to zooarchaeological remains is advantageous because the isotopic compositions of an animal's tissues record information about its relationship to the environment and the environment itself, and this information is independent of the structure of the zooarchaeological assemblage. This means that we can compare the isotopic compositions of bone fragments from the earliest, most ephemeral sites on Banks Island with faunal remains from later, more complex sites, and from modern bone samples to reconstruct caribou and muskox ecology on the island.

3.1.4 Isotopic and Ecological Niche

Stable isotope analysis is a methodology frequently used to reconstruct trophic relationships in ecological or paleoecological communities. In this application, the most commonly-measured stable isotope ratios are $^{13}C/^{12}C$ and $^{15}N/^{14}N$, (notated as $\delta^{13}C$ and $\delta^{15}N$, respectively), both because carbon and nitrogen are abundant in organic tissues, and because both stable isotope systems reflect the routing of energy in foodwebs. For instance, the $\delta^{13}C$ and $\delta^{15}N$ of terrestrial herbivore tissues reflects the $\delta^{13}C$ and $\delta^{15}N$ of assimilated

forage[12] macromolecules. The $\delta^{13}C$ and $\delta^{15}N$ of those macromolecules is ultimately determined by the photosynthetic pathway and nitrogen sources, respectively, utilized by the plant or primary producer, as well as equilibrium and kinetic reactions that occur within the primary producer following fixation. Isotopic variation in forage is then passed through successive trophic levels in the food chain.

Carbon and nitrogen isotope compositions are typically presented in a biplot. Though this biplot simply describes the bivariate coordinates of carbon and nitrogen isotope compositions, it has come to represent an ecological space – what Newsome et al. (2007) call "δ-space" – where $\delta^{13}C$ and $\delta^{15}N$ correspond to bionomic (resource-related) and scenopoetic (environmental) variables (Hutchinson 1978; Soberón 2007). As Newsome et al. (2007) also point out, the δ-space model parallels Hutchinson's (1957:416) concept of fundamental ecological niche, which he defines as "an *n*-dimensional hypervolume…every point in which corresponds to a state of the environment which would permit the species…to exist indefinitely." In Hutchinson's conception, the fundamental ecological niche exists only in abstract space and is never completely quantifiable. Because isotopic data encode information about multiple bionomic and scenopoetic axes that are not otherwise easily measured, however, the "isotopic niche" of an individual, population, or species in δ-space is a useful approximation of their fundamental ecological niche.

The Hutchinsonian niche model also follows Gause's (1936) law of competitive exclusion: a species will maximize its ecological niche whenever possible, but no two species can occupy the same ecological niche without either the expulsion of one species from the niche, or a decrease in fitness. Subsequently, sympatric species like caribou and muskoxen should exhibit larger ecological, and by extension, isotopic, niches when inter-specific competition is low (Figure 3.4a), and smaller ecological and isotopic niches when inter-specific competition is high (Figure 3.4b). As Jackson et al. (2012) point out, however, recent work (Bolnick 2001; Bolnick et al. 2003; Svanbäck and Bolnick 2007) drawing on

[12]As in Chapter 2, we use the term "forage" to refer to all photosynthetic vegetation potentially consumed by caribou and muskoxen on Banks Island, including vascular plants, mosses (non-vascular plants), and lichens (organisms composed of symbiotic fungi and algae or cyanobacteria).

the Ecological Character Displacement model (Grant 1972; Dayan and Simberloff 2005) suggests that when intra- or inter-specific niche competition is high, a species' total niche area will expand, as individuals are forced to seek alternatives to their preferred forage types. Consequently, smaller isotopic niches correspond to reduced competition (Figure 3.4c), while larger isotopic niches correspond to competitive diversification (Figure 3.4d). By attempting to establish which niche model better accounts from observed trends in caribou and muskox bone collagen carbon and nitrogen isotope compositions across cultural periods on Banks Island, we can make inferences about potential niche variation and forage competition that may have reduced their availability to ancient hunters.

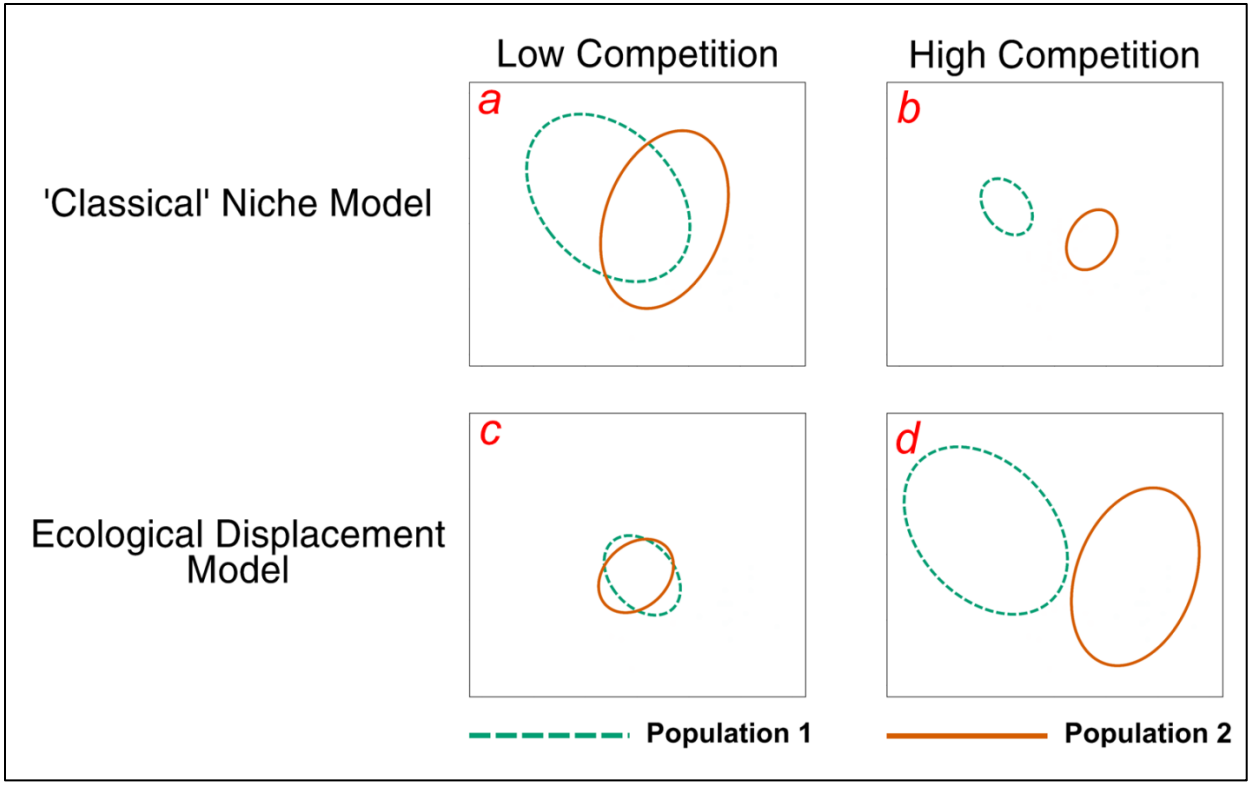


Figure 3.4. Simplified illustration of isotopic niche relationships between two sympatric populations, as hypothesized by the "classical" Hutchinsonian niche model, and by the ecological displacement model. The x and y axes represent any two stable isotope systems (e.g. carbon, nitrogen, sulphur, hydrogen).

3.1.5 Bone Collagen $\delta^{13}C$ and $\delta^{15}N$

Bone is a common analyte in stable isotope paleoecology because bones are commonly the only faunal tissues remaining at paleontological or archaeological sites. The collagen component of bone has properties ideal for this application. Collagen is abundant in fresh or well-preserved bone, accounting for ~ 25% of bone by weight (Schoeninger et al. 1989; Ambrose 1990; Ambrose and Norr 1993; van Klinken 1999; Jørkov et al. 2007), and is simple and relatively inexpensive to extract and analyze.

The $\delta^{13}C$ and $\delta^{15}N$ of bone collagen in carnivores and omnivores are typically dominated by those of dietary protein sources because dietary amino acids can be routed directly to proteinaceous body tissues, or used to synthesize nonessential amino acids (Hare et al. 1991; Tieszen and Fagre 1993). Vegetation, however, is generally protein-poor, being composed almost entirely of carbohydrates. Many herbivores must therefore synthesize amino acids necessary for tissue development *de novo* from carbohydrates (Krueger and Sullivan 1984; Ambrose and Norr 1993; Dewhurst et al. 2000; Atasoglu et al. 2004). The stable isotopic compositions of herbivore bone collagen should therefore exhibit less of a bias towards dietary sources with high crude protein contents.

Because bone remodels slowly (Tieszen et al. 1983; Ambrose and Norr 1993), bulk bone collagen $\delta^{13}C$ and $\delta^{15}N$ (hereafter, $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$, respectively) should provide the signature of the averaged $\delta^{13}C$ and $\delta^{15}N$ of dietary sources assimilated during approximately the last decade of life. Consequently, caribou and muskox $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$, compared across cultural periods on Bank Island, can reveal: (1) whether caribou and muskox dietary compositions varied over time; and (2) whether there were periods of dietary convergence, and potential dietary competition, that may have resulted in population declines and decreased availability to hunters.

3.1.6 Dentin Collagen $\delta^{13}C$ and $\delta^{15}N$

Dentin development, and the information recorded by dentin collagen $\delta^{13}C$ and $\delta^{15}N$ (hereafter, $\delta^{13}C_{dc}$ and $\delta^{15}N_{dc}$, respectively), is considerably different than in bone. In most mammals, tooth formation begins at the apex of the tooth crown and proceeds towards the

roots (Figure 3.5a), with dentin and enamel both developing outwards and downwards from the dentinoenamel junction (DEJ) (Figure 3.5b, c). The formation of dentin precedes that of enamel and is completed in two main phases: the secretion of an organic collagen-rich matrix by odontoblasts, and the "seeding" (Hillson 2000:185) of this matrix with inorganic crystallites, which immediately develop outwards in all directions to mineralize the organic matrix (Linde and Goldberg 1993). Dentin in the tooth crown is formed in sequential, cone-like layers (Figure 3.5c) (Carlson 1990; Hillson 2000; Zazzo et al. 2006) and is not resorbed or remodeled after apposition (Gage et al. 1989; Lowenstam and Weiner 1989; Balasse 2003). As a result, the $\delta^{13}C$ and $\delta^{15}N$ of dentin collagen from the tooth crown may permanently record dietary variation during the months or years in which the tooth crown develops. As in bone collagen, there are trophic enrichments in ^{13}C and ^{15}N between dietary items and dentin collagen, and these trophic enrichments are presumably the same in both structures (LeGeros 1991; Koch 2007). Consequently, the temporal resolution of dentin collagen $\delta^{13}C$ and $\delta^{15}N$ is more fine-grained than – but still comparable to – bulk bone collagen $\delta^{13}C$ and $\delta^{15}N$. Since the diets of caribou and muskoxen should vary considerably between seasons, the $\delta^{13}C$ and $\delta^{15}N$ of sequentially-sampled crown dentin collagen samples are potentially useful for determining whether overlap in bulk bone collagen isotopic compositions during certain cultural periods corresponds to overlap in summer diets, winter diets, or both, or if there are seasonal trade-offs in forage resources between caribou and muskoxen.

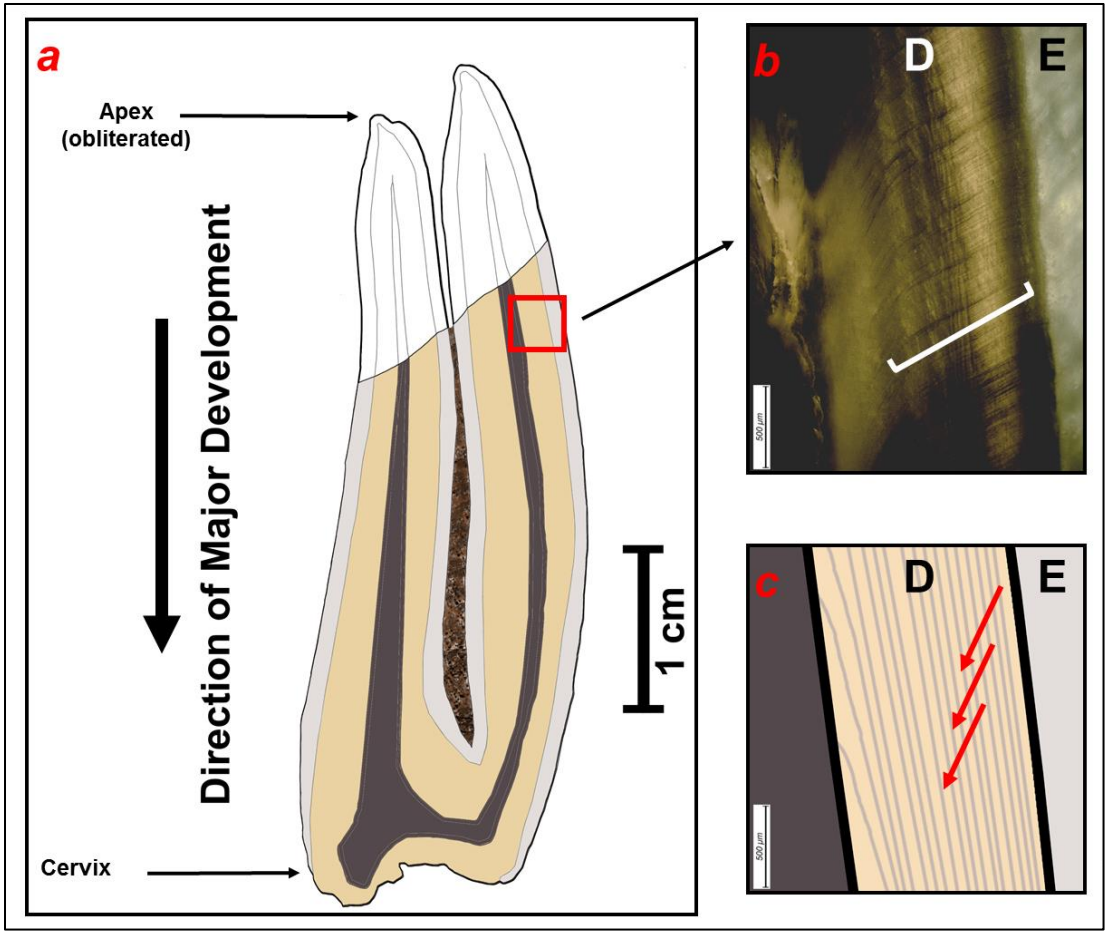


Figure 3.5. Diagram of a typical hypsodont tooth crown, reproduced from Chapter 2. **(*a*)** buccolingual cross-section showing apical section obliterated through occlusal wear; **(*b*)** image of the dentinoenamel junction (DEJ) in a muskox M2, taken at 5x magnification using differential interference contrast (DIC) microscopy. "E" is enamel and "D" is dentin; small, near-horizontal lines (white bracket) are individual dentin tubules; **(*c*)** idealized illustration of diagram *b*, depicting sequentially-developed dentin cones (gray lines). Red arrows indicate the direction of successive dentin apposition away from the DEJ.

3.1.7 Tooth Development in Caribou and Muskoxen

There are no published studies of the tooth development sequence in caribou or muskoxen. Several researchers (Tener 1965; Miller 1974; Henrichsen and Grue 1980), however, have documented the tooth eruption sequences of both species (Figures 3.6 and 3.7) and since formation necessarily precedes eruption, it is possible to infer the approximate period of formation in each tooth. In both caribou and muskoxen, first molar (M1) eruption begins shortly after birth and continues over the first year of life. In caribou, second molar (M2) eruption begins late in the first year of life and continues into the second fall or winter of life, while in muskoxen, M2 eruption begins around the second summer of life and continues into the third winter of life. In caribou, the third molar (M3) eruption begins around the second summer of life and continues into the third winter of life, while the adult fourth premolar (P4) erupts between the third summer and winter of life. In muskoxen, the M3 erupts between the third summer and fifth winter of life, and the P4 erupts between the fourth and fifth summers of life. Anatomical (Knott et al. 2004, 2005) and observational studies (Tener 1965; Kelsall 1968; Skoog 1968) suggest that caribou and muskoxen are capable of transitioning from milk to forage within the first several weeks of life. Observational studies, however, also suggest that caribou and muskox calves may both prolong suckling when adequate forage is not available during the first fall and winter (Banfield 1954; Kelsall 1968; Parker et al. 1990; Knott et al. 2005).

Published research on the link between nursing and maternal health (Parker et al. 1990; White et al. 1997) suggests that, unlike muskoxen, caribou experience lactational anestrus. Caribou cows therefore have a strong physiological motivation to completely wean their calves as soon as possible, while, if forage conditions are appropriate, muskox cows may continue nursing a yearling while pregnant. Because milk is synthesized from fat and protein stores, a nursing mammal sits one trophic level above the animal nursing it, and its tissues will experience a trophic enrichment in ^{15}N of +2 to 3‰ (Fogel et al. 1989; Jenkins et al. 2001; Balasse and Tresset 2002). In Chapter 2, we demonstrate that the enrichment in ^{15}N, and the subsequent shift towards lower $\delta^{15}N$ at the completion of weaning, is recorded in the $\delta^{15}N_{dc}$ of adult teeth from modern caribou and muskoxen. If the duration of the weaning process in caribou and muskoxen is largely dependent on forage conditions,

as we argue in Chapter 2, the $\delta^{15}N_{dc}$ of archaeological caribou and muskox teeth may also provide further information about links between climatically-induced changes in forage and range conditions, forage competition, and demography on Banks Island over the last 4000 years.

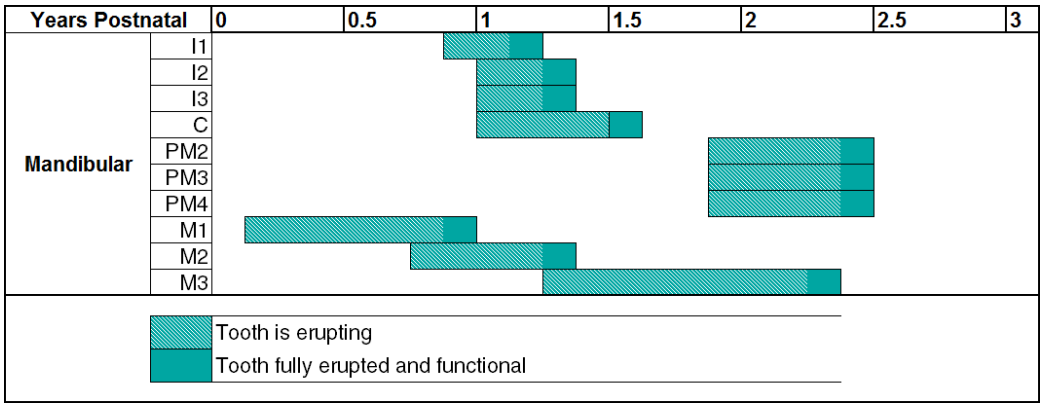


Figure 3.6. Eruption sequence of permanent dentition in barren ground caribou, reproduced from Chapter 2. “I” = incisor, “C” = canine, “PM” = premolar, and “M” = molar. Data are from Banfield (1954) and Miller (1974).

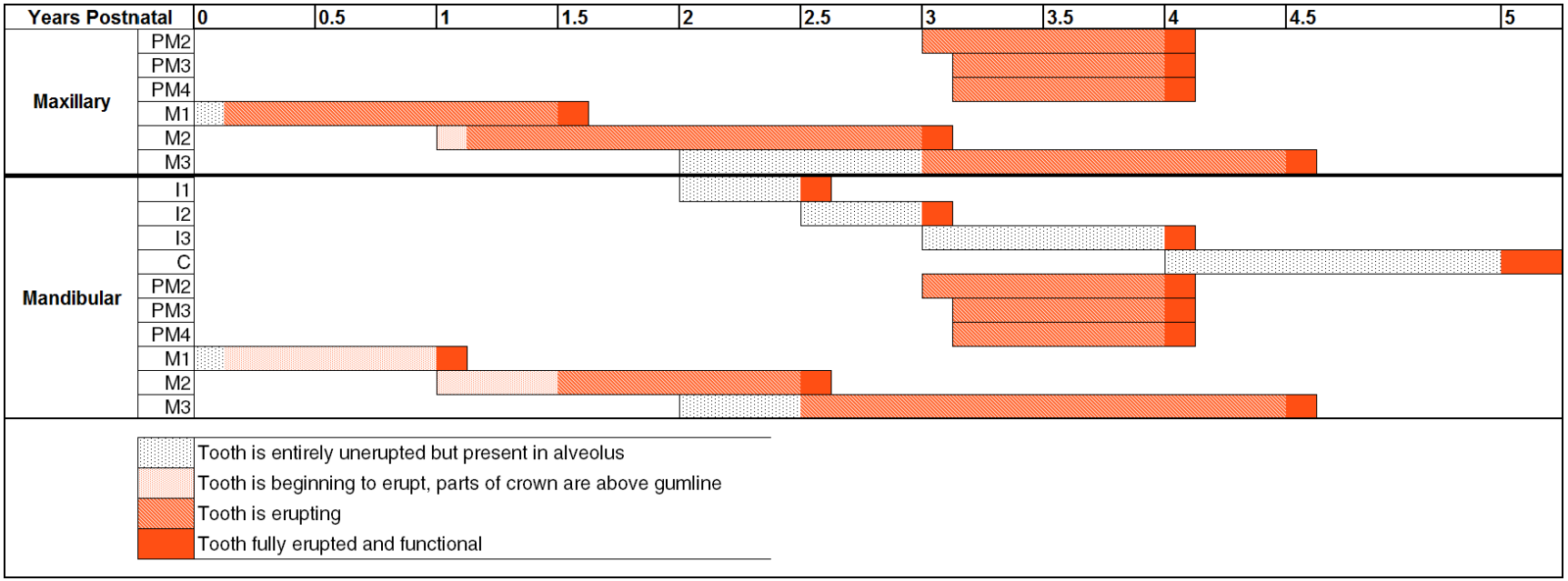


Figure 3.7. Eruption sequence of permanent dentition in muskoxen, reproduced from Chapter 2. "I" = incisor, "C" = canine, "PM" = premolar, and "M" = molar. Data are from Tener (1965) and Henrichsen and Grue (1980).

3.2 Materials

3.2.1 Bone and Dentin Collagen

In 2014, we visited fourteen archaeological sites on Banks Island (Figure 3.1) by helicopter and surface-collected caribou and muskox skeletal elements. These archaeological sites span all documented human occupational periods on Banks Island. We prioritized the collection of mandibles and maxillae because they allow rapid taxonomic identifications in the field, and provide both bone and teeth for sampling. In many cases, particularly at small Pre-Dorset and Lagoon period camp sites, surficial faunal remains were limited to bone fragments. Forthcoming DNA analysis (Rodrigues, Yang, and Hodgetts, unpublished data) resolved the taxonomic assignments of many of the fragmentary bone samples, but where DNA amplification failed and no definitive taxonomic assignment could be made with reference specimens, samples were omitted from further analysis.

We also include isotopic and elemental data for modern and archaeological bone collagen samples prepared and analyzed as part of a pilot project on caribou and muskoxen from Banks Island (Masoner, Hodgetts, White, and Longstaffe, unpublished data). Bone collagen from these pilot project samples was extracted and analyzed in the same manner as described below. The Pre-Dorset dataset includes published $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ data from adult (i.e. $\geq$ 2.5 years) caribou and muskoxen excavated at the Umingmak site (PjRa-2) (Bocherens et al. 2016). Finally, we compare archaeological bone and dentin collagen isotopic compositions with those of modern caribou and muskox from Banks Island, as described in Chapter 2. Bone collagen isotopic data are listed by cultural period in Table 3.2. Data for sequential microbulk dentin collagen samples from caribou and muskox tooth crowns are presented in Tables 3.3 and 3.4, respectively.

Table 3.2. Isotopic, elemental, and percent collagen content data for caribou and muskox bulk bone collagen samples from Banks Island. All modern bone collagen carbon isotope compositions are corrected by +1.7‰ for comparability with archaeological bone collagen data.

Sample ID	Site Name	Borden	Taxon	Element	$\delta^{13}C$ (‰, VPDB)	$\delta^{15}N$ (‰, AIR)	C%	N%	Atomic C:N Ratio	Wt% Coll
Pre-Dorset										
BIBS14-430	Twin Lakes	PjPx-10	Caribou	Metapodial	–19.2	+2.5	46.2	16.7	3.2	16.7
BIBS14-435	Twin Lakes	PjPx-10	Caribou	Metapodial	–19.8	+2.1	44.7	16.3	2.9	18.2
BIBS14-463	Shoran Lake	PjRa-1	Caribou	Tibia	–18.8	+3.3	45.4	16.5	3.2	17.2
PjRa1-1†	Shoran Lake	PjRa-1	Caribou	Radioulna	–19.3	+1.9	41.6	15.5	3.1	
PjRa1-4†	Shoran Lake	PjRa-1	Caribou	Metatarsus	–19.4	+2.5	44.0	16.4	3.1	
PjRa1-5†	Shoran Lake	PjRa-1	Caribou	Metatarsus	–19.3	+2.9	43.9	16.4	3.1	
BIBS14-151	Umingmak	PjRa-2	Caribou	Metatarsus	–19.2	+2.0	44.7	16.1	3.2	19.6
PjRa2-U83B†	Umingmak	PjRa-2	Caribou	Radioulna	–18.9	+2.2	44.8	16.7	3.1	
UMK-14*	Umingmak	PjRa-2	Caribou	Metatarsus	–19.2	+1.4	42.9	15.1	3.3	
UMK-15*	Umingmak	PjRa-2	Caribou	Metatarsus	–18.8	+2.9	41.7	14.9	3.3	
UMK-16*	Umingmak	PjRa-2	Caribou	Metatarsus	–18.8	+3.6	40.5	14.5	3.3	
UMK-17*	Umingmak	PjRa-2	Caribou	Metatarsus	–18.3	+1.8	40.5	14.6	3.2	
UMK-18*	Umingmak	PjRa-2	Caribou	Metatarsus	–19.3	+2.5	42.8	15.1	3.3	
BIBS14-134	Twin Lakes	PjPx-10	Muskox	Femur	–20.7	+3.7	45.5	16.4	3.2	15.2
BIBS14-431	Twin Lakes	PjPx-10	Muskox	Humerus	–20.6	+3.2	46.5	16.9	3.2	12.3
BIBS14-432	Twin Lakes	PjPx-10	Muskox	Long bone	–20.8	+3.0	46.6	16.8	3.2	16.4
BIBS14-407§	Shoran Lake	PjRa-1	Muskox	Mandible	–20.3	+0.9	45.6	16.3	3.3	20.4

BIBS14-424	Shoran Lake	PjRa-1	Muskox	Metacarpus	–21.1	+3.4	45.3	16.5	3.2	16.2
BIBS14-444	Shoran Lake	PjRa-1	Muskox	Femur	–20.9	+3.7	45.5	16.5	3.2	15.0
PjRa1-2†	Shoran Lake	PjRa-1	Muskox	Metatarsus	–21.0	+2.3	41.8	15.7	3.1	
PjRa1-3†	Shoran Lake	PjRa-1	Muskox	Metacarpus	–20.9	+2.8	44.0	16.5	3.1	
PjRa1-6†	Shoran Lake	PjRa-1	Muskox	Metatarsus	–21.5	+2.9	43.9	16.4	3.1	
PjRa1-7†	Shoran Lake	PjRa-1	Muskox	Metatarsus	–21.5	+3.1	44.5	16.7	3.1	
PjRa1-8†	Shoran Lake	PjRa-1	Muskox	Mandible	–21.5	+3.0	44.5	16.7	3.1	
BIBS15-51	Umingmak	PjRa-2	Muskox	Metacarpus	–21.1	+3.0	42.5	16.0	3.1	
BIBS14-409§	Umingmak	PjRa-2	Muskox	Mandible	–20.9	+4.1	45.9	16.4	3.3	19.9
BIBS14-413	Umingmak	PjRa-2	Muskox	Maxilla	–20.9	+3.5	45.7	16.5	3.2	19.8
BIBS15-52	Umingmak	PjRa-2	Muskox	Astragalus	–21.2	+2.6	45.0	16.4	3.2	19.4
BIBS15-54	Umingmak	PjRa-2	Muskox	Astragalus	–21.2	+2.2	45.5	16.5	3.2	21.2
PjRa2-1†	Umingmak	PjRa-2	Muskox	Astragalus	–21.0	+3.8	44.1	16.6	3.1	
PjRa2-2†	Umingmak	PjRa-2	Muskox	Astragalus	–20.8	+3.1	44.5	16.8	3.1	
PjRa2-3†	Umingmak	PjRa-2	Muskox	Astragalus	–21.0	+2.5	44.3	16.8	3.1	
PjRa2-4†	Umingmak	PjRa-2	Muskox	Calcaneus	–21.1	+3.4	44.0	16.6	3.1	
PjRa2-5†	Umingmak	PjRa-2	Muskox	Calcaneus	–21.2	+2.7	43.7	16.2	3.1	
PjRa2-6†	Umingmak	PjRa-2	Muskox	Phalanx	–21.1	+3.0	40.2	15.2	3.1	
PjRa2-7†	Umingmak	PjRa-2	Muskox	Phalanx	–20.8	+2.4	43.4	16.3	3.1	
PjRa2-8†	Umingmak	PjRa-2	Muskox	Phalanx	–20.7	+3.0	42.1	15.8	3.1	
PjRa2-9†	Umingmak	PjRa-2	Muskox	Metatarsus	–21.1	+2.9	42.5	16.0	3.1	
PjRa2-u9d†	Umingmak	PjRa-2	Muskox	Humerus	–20.8	+3.4	42.9	16.1	3.1	
UMK-11*	Umingmak	PjRa-2	Muskox	Mandible	–20.9	+3.9	44.2	16.0	3.2	
UMK-12*	Umingmak	PjRa-2	Muskox	Mandible	–20.9	+3.2	43.3	15.3	3.3	

UMK-13*	Umingmak	PjRa-2	Muskox	Mandible	–20.5	+3.8	44.6	15.9	3.3	
UMK-5*	Umingmak	PjRa-2	Muskox	Mandible	–21.1	+2.6	42.7	15.1	3.3	
UMK-6*	Umingmak	PjRa-2	Muskox	Mandible	–20.4	+2.2	42.4	15.1	3.3	
UMK-7*	Umingmak	PjRa-2	Muskox	Mandible	–20.8	+2.8	43.1	15.4	3.3	
Lagoon										
BIBS14-199	Lagoon	OjRl-3	Caribou	Scapula	–21.3	+5.7	44.3	15.9	3.2	20.4
BIBS14-218	Lagoon	OjRl-3	Caribou	Tibia	–19.3	+2.4	44.5	16.2	2.5	20.9
BIBS14-234	Arviq	QaPv-5	Caribou	Cranium	–19.4	+2.7	44.7	15.8	3.3	21.2
BIBS14-109		PkPx-18	Caribou	Scapula	–20.2	+3.8	44.2	15.9	3.2	18.4
BIBS14-246		PkPx-18	Caribou	Radioulna	–20.7	+3.9	45.9	16.7	3.2	17.2
BIBS14-141	Lagoon	OjRl-3	Muskox	Occipital	–21.1	+2.0	44.5	16.0	3.3	20.7
BIBS14-162§	Arviq	QaPv-5	Muskox	Mandible	–20.4	+3.2	43.4	15.6	3.3	22.9
BIBS14-208	Arviq	QaPv-5	Muskox	Mandible	–21.1	+4.0	45.3	16.4	3.2	22.1
BIBS14-209§	Arviq	QaPv-5	Muskox	Mandible	–20.8	+4.2	45.0	16.5	3.2	20.2
BIBS14-231	Arviq	QaPv-5	Muskox	Mandible	–21.5	+5.4	44.7	15.8	3.3	16.4
BIBS14-323	Arviq	QaPv-5	Muskox	Maxilla	–21.8	+3.8	45.3	16.3	3.2	19.7
BIBS14-324	Lagoon	OjRl-3	Muskox	Scapula	–21.0	+4.5	39.2	14.2	3.2	19.3
BIBS14-340	Lagoon	OjRl-3	Muskox	Rib	–20.7	+1.8	45.0	16.4	3.2	21.7
BIBS14-341	Lagoon	OjRl-3	Muskox	Rib	–21.1	+3.6	45.3	16.5	3.2	15.6
BIBS14-414	Lagoon	OjRl-3	Muskox	Cranium	–20.8	+2.5	43.3	15.8	2.4	20.7
BIBS14-117		PkPx-18	Muskox	Vertebra	–20.9	+3.5	44.2	15.9	3.2	23.9
BIBS14-428		PkPx-18	Muskox	Horn core	–20.9	+3.8	44.8	15.7	3.3	20.6

Early Thule										
BIBS15-58	Nelson River	OhRh-1	Caribou	Rib	–21.0	+3.2	44.2	16.2	3.2	19.5
BIBS15-61	Nelson River	OhRh-1	Caribou	Humerus	–20.4	+5.5	45.1	16.6	3.2	18.0
BIBS15-63	Nelson River	OhRh-1	Caribou	Mandible	–20.8	+4.7	45.1	16.4	3.2	15.7
BIBS15-65	Nelson River	OhRh-1	Caribou	Radioulna	–18.8	+2.2	39.9	14.5	3.2	
BIBS16-22	Nelson River	OhRh-1	Caribou	Metacarpus	–18.7	+3.7	45.4	16.7	3.2	21.0
BIBS16-28	Nelson River	OhRh-1	Caribou	Vertebra	–19.2	+2.9	45.0	16.4	3.2	20.2
BIBS16-38	Nelson River	OhRh-1	Caribou	Metatarsus	–18.5	+2.2	42.2	15.4	3.2	21.8
BIBS16-39	Nelson River	OhRh-1	Caribou	Scapula	–21.6	+4.2	44.8	16.2	3.2	25.7
BIBS14-372	Cape Kellett	OlRr-1	Caribou	Mandible	–19.5	+2.9	44.6	16.2	3.2	17.4
BIBS15-62	Nelson River	OhRh-1	Muskox	Humerus	–20.5	+4.3	45.5	16.8	3.2	16.4
BIBS15-66	Nelson River	OhRh-1	Muskox	Maxilla	–21.3	+2.0	45.6	16.7	3.2	15.0
BIBS16-21	Nelson River	OhRh-1	Muskox	Femur	–20.4	+4.8	44.7	16.4	3.2	18.3
BIBS16-23	Nelson River	OhRh-1	Muskox	Femur	–20.5	+6.7	45.3	16.4	3.2	21.0
BIBS16-24	Nelson River	OhRh-1	Muskox	Mandible	–20.0	+2.5	44.0	15.9	3.2	22.5
BIBS16-25	Nelson River	OhRh-1	Muskox	Mandible	–19.9	+3.0	43.7	15.8	3.2	20.5
BIBS16-26	Nelson River	OhRh-1	Muskox	Femur	–21.0	+4.7	45.8	16.7	3.2	17.9
BIBS16-27	Nelson River	OhRh-1	Muskox	Femur	–20.6	+4.0	45.9	16.8	3.2	18.5
BIBS16-29	Nelson River	OhRh-1	Muskox	Femur	–20.6	+2.5	45.2	16.4	3.2	11.4
BIBS16-30	Nelson River	OhRh-1	Muskox	Mandible	–20.5	+2.5	44.2	16.0	3.2	24.4
BIBS16-31[§]	Nelson River	OhRh-1	Muskox	Mandible	–19.8	+3.1	44.4	16.0	3.2	18.4
BIBS16-32	Nelson River	OhRh-1	Muskox	Metacarpus	–20.7	+4.4	43.9	16.1	3.2	22.4
BIBS16-33	Nelson River	OhRh-1	Muskox	Metacarpus	–20.6	+3.7	45.2	16.5	3.2	21.7

BIBS16-34	Nelson River	OhRh-1	Muskox	Metacarpus	–20.8	+4.4	45.9	16.8	3.2	20.7
BIBS16-35	Nelson River	OhRh-1	Muskox	Metacarpus	–21.2	+3.7	44.4	16.2	3.2	21.0
BIBS16-36	Nelson River	OhRh-1	Muskox	Metacarpus	–21.1	+2.8	45.7	16.7	3.2	21.4
BIBS16-37	Nelson River	OhRh-1	Muskox	Metacarpus	–20.4	+3.8	45.6	16.7	3.2	22.0
OhRh1-1†	Nelson River	OhRh-1	Muskox	Calcaneus	–20.9	+4.2	43.3	16.4	3.1	
BIBS14-106	Umingmak	PjRa-2	Muskox	Mandible	–20.3	+5.0	44.3	16.0	3.2	19.1
BIBS14-108		PkPx-18	Muskox	Ischium	–21.3	+3.6	44.1	15.9	3.2	20.6
Classic Thule										
BIBS14-494§	Agvik	OkRn-1	Caribou	Mandible	–19.3	+2.6	45.4	16.6	3.2	12.5
BIBS14-496	Agvik	OkRn-1	Caribou	Mandible	–19.7	+3.0	46.0	16.8	3.2	13.0
BIBS14-502§	Agvik	OkRn-1	Caribou	Mandible	–19.2	+2.9	46.2	16.8	3.2	13.9
BIBS16-8	Agvik	OkRn-1	Caribou	Femur	–19.8	+2.4	45.3	16.8	3.1	16.6
OkRn1-137†	Agvik	OkRn-1	Caribou	Metatarsus	–20.2	+2.5	44.5	16.8	3.1	
OkRn1-164†	Agvik	OkRn-1	Caribou	Humerus	–19.4	+3.3	44.6	16.7	3.1	
OkRn1-167†	Agvik	OkRn-1	Caribou	Maxilla	–19.4	+2.8	41.2	15.7	3.1	
OkRn1-266†	Agvik	OkRn-1	Caribou	Metatarsus	–19.3	+3.5	43.5	16.2	3.1	
OkRn1-60†	Agvik	OkRn-1	Caribou	Radioulna	–19.4	+2.8	42.8	16.3	3.1	
OkRn1-88†	Agvik	OkRn-1	Caribou	Metatarsus	–19.6	+3.1	45.3	17.1	3.1	
OkRn1-89†	Agvik	OkRn-1	Caribou	Metatarsus	–19.2	+2.2	41.6	15.8	3.1	
BIBS14-261	Cape Kellett	OlRr-1	Caribou	Mandible	–19.0	+4.4	45.5	16.4	3.2	16.8
BIBS14-298§	Cape Kellett	OlRr-1	Caribou	Mandible	–18.9	+2.7	45.3	16.1	3.3	15.3
BIBS14-329	Cape Kellett	OlRr-1	Caribou	Radioulna	–18.5	+2.7	45.3	16.6	3.2	18.1
BIBS14-354	Cape Kellett	OlRr-1	Caribou	Scapula	–20.7	+3.4	45.1	16.5	3.2	20.7

BIBS14-355	Cape Kellett	OlRr-1	Caribou	Scapula	–19.4	+3.0	45.0	16.5	3.2	18.1
BIBS14-260	Cape Kellett	OlRr-1	Muskox	Tibia	–21.5	+5.4	45.1	16.5	3.2	20.3
BIBS14-297	Cape Kellett	OlRr-1	Muskox	Rib	–21.6	+3.5	43.9	16.0	3.2	20.2
BIBS14-330	Cape Kellett	OlRr-1	Muskox	Sternum	–21.4	+5.1	44.2	16.1	3.2	23.7
BIBS14-353	Cape Kellett	OlRr-1	Muskox	Tibia	–21.5	+4.9	43.9	16.0	3.2	18.8
BIBS14-356	Cape Kellett	OlRr-1	Muskox	Radioulna	–21.5	+5.2	45.5	16.5	3.2	20.0
BIBS14-474§	Back Point	QbPu-3	Muskox	Mandible	–21.0	+3.6	45.2	16.7	3.2	17.6
BIBS14-485	Back Point	QbPu-3	Muskox	Mandible	–21.3	+4.1	45.1	16.4	3.2	19.8
				Inuit						
BIBS14-182		OjRk-1	Caribou	Tibia	–19.8	+3.2	46.7	17.0	3.2	13.7
BIBS14-125		OjRl-2	Caribou	Vertebra	–20.3	+3.3	45.0	16.2	3.2	16.3
BIBS14-127		OjRl-2	Caribou	Phalanx	–19.9	+2.5	45.7	16.9	3.2	19.1
BIBS14-132		OjRl-2	Caribou	Maxilla	–19.8	+2.0	44.5	16.0	3.2	22.8
BIBS14-189		OjRl-2	Caribou	Mandible	–19.8	+3.1	45.0	16.3	3.2	18.6
BIBS14-191		OjRl-2	Caribou	Maxilla	–20.0	+2.6	45.3	16.5	3.2	18.7
BIBS14-214§	Sunnguqpaaluk	PdRi-1	Caribou	Maxilla	–20.2	+2.6	45.7	16.7	3.2	17.7
BIBS14-418	Sunnguqpaaluk	PdRi-1	Caribou	Scapula	–19.7	+2.4	45.8	16.6	3.2	20.3
BIBS15-21	Nasogaluak	PgPw-3	Caribou	Metacarpus	–20.7	+2.8	45.5	16.6	3.2	16.3
BIBS15-22	Nasogaluak	PgPw-3	Caribou	Metatarsus	–19.2	+4.9	45.3	16.3	3.3	20.4
PgPw3-B†	Nasogaluak	PgPw-3	Caribou	Metatarsus	–20.4	+3.1	42.9	16.0	3.1	
BIBS14-360§	Head Hill	PlPx-1	Caribou	Mandible	–19.3	+4.5	45.1	16.3	3.2	16.0
BIBS14-416		OjRl-2	Muskox	Cranium	–21.1	+4.3	44.7	16.4	3.2	20.5
BIBS14-419	Sunnguqpaaluk	PdRi-1	Muskox	Atlas	–21.6	+5.9	45.6	16.4	3.2	24.1

PgPw3-1†	Nasogaluak	PgPw-3	Muskox	Mandible	–21.4	+4.8	42.9	15.9	3.1	
PgPw3-1053†	Nasogaluak	PgPw-3	Muskox	Mandible	–21.4	+3.8	41.9	15.7	3.1	
PgPw3-1069†	Nasogaluak	PgPw-3	Muskox	Mandible	–21.3	+4.1	42.8	16.0	3.1	
PgPw3-1099†	Nasogaluak	PgPw-3	Muskox	Maxilla	–21.7	+4.4	43.4	16.4	3.1	
PgPw3-1618†	Nasogaluak	PgPw-3	Muskox	Mandible	–21.2	+4.6	43.4	16.5	3.1	
PgPw3-2†	Nasogaluak	PgPw-3	Muskox	Mandible	–21.5	+4.1	41.9	15.5	3.2	
PgPw3-3†	Nasogaluak	PgPw-3	Muskox	Mandible	–21.2	+4.4	42.6	15.9	3.1	
PgPw3-4†	Nasogaluak	PgPw-3	Muskox	Mandible	–21.4	+3.9	42.5	15.9	3.1	
PgPw3-5†	Nasogaluak	PgPw-3	Muskox	Mandible	–21.9	+4.4	42.0	15.7	3.1	
PgPw3-6†	Nasogaluak	PgPw-3	Muskox	Mandible	–21.5	+6.8	44.0	16.6	3.1	
PgPw3-6148†	Nasogaluak	PgPw-3	Muskox	Mandible	–21.1	+4.0	42.3	15.7	3.1	
PgPw3-6149†	Nasogaluak	PgPw-3	Muskox	Mandible	–21.4	+3.8	43.4	16.3	3.1	
PgPw3-7†	Nasogaluak	PgPw-3	Muskox	Mandible	–21.1	+4.7	42.6	15.8	3.2	
BIBS14-165	Head Hill	PlPx-1	Muskox	Mandible	–22.5	+4.3	44.5	16.1	3.2	22.4
BIBS14-287	Head Hill	PlPx-1	Muskox	Mandible	–22.0	+6.1	44.9	16.3	3.2	21.8
BIBS14-288	Head Hill	PlPx-1	Muskox	Mandible	–21.8	+5.7	45.6	16.4	3.2	20.4
BIBS14-289	Head Hill	PlPx-1	Muskox	Mandible	–22.1	+6.2	44.7	15.9	3.3	23.1
BIBS14-291	Head Hill	PlPx-1	Muskox	Mandible	–21.4	+5.3	46.4	17.0	3.2	20.3
BIBS14-361	Head Hill	PlPx-1	Muskox	Mandible	–21.4	+3.6	45.7	16.4	3.2	19.1
BIBS14-362	Head Hill	PlPx-1	Muskox	Mandible	–21.7	+5.1	45.8	16.7	3.2	23.3
BIBS14-364	Head Hill	PlPx-1	Muskox	Mandible	–21.7	+4.9	44.6	16.1	3.2	24.5
BIBS14-447	Head Hill	PlPx-1	Muskox	Mandible	–22.2	+4.5	46.5	17.0	3.2	20.2
BIBS14-449	Head Hill	PlPx-1	Muskox	Mandible	–21.8	+5.0	46.4	17.0	3.2	22.5
BIBS14-454	Head Hill	PlPx-1	Muskox	Mandible	–22.1	+3.9	44.7	16.1	3.2	22.0

BIBS14-456§	Head Hill	PlPx-1	Muskox	Mandible	–21.8	+4.8	46.7	17.1	3.2	20.5
BIBS14-457	Head Hill	PlPx-1	Muskox	Mandible	–21.8	+4.4	45.3	16.4	3.2	20.3
				Modern						
BKS-001†			Caribou	Cranium	–20.2	+2.9	42.8	16.1	3.1	
BIBS15-67§			Caribou	Cranium	–20.4	+4.1	45.2	16.5	3.2	20.2
BIBS15-68			Caribou	Cranium	–20.1	+3.2	45.3	16.8	3.2	19.1
BIBS16-19§			Caribou	Mandible	–19.8	+4.5	44.7	16.3	3.2	21.6
BIBS16-20			Caribou	Rib	–20.2	+3.7	44.4	16.3	3.2	21.7
BIBS16-40			Caribou	Rib	–20.3	+3.6	45.9	16.8	2.4	22.0
BIBS16-41			Caribou	Mandible	–20.0	+3.0	44.3	16.3	2.7	18.9
BIBS16-42			Caribou	Humerus	–20.4	+3.4	45.6	16.7	3.5	15.3
BIBS16-43			Caribou	Rib	–20.6	+5.0	44.6	16.4	2.3	22.2
BIBS16-44			Caribou	Rib	–21.0	+5.5	44.5	16.4	2.4	21.6
BNK-7**			Caribou	Mandible	–19.9	+3.2				
BNK-18**			Caribou	Mandible	–19.9	+3.5				
BNK-4***			Caribou	Mandible	–20.3	+3.7				
BNK-11***			Caribou	Mandible	–20.6	+3.1				
BNK-15***			Caribou	Mandible	–20.7	+3.6				
BKS-0190†			Muskox	Mandible	–20.9	+4.5	42.9	16.3	3.1	
BKS-0191†			Muskox	Cranium	–20.6	+3.7	40.4	15.1	3.1	
BIBS14-168‡			Muskox	Tibia	–20.4	+3.9	44.1	16.0	3.2	18.0
BIBS14-169‡§			Muskox	Mandible	–21.7	+4.0	43.4	15.8	3.2	20.8
BIBS14-445‡§			Muskox	Mandible	–21.0	+5.4	46.1	16.9	3.2	21.1

BIBS16-9	Muskox	Mandible	–21.2	+4.8	43.3	15.9	3.2	25.7
BIBS16-10	Muskox	Mandible	–21.1	+4.4	43.3	15.9	3.2	23.5
BIBS16-11	Muskox	Mandible	–21.0	+3.9	43.4	16.0	3.2	22.5
BIBS16-12	Muskox	Mandible	–20.8	+4.6	43.5	16.0	3.2	24.1
BIBS16-13	Muskox	Mandible	–21.0	+4.0	43.5	16.0	3.2	23.1
BIBS16-14	Muskox	Mandible	–20.6	+4.0	44.0	16.2	3.2	23.8
BIBS16-15	Muskox	Mandible	–21.0	+4.6	44.6	16.5	3.2	22.2
BIBS16-16	Muskox	Mandible	–21.3	+4.0	44.6	16.5	3.2	23.2
BIBS16-17	Muskox	Mandible	–20.6	+4.3	43.8	16.1	3.2	22.8
BIBS16-18	Muskox	Mandible	–20.5	+5.1	44.4	16.4	3.2	25.9

† From pilot study

*Data from Bocherens et al. (2016)

** Data from Drucker et al. (2012); $\delta^{13}C$ has been corrected by –1.43‰

*** Data from Drucker et al. (2012); $\delta^{13}C$ has been corrected by –1.32‰

§ Dentin collagen sampled from tooth belonging to this individual

‡ Recently deceased individual collected at or near archaeological site

Table 3.3. Isotopic, elemental, and percent collagen content data for caribou sequential crown dentin collagen samples from Banks Island. All modern dentin collagen carbon isotope compositions are corrected by +1.7‰ for comparability with archaeological bone collagen data.

Sample ID	Site Name	Borden	Taxon	Microbulk Sample	$\delta^{13}C$ (‰, VPDB)	$\delta^{15}N$ (‰, AIR)	C%	N%	Atomic C:N Ratio	Wt% Coll
Classic Thule										
BIBS14-298 M1	Cape Kellett	OlRr-1	Caribou	BULK	–18.8	+5.7	44.4	16.2	3.2	8.0
BIBS14-298 M2	Cape Kellett	OlRr-1	Caribou	DC1	–19.0	+5.5	42.9	15.5	3.2	6.2
				DC2	–18.5	+5.1	44.3	16.1	3.2	10.6
BIBS14-298 M3	Cape Kellett	OlRr-1	Caribou	DC1	–18.0	+4.4	43.4	15.4	3.3	5.2
				DC2	–18.0	+4.3	44.9	16.2	3.2	11.2
BIBS14-494 M1	Agvik	OkRn-1	Caribou	BULK	–18.9	+5.4	45.4	16.1	3.3	12.3
BIBS14-502 M1	Agvik	OkRn-1	Caribou	BULK	–18.9	+5.2	45.1	16.3	3.2	11.4
Inuit										
BIBS14-214 M1	Sunnguqpaaluk	PdRi-1	Caribou	BULK	–19.5	+5.4	44.8	16.3	3.2	14.2
BIBS14-214 M2	Sunnguqpaaluk	PdRi-1	Caribou	BULK	–19.8	+5.0	45.4	16.5	3.2	12.6
BIBS14-214 M3	Sunnguqpaaluk	PdRi-1	Caribou	BULK	–20.1	+5.1	46.2	16.7	3.2	11.9
BIBS14-214 P4	Sunnguqpaaluk	PdRi-1	Caribou	BULK	–19.8	+4.9	45.0	16.3	3.2	12.5
BIBS14-360 M1	Head Hill	PlPx-1	Caribou	BULK	–19.0	+6.4	45.5	16.6	3.2	11.3

Modern								
BIBS15-67 M2	Caribou	DC1	–19.3	+4.0	43.2	15.5	3.3	8.7
		DC2	–19.4	+4.5	44.9	16.3	3.2	14.0
BIBS16-19 dp4	Caribou	BULK	–19.4	+6.2	42.5	15.3	3.2	12.3
BIBS16-19 M1	Caribou	DC1	–19.6	+6.2	42.7	15.3	3.3	5.4
		DC2	–19.8	+6.1	42.7	15.4	3.2	11.4
		DC3	–19.5	+6.2	43.8	15.9	3.2	14.6
BIBS16-19 M2	Caribou	DC1	–20.2	+6.0	43.1	15.7	3.2	5.6
		DC2	–19.6	+5.7	43.3	15.5	3.3	8.3

Table 3.4. Isotopic, elemental, and percent collagen content data for muskox sequential crown dentin collagen samples from Banks Island. All modern dentin collagen carbon isotope compositions are corrected by +1.7‰ for comparability with archaeological bone collagen data.

Sample ID	Site Name	Borden	Taxon	Microbulk Sample	$\delta^{13}C$ (‰, VPDB)	$\delta^{15}N$ (‰, AIR)	C%	N%	Atomic C:N Ratio	Wt% Coll
Pre-Dorset										
BIBS14-407 M1	Shoran Lake	PjRa-1	Muskox	DC1	–20.9	+5.0	43.9	16.0	3.2	9.7
				DC2	–20.7	+5.2	44.4	16.3	3.2	10.7
				DC3	–20.8	+4.8	44.6	16.4	3.2	11.2
				DC4	–20.7	+5.1	45.3	16.6	3.2	12.0
				DC5	–20.4	+5.3	45.4	16.7	3.2	15.6
BIBS14-409 M1	Umingmak	PjRa-2	Muskox	DC1	–21.3	+6.6	42.2	15.5	3.2	13.5
				DC2	–20.7	+6.7	44.3	16.2	3.2	13.1
				DC3	–20.8	+6.7	44.8	16.5	3.2	11.5
				DC4	–20.8	+6.7	43.3	16.0	3.2	13.3
				DC5	–20.7	+6.5	46.1	17.1	3.1	16.9
Lagoon										
BIBS14-162 M1		QaPv-5	Muskox	BULK	–19.8	+6.2	44.7	16.1	3.2	13.5
BIBS14-209 M1		QaPv-5	Muskox	DC1	–21.0	+7.6	43.0	15.4	3.3	8.5
				DC2	–20.8	+7.4	44.7	16.2	3.2	12.2
				DC3	–20.9	+7.4	44.8	16.3	3.2	13.5
				DC4	–21.0	+7.2	45.7	16.7	3.2	16.8

Early Thule										
BIBS16-30 M1	Nelson River	OhRh-1	Muskox	DC1	–20.5	+7.0	38.1	13.6	3.3	8.4
				DC2	–20.4	+7.1	43.9	15.7	3.3	10.7
				DC3	–20.5	+7.3	43.8	15.6	3.3	11.9
				DC4	–20.6	+7.1	43.8	15.6	3.3	12.8
				DC5	–20.2	+6.9	44.9	16.1	3.2	14.6
Classic Thule										
BIBS14-474 M1	Back Point	QbPu-1	Muskox	DC1	–21.3	+5.1	43.3	15.7	3.2	12.6
				DC2	–19.9	+5.4	44.1	16.0	3.2	14.2
				DC3	–19.9	+5.7	44.1	15.8	3.2	15.6
Inuit										
BIBS14-456 M1	Head Hill	PlPx-1	Muskox	DC1	–21.6	+7.6	43.5	15.8	3.2	9.4
				DC2	–21.9	+7.5	44.2	16.1	3.2	10.3
				DC3	–21.9	+7.3	43.9	15.8	3.2	10.1
				DC4	–21.8	+7.2	44.5	16.2	3.2	12.0
				DC5	–21.9	+7.1	43.4	15.7	3.2	14.1
				DC6	–21.6	+7.4	44.7	16.2	3.2	14.9
				DC7	–21.5	+6.9	44.1	16.0	3.2	15.8
Modern										
BIBS14-169 M1			Muskox	DC1	–21.2	+7.9	42.8	15.6	3.2	14.5
				DC2	–20.9	+7.7	44.8	16.3	3.2	14.4
				DC3	–21.1	+8.0	44.9	16.4	3.2	14.5
				DC4	–20.8	+7.9	45.3	16.5	3.2	16.0

		DC1	–20.6	+7.2	42.2	15.4	3.2	11.0
		DC2	–20.7	+7.3	43.8	15.9	3.2	14.3
BIBS14-445 M1	Muskox	DC3	–20.3	+7.4	44.9	16.3	3.2	15.2
		DC4	–20.4	+7.5	44.7	16.3	3.2	16.8
		DC5	–20.0	+7.2	44.7	16.4	3.2	18.7

3.3 Methods

3.3.1 Sample Preparation

Approximately 1 g of material was removed from each bone sample using a Dremel® rotary tool. Where possible, we favored cortical bone for isotopic analysis because the turnover rate is slightly slower than in trabecular bone, and is therefore less affected by short periods of dietary fluctuation (Cox and Sealy 1997; Hill and Orth 1998; Hedges et al. 2007). Similarly, we avoided unfused skeletal elements and mandibles or maxillae with less than two erupted permanent molars. Because nitrogen isotope compositions, and to a smaller extent, carbon isotope compositions are influenced by the consumption of milk (Fogel et al. 1989; Jenkins et al. 2001) the inclusion of bone samples from young individuals, who were still nursing, in our analysis could affect shape-based metrics based on isotopic compositions.

We also sampled 2-3 g of bone from each element for radiocarbon dating, and a further 2-3 g of bone for ancient DNA analysis (Rodrigues et al. forthcoming). Where present, crustose lichen was removed from bone surfaces with a dental scaler, and soil and dust were removed via ultrasonication for several minutes in distilled water. Bone samples were then dried at low temperature (~ 60°C) and crushed to grain sizes between 0.18 and 0.84 mm. Bulk collagen was extracted using a modified version of the protocol described by Longin (1971). This process involves removal of lipids and any residual soft-tissue with three rinses in 2:1 chloroform-methanol, demineralization in 0.50 M HCl, removal of humic and fulvic acids in 0.1 M NaOH, solubilization in weak acid (10^{-3} M HCl), and evaporation of water to yield dry collagen. In all cases, the demineralization process took less than two weeks.

We selected only M1s from archaeological muskoxen, while in caribou we selected all available molars in a single tooth row. The difference in tooth sampling strategies is due to the size disparity between caribou and muskox teeth. The molars and adult premolars of muskoxen are much larger than those of caribou. Hence, while it is possible to obtain a sequence of microbulk dentin samples from muskox molar and adult premolar crowns, we were often required to sample all crown dentin in a caribou molar to obtain the minimum

amount of collagen required for analysis. We also hypothesized that due to their size, formation schedule (Figure 3.7), and the supposedly rapid weaning process in muskoxen (Tener 1965; Kelsall 1968), the isotopic compositions of sequential dentin collagen samples from muskox M1s would capture the transition from nursing to adult diet. Additionally, the focus of Chapter 4 is the reconstruction of the movements of caribou and muskoxen using oxygen isotope compositions of enamel structural carbonate in tooth crowns. For caribou, we therefore sampled as many teeth in a tooth row as possible to reconstruct potential seasonal movements over the course of an individual's life.

Sequential dentin "microbulk"[13] collagen samples were obtained from tooth crowns and prepared in the same fashion as in Chapter 2, and follow the same collagen extraction methods used for bone collagen samples. Briefly described, selected teeth were extracted from mandibles or maxillae, cleaned of dust, debris, and residual cementum using ultrapure water, a toothbrush, and a dental scaler, and allowed to dry under continuous air flow in a fume hood (Figure 3.8a). Because the size of the muskox teeth exceeded all commercially-available embedding molds, we instead employed inexpensive silicone cigarette cases purchased from a variety store as reusable embedding molds. Teeth were fully embedded in epoxy resin (Struers EpoFix®) (Figure 3.8b) and each epoxy "block" cured at room temperature for at least a week. After curing, we used a Buehler® IsoMet™ low-speed saw to produce two 250 μm-thick buccolingual thick sections (henceforth the "A-section" and "B-section") through the highest point of the least worn tooth loph (Figure 3.8c). After microsampling enamel from each A-section for related research (see Chapter 4; B-sections were used exclusively for the analysis of tooth enamel $\delta^{13}C$ and $\delta^{18}O$ in that chapter as well), we used a second, smaller sectioning machine to divide each tooth crown into ~ 5 mm transverse "slices" (Figure 3.8d, e). Because the degree of occlusal wear in each tooth varies (Appendix B, Supplemental Figures B1 and B2), the root-enamel junction (REJ) of

[13]Since it is not possible to obtain collagen from individual dentin appositional layers with the sampling methodology we employ here, the isotopic compositions of each sequential dentin sample reflect the averaged isotopic compositions of multiple, cross-cut dentin appositional layers. We use the term "microbulk" to distinguish from studies where whole-tooth, homogenized dentin samples are analyzed.

each tooth crown was used as a common “anchor point” for each sampling “grid” of 5 mm transverse sections.

As with modern tooth samples (Chapter 2), archaeological microbulk dentin collagen samples were not crushed to uniform grain sizes prior to demineralization. This procedural change was made to minimize sample loss during grinding and facilitate the removal of residual embedding epoxy. All microbulk dentin collagen samples were rinsed three times in 2:1 chloroform-methanol prior to the collagen extraction process to dissolve as much adhering epoxy as possible.

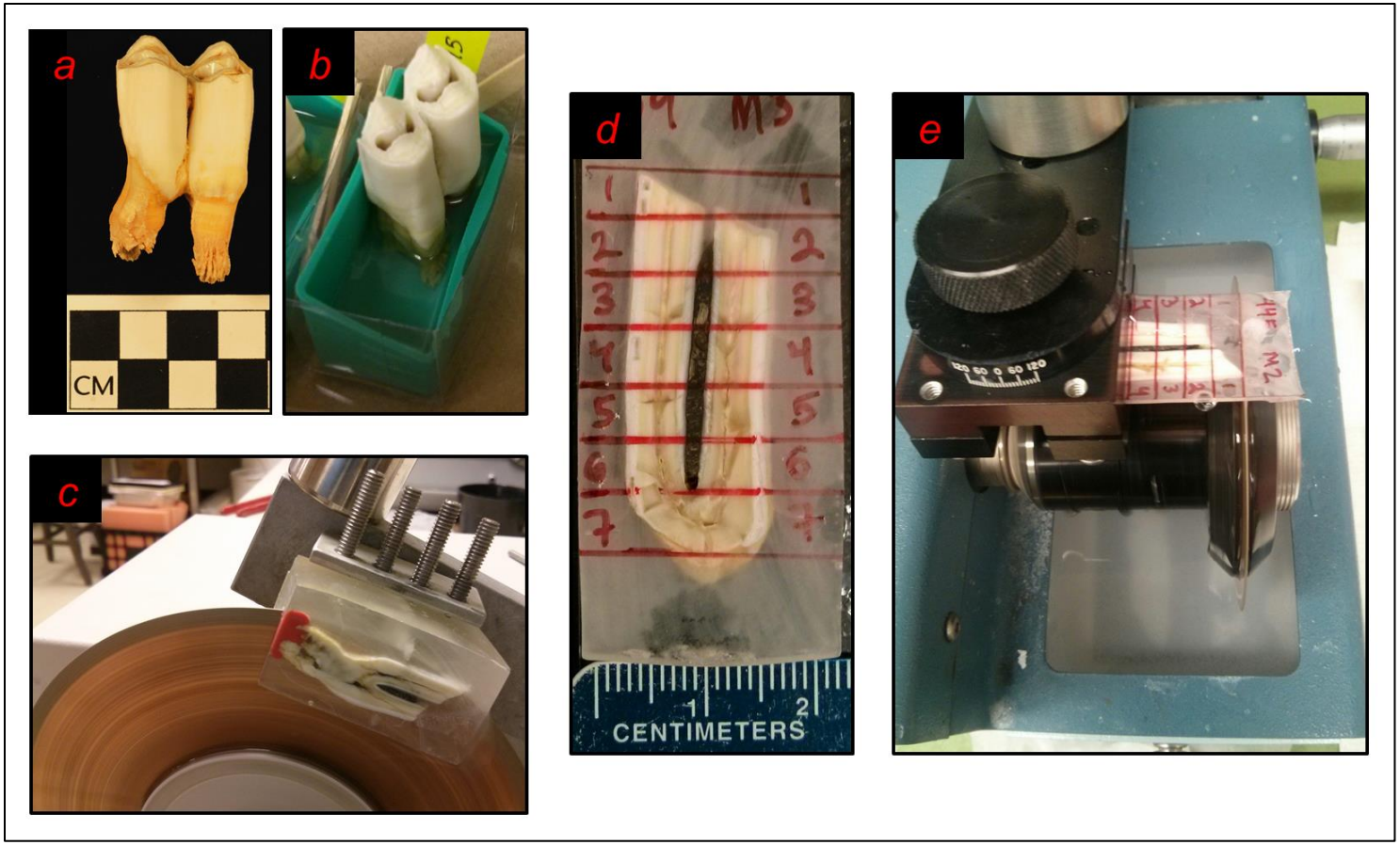


Figure 3.8. The dentin collagen sampling process, reproduced from Chapter 2: **(*a*)** intact tooth after being removed, cleaned, and dried; **(*b*)** embedding in epoxy resin using silicone cigarette cases as molds; **(*c*)** obtaining one of two thick sections from the epoxy block; the first section (the "A-section") is used for obtaining dentin samples (red material is modeling clay used to position tooth during embedding); **(*d*)** an A-section marked for transverse sectioning; numbers correspond to sequential dentin sample IDs. Each section is approximately 5 mm in height with the sampling "grid" anchored at the root-enamel junction (REJ); **(*e*)** obtaining sequential dentin samples from an A-section using the second sectioning machine.

3.3.2 Isotopic Analysis

All isotopic analyses, including those from the pilot project, were performed at the Laboratory for Stable Isotope Science (LSIS) at the University of Western Ontario, London, Ontario, Canada using a Costech™ 4010 Elemental Combustion System interfaced with either a Thermo Scientific™ DELTA^{plus} XL® or Thermo Scientific™ DELTA V Plus® isotope ratio mass spectrometer (IRMS) operating in continuous flow (CF) mode. All isotopic compositions are reported in per mil (‰) using delta notation (δ) (Equation 3.1):

$$\delta = \left[\frac{R_{Sample}}{R_{Standard}} - 1\right]$$

[Equation 3.1]

where R is the ratio of heavy to light isotopes in the analyte. Carbon isotope compositions are calibrated to Vienna Pee Dee Belemnite (VPDB) (δ^{13}C = 0‰) and nitrogen isotope compositions are calibrated to atmospheric N_2 (AIR) (δ^{15}N = 0‰) using USGS40 (L-glutamic acid; accepted δ^{13}C and δ^{15}N = –26.39‰ and –4.52‰, respectively) and USGS41 (L-glutamic acid; accepted δ^{13}C and δ^{15}N = +37.63‰ and +47.57‰, respectively) (Qi et al. 2004). An internal keratin standard (MP Biomedicals Inc., Cat No. 90211, Lot No. 9966H), and an international standard (IAEA-CH-6) were used to measure instrument analytical accuracy throughout each analytical session.

For all samples, weight percent carbon (C%) and nitrogen (N%) were not measured directly but were calculated using Equation 2.2:

$$\frac{\frac{\%E_{Standard} * Amplitude_{Sample}}{Amount_{Sample}}}{K-Factor}$$

[Equation 3.2]

where "$\%E_{Standard}$" equals the accepted elemental (C or N) weight percentage of the reference standard (here, either USGS-40 or USGS-41), "$Amplitude_{Sample}$" equals the amplitude of ions with a mass-to-charge (m/z) ratio of 44 (for carbon) or 28 (for nitrogen) measured in the sample, and "$Amount_{Sample}$" equals the sample weight (in mg). The "*K-factor*", used to correct for instrumental mass discrimination, and is derived from Equation 2.3:

$$\frac{Average\ Amplitude_{Standard}}{Average\ Amount_{Standard}}$$

[Equation 3.3]

where "$Average\ Amplitude_{Standard}$" equals the average amplitude of ions with a mass-to-charge (m/z) ratio of 44 (for carbon) or 28 (for nitrogen) measured in all analyses of a reference standard (here, either USGS-40 or USGS-41) during the analytical session, and "$Average\ Amount_{Standard}$" equals the average weight (in mg) of all reference standards (again, either USGS-40 or USGS-41) analyzed during the analytical session.

For every ~ 20 bone or dentin collagen samples selected, we created two method duplicates to assess the effect of the collagen extraction process on the reproducibility of isotopic and elemental data. We also analyzed duplicate bone and dentin samples (i.e. instrumental duplicates) at regular intervals to assess instrumental precision. The standard deviation of method duplicates and instrumental duplicates reported here reflect the differences between the average value (δ^{13}C, δ^{15}N, C%, N%) of all method or instrumental duplicates, and the average value (δ^{13}C, δ^{15}N, C%, N%) of their parent samples.

3.3.3 Convex Hulls and Layman Metrics

Several quantitative methods are available for evaluating isotopic niche position and overlap in species. The most straightforward is the convex hull approach (Layman et al. 2007a, 2007b, 2012). Here, the *outermost* isotopic values (in δ-space) for a given species delineate its isotopic niche, and different metrics (i.e. "Layman" metrics, after Layman et al. (2007a, 2007b)), such as the range of carbon and nitrogen isotope compositions (CR

and NR, respectively), the total area encapsulated by the convex hull (CHA, but often referred to as "total area" or "TA"), and the "packing" of the data points inside each hull (Table 3.5). As several researchers (Jackson et al. 2011, 2012; Syväranta et al. 2013) point out, however, convex hulls and Layman metrics, as measures of extreme value (i.e. the outermost isotopic values for a given sample population) are prone to exaggerating isotopic niche area (see also Hoeinghaus and Zeug 2008). Additionally, the area of a convex hull, and therefore other Layman metrics, can change substantively with the addition of new data. Through simulation, Jackson et al. (2011) demonstrated that TA will increase indefinitely with the addition of more data. This makes valid comparisons of estimated isotopic niche areas from datasets difficult, though other Layman metrics may provide useful information about niche characteristics.

Table 3.5. Descriptions of different Layman metrics presented in this chapter.[14]

Layman Metric	Description
Carbon range (CR)	Difference (in ‰) between the maximum and minimum values of $\delta^{13}C$ in the sample dataset; provides a measure of forage resource diversity
Nitrogen range (NR)	Difference (in ‰) between the largest and smallest values of $\delta^{15}N$ in the sample dataset; provides a measure of forage resource diversity
Mean distance to centroid (CD)	Average distance (in ‰^{2}) between each data point in Cartesian space, and the centroid of the convex hull; provides a measure of intra-species isotopic diversity (i.e. "packing").
Mean Nearest Neighbor Distance (MNND)	Average of the distances () to each data point's nearest neighbor in Cartesian space; provides a measure of intra-species isotopic diversity (i.e. "packing").
Standard Deviation of Nearest Neighbor Distance (SDNND)	A measure of the "evenness" in the packing of $\delta^{13}C$ and $\delta^{15}N$, which provides additional information about intra-species isotopic diversity
Convex Hull Area (CHA)	Smallest area encompassed by all $\delta^{13}C$ and $\delta^{15}N$ in a sample dataset; provides a measure of total niche space occupied

[14]Although isotopic data expressed in ‰ are dimensionless, where used, "‰^{2}" expresses the area of a two-dimensional shape in Cartesian space created by the $\delta^{13}C$ and $\delta^{15}N$ of a sample or samples.

3.3.4 Multivariate and Bayesian Ellipses

Multivariate ellipse-based metrics are now commonly used alongside, or as an alternative to convex hulls. We use the "Stable Isotope Bayesian Ellipses in R" (SIBER) function inside the "Stable Isotopes in R" (SIAR) package (version 4.2) for the R open source software environment (version 3.2.4) (R Development Core Team 2009)[15]. Developed by Jackson et al. (2011), SIBER allows users to create estimates of consumer isotopic niche widths that are, unlike convex hulls, nearly independent of sample size. Because multivariate ellipses describe the central tendencies of a dataset, rather than its extreme values, and because the multivariate ellipse always contains ~ 40% of the data irrespective of sample size (Batschelet 1981, Jackson et al. 2011), they integrate more uncertainty into the isotopic niche estimate than convex hulls (Jackson et al. 2011).

The mathematics of multivariate ellipses are described in detail by Batschelet (1981), Ricklefs and Nealen (1998), and Jackson et al. (2011) and summarized in plain language here. For a given set of data x and y (in this context, $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$, respectively), the centroid of the ellipse drawn in two-dimensional space is located at the mean values of x and y. The size and orientation of the ellipse is determined by first calculating the covariance of the x and y data [$\sigma(x,y)$], which is summarized in a covariance matrix. This covariance matrix describes the spread and orientation of the x-y point cloud in Cartesian space. The semi-major (a) and semi-minor axes (b) of the ellipse correspond to the largest and second largest eigenvectors, respectively, of the covariance matrix, which reflect the largest and second largest variances in the data. The magnitudes (i.e. the lengths) of the axes correspond to the square roots of the largest and second largest eigenvalues, and the shape of the ellipse is determined by the square root of the ratio of the largest eigenvalue to the second eigenvalue (i.e. the square root of the ratio of the semi-major to semi-minor

[15] At the time of our data analysis, SIBER existed as a function inside the "Stable Isotope Analysis in R" (SIAR) package. SIBER is now offered as a standalone R package (https://cran.r-project.org/web/packages/SIBER).

axis length). The area of the ellipse, or "Standard Ellipse Area" (SEA) is then given by πab.

In practice, ellipses are plotted and their metrics calculated automatically using the code within SIBER. Jackson et al. (2011) demonstrate that above a sample size of n = 30, estimated SEA does not change as it does with convex hull area. Realistically however, sample sizes for isotopic data sets are often much smaller than n = 30, and so an SEA estimate corrected for small sample sizes, SEA_c, is also available. In simulation, Jackson et al. (2011) demonstrate that ellipse area estimates provided by the SEA_c metric change little over the minimum sample size of n = 3 (but see Syväranta et al. 2013). Finally, a Bayesian ellipse area estimate (SEA_B) can be produced by using Markov Chain Monte Carlo (MCMC) (Parnell et al. 2010; Jackson et al. 2011), and different ellipse-based metrics can be calculated.

3.4 Results

3.4.1 Bone Collagen $\delta^{13}C$ and $\delta^{15}N$ Results

Archaeological bone collagen carbon and nitrogen isotope and elemental compositions were measured in ten analytical sessions, including those that produced the pilot project data. The modern bone collagen samples considered in this chapter but discussed in detail in Chapter 2 were also analyzed in these sessions. Across 72 analyses of the internal keratin standard (mean $\delta^{13}C$ and $\delta^{15}N$ = –24.04‰ and +6.36‰, respectively), $\delta^{13}C$ was –24.10±0.16‰ and $\delta^{15}N$ was +6.40±0.13‰. Across 28 analyses of IAEA-CH-6 (accepted $\delta^{13}C$ = –10.45‰ (Hut 1987)), $\delta^{13}C$ was –10.44±0.07‰. The standard deviation of bone collagen samples analyzed as instrumental duplicates (n = 14) is $\delta^{13}C$ = ±0.0‰, $\delta^{15}N$ = ±0.1‰, C% = ±0.1, and N% = ±0.1. The standard deviation of bone collagen samples analyzed as methodological duplicates (n = 14) is $\delta^{13}C$ = ±0.0‰, $\delta^{15}N$ = ±0.1‰, C% = ±0.1, and N% = ±0.1.

The collagen content, as a percentage of sample weight ("wt% coll") for archaeological bone samples averages 19.8% (min = 11.4%; max = 25.9%), with no significant differences across cultural periods. Percent collagen content data from the pilot project samples are not available to us, but based on their calculated percent carbon (C%) and nitrogen (N%)

contents, and the percent collagen content of bone samples from concurrent cultural periods, we assume that they are of comparable preservation. These collagen percentages are typical of those observed in modern or well-preserved bone collagen (wt% coll = ~ 20-30%) (Schoeninger et al. 1989; Ambrose 1990; Ambrose and Norr 1993; van Klinken 1999; Jørkov et al. 2007). Including the pilot project samples, C% and N% average 44.3% (min = 39.2%, max = 46.7%) and 16.2% (min = 14.2%, max = 17.1%), respectively. Atomic C:N ratios average 3.2 (min = 3.1; max = 3.3). Elemental abundances and atomic C:N ratios from all archaeological bone collagen samples are both within commonly accepted ranges for isotopically-unaltered bone collagen (C% = 15.3 to 47.0%; N% = 5.5 to 17.3%; atomic C:N = 2.9 to 3.6) (DeNiro 1985; Ambrose 1990; van Klinken 1999). Reproducibility and preservation data for modern bone collagen samples included here are likewise good, as discussed fully in Chapter 2.

The $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ of caribou and muskoxen from all cultural periods are listed in Table 3.2. Modern bone collagen carbon isotope compositions from Chapter 2 are corrected here by +1.7‰ to achieve comparability with the archaeological data. This difference is the result of gradual depletion of ^{13}C in atmospheric CO_2 (i.e. the "Suess Effect") over the last ~ 150 years due to the anthropogenic combustion of ^{13}C-depleted fossil fuels (Keeling et al. 1979; Tans 1979; Friedli et al. 1986).

3.4.2 Trophic Discrimination Factors and Niche Overlap

In terms of multivariate ellipse metrics, our primary interests are the *relative locations of caribou and muskox ellipses in δ-space,* and the *degree of caribou-muskox ellipse overlap* across cultural periods. The use of multivariate ellipse overlap as a proxy for ecological niche overlap, however, depends in part on the isotopic trophic discrimination factors (TDFs) of the species under comparison. If the TDFs for the analyzed isotopic systems are the same in both species then the isotopic compositions of the analyzed tissues, and their associated multivariate ellipse metrics, are directly comparable in δ-space. Consequently, significant overlap of multivariate ellipses in this scenario could point towards dietary or ecological niche overlap. This, however, is not necessarily the case if the TDFs for the species in question are markedly different.

In Chapter 2, we used the Stable Isotope Discrimination Estimation in R (SIDER) package for R (https://github.com/healyke/SIDER) to obtain carbon and nitrogen TDF estimates ($\Delta^{13}C_{coll\text{-}diet}$ and $\Delta^{15}N_{coll\text{-}diet}$, respectively) plus associated measures of uncertainty, for modern caribou and muskoxen. The use of SIDER-derived TDFs in Bayesian dietary mixing models is advantageous because SIDER also provides and error range around TDF estimate (Healy et al. 2016). Consequently, the probability distributions for different source contributions, when calculated by MixSIAR, incorporate a greater degree of uncertainty than if generalized TDFs and SD values are used. The SIDER-derived $\Delta^{13}C_{coll\text{-}diet}$ estimate for caribou is 4.7‰ (SD = 1.5‰), while the $\Delta^{13}C_{coll\text{-}diet}$ estimate for muskoxen is 2.6‰ (SD = 1.9‰). Turning to nitrogen, the $\Delta^{15}N_{coll\text{-}diet}$ estimate for caribou is 3.3‰ (SD = 1.1‰), and that for muskoxen is 3.7‰ (SD = 1.3‰). In order to compare caribou and muskox $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ across cultural periods, and hence to evaluate the evidence for niche overlap, we must first account for the different $\Delta^{13}C_{coll\text{-}diet}$ and $\Delta^{15}N_{coll\text{-}diet}$ of each species. Otherwise, there is an obvious disjuncture between our interpretation of modern caribou and muskox diet, which is derived from mixing models utilizing Bayesian TDFs, and interpretations of archaeological caribou and muskox isotopic niche variation derived from non-transposed bone collagen isotopic data and their shape-based metrics (i.e. ellipse and convex hull metrics) (Newsome et al. 2012).

While workers in wildlife and applied ecology have recognized the significance of taxon-specific variation in trophic discrimination factors (Bearhop et al. 1999; Bocherens and Drucker 2003; Caut et al. 2009; Halley et al. 2010; Kelly et al. 2012; Derbridge et al. 2015; Holá et al. 2015; Dionne et al. 2016; Healy et al. 2016; Matley et al. 2017), we know of no published studies at the time of writing that have attempted to rationalize the assumptions of overlap in shape-based metrics with the possibility that members of the same trophic level in *paleoecological* communities may have had different carbon and nitrogen TDFs. Indeed, investigations into paleoecological niche relationships, particularly those dealing with sympatric ungulate species, typically assume either implicitly or explicitly that consumer isotopic compositions directly reflect niche relationships (Iacumin et al. 2000; Ben-David et al. 2001; Drucker et al. 2003; Feranec 2007; Feranec and MacFadden 2006; France et al. 2007; Fox-Dobbs et al. 2008; Mann et al. 2013; Bocherens et al. 2015a, b), and that shape-based metrics can be used as direct measures of niche overlap or

partitioning. Because this dissertation takes as its study subjects both modern and comparatively-recent Holocene archaeological caribou and muskoxen, we are uniquely-positioned to consider this problem.

Several factors complicate the use of Bayesian mixing models to formally investigate the proportional contributions of different forage sources to archaeological bone collagen isotopic compositions. Most obviously, we have no archaeological source (i.e. forage) isotopic data. The use of modern forage isotopic data in the mixing model is also inappropriate, as we do not know whether or how the $\delta^{13}C$ and $\delta^{15}N$ of different forage species on Banks Island have varied across time. Overall, phytodiversity in the Canadian Arctic has remained the same since deglaciation, but the aboveground productivity (i.e. *phytomass*) of different forage species has varied (Gajewski et al. 2000; Gajewski 2015a). Consequently, some forage sources consumed by caribou and muskoxen today may have been unavailable at certain times in the past and *vice versa*. Finally, it is not clear whether carbon and particularly nitrogen TDFs for caribou and muskoxen have varied through time with factors such as dietary protein content (Fantle et al. 1999; Oelbermann and Scheu 2002; Martinez del Rio and Wolf 2005; Robbins et al. 2005, 2010; Greer et al. 2015).

In light of these complexities, we attempt to model actual niche overlap between caribou and muskoxen as follows. Figure 3.9 presents the $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ of caribou and muskoxen from each cultural period, along with convex hulls and SEA_c ellipses (again with modern $\delta^{13}C_{bc}$ corrected by +1.7‰ for comparability with archaeological bone collagen data). In Figure 3.10, we then replot these data, along with convex hulls and SEA_c ellipses, transposed into what we refer to as "quasi-IsoSpace" (after Newsome et al. 2012), using the mean values of the respective SIDER-derived $\Delta^{13}C_{coll\text{-}diet}$ and $\Delta^{15}N_{coll\text{-}diet}$ estimates for caribou and muskoxen. There are some drawbacks to this approach: it introduces potential error into the ellipse overlap calculation, due to the possibility that the SIDER-derived TDFs may be incorrect, and it ignores uncertainty around each SIDER-derived TDF estimate. Nonetheless, it more accurately reflects the relationships between caribou and muskox isotopic compositions and their probable dietary niches than isotopic data not adjusted for the potentially unique TDFs of caribou versus muskoxen. Multivariate and Bayesian ellipse metrics for non-transposed and transposed data are presented in Table

3.6 and summary and Layman metrics are presented in Table 3.7. The 95% credible intervals for SEA_B ellipse estimates in each cultural period, at 10^4 iterations, are shown in Figure 3.11. Intra-specific, shape-based metrics (e.g. change in mean $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ across time, CR, NR, CHA, SEA_c, SEA_B) do not change regardless of any data transpositions.

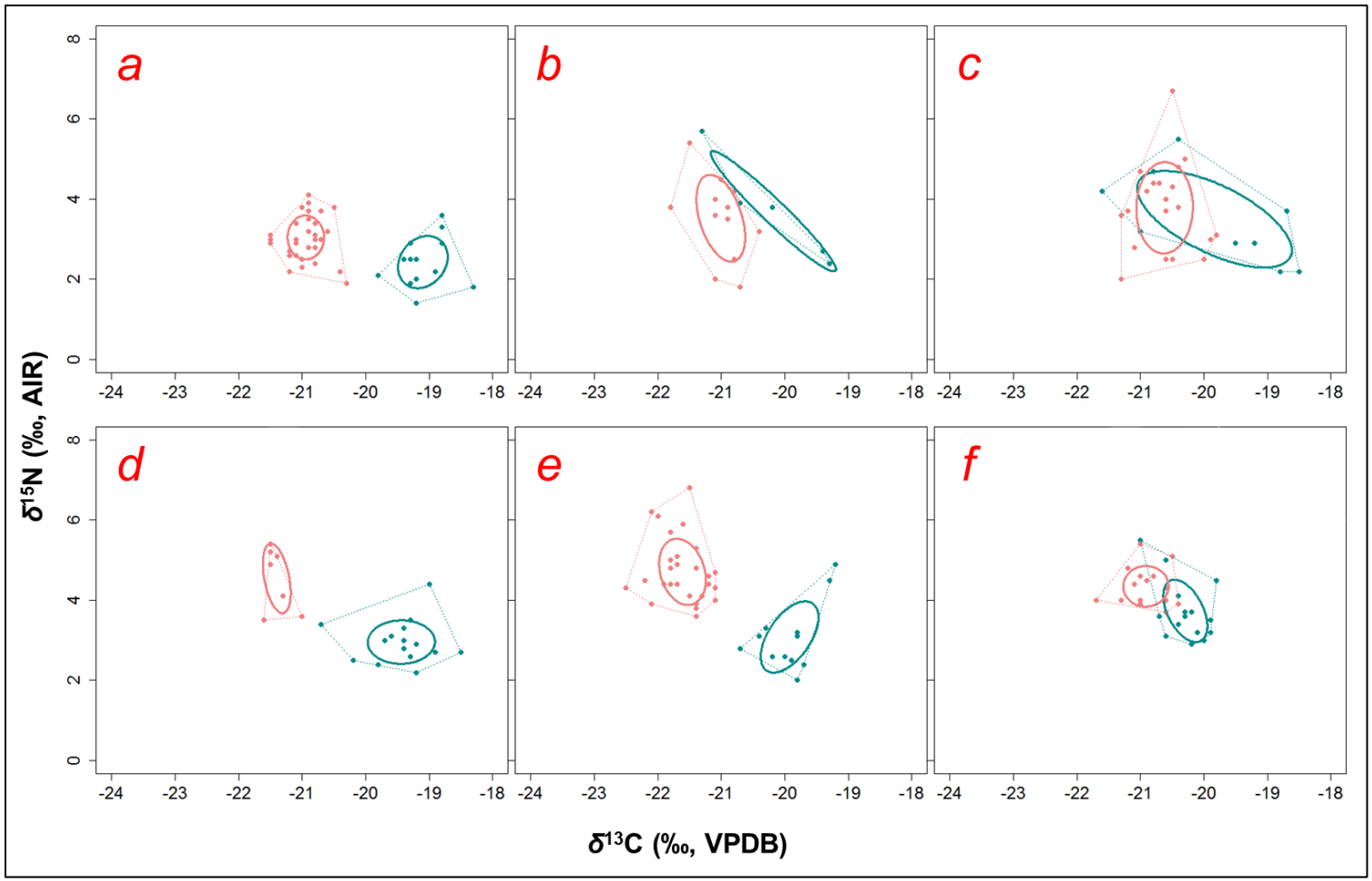


Figure 3.9. Non-transposed bone collagen $\delta^{13}C$ and $\delta^{15}N$, convex hulls and SEA_c ellipses derived from caribou (turquoise) and muskoxen (coral) bone collagen isotopic compositions across cultural periods on Banks Island. **(*a*)** Pre-Dorset period; **(*b*)** Lagoon period; **(*c*)** Early Thule period; **(*d*)** Classic Thule period; **(*e*)** Inuit period; **(*f*)** modern period. Modern carbon isotope compositions have been adjusted by +1.7‰ for comparability with archaeological data.

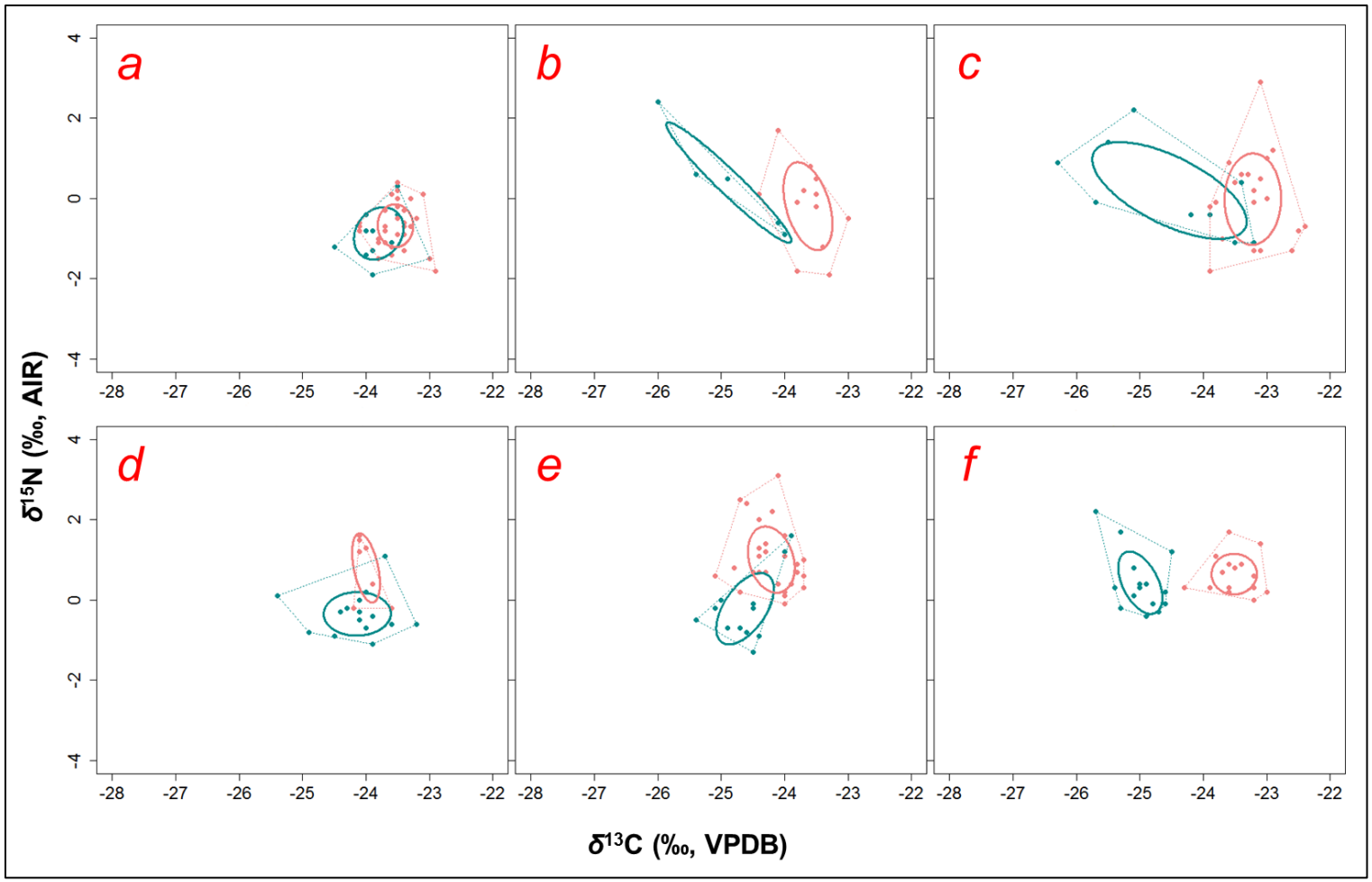


Figure 3.10. TDF-transposed convex hulls and SEA_c ellipses derived from caribou (turquoise) and muskoxen (coral) bone collagen isotopic compositions across cultural periods on Banks Island. **(*a*)** Pre-Dorset period; **(*b*)** Lagoon period; **(*c*)** Early Thule period; **(*d*)** Classic Thule period; **(*e*)** Inuit period; **(*f*)** modern period. Modern carbon isotope compositions have been adjusted by +1.7‰ for comparability with archaeological data.

Table 3.6. Multivariate and Bayesian ellipse metrics for non-transposed and transposed caribou and muskox bone collagen isotopic data from Banks Island.

Taxon	Ellipses Area Comparisons (‰^{2})					Ellipse Metrics				
	SEA	SEA_c	SEA_B (10^4)	SEA_B (10^5)	SEA_B (10^6)	$SEA_{B(C>M)}$ (%)	$SEA_{c(O)}$ (‰^{2})	$\%SEA_{c(O)}$	Transposed $SEA_{c(O)}$ (‰^{2})	Transposed $\%SEA_{c(O)}$
Pre-Dorset										
Caribou	0.7	0.8	1.1	1.1	1.1	0.04	0.00	0.00	0.32	0.41
Muskox	0.5	0.5	0.7	0.7	0.7			0.00		0.66
Lagoon										
Caribou	0.9	1.2	2.4	2.3	2.4	0.14	0.00	0.00	0.00	0.00
Muskox	1.1	1.2	1.6	1.6	1.6			0.00		0.00
Early Thule										
Caribou	3.1	3.5	3.0	3.0	3.0	0.06	1.05	0.30	0.26	0.07
Muskox	1.5	1.6	1.8	1.8	1.8			0.66		0.16
Classic Thule										
Caribou	0.8	0.9	1.1	1.1	1.1	0.78	0.00	0.00	0.04	0.04
Muskox	0.5	0.5	1.4	1.4	1.4			0.00		0.07
Inuit										
Caribou	1.0	1.1	1.4	1.4	1.4	0.19	0.00	0.00	0.09	0.08
Muskox	0.9	0.9	1.1	1.1	1.1			0.00		0.09
Modern										
Caribou	0.7	0.7	1.1	1.1	1.1	0.24	0.02	0.03	0.00	0.00
Muskox	0.5	0.6	0.9	0.9	0.9			0.04		0.00

Table 3.7. Summary and Layman metrics for non-transposed and transposed caribou and muskox bone collagen isotopic data from Banks Island. Modern $\delta^{13}C_{bc}$ data are adjusted by +1.7‰ for comparability with archaeological bone collagen isotopic data.

Taxon	*n*	Mean $\delta^{13}C_{bc}$ (‰, VPDB)	Mean $\delta^{15}N_{bc}$ (‰, AIR)	CR (‰)	NR (‰)	CD (‰^{2})	MNND (‰^{2})	SDNND (‰^{2})	CHA (TA) (‰^{2})	$CHA_{(C>M)}$ (%)	$CHA_{(o)}$ (‰^{2})	$\%CHA_{(O)}$	Transposed $CHA_{(o)}$ (‰^{2})	Transposed $\%CHA_{(O)}$
Pre-Dorset														
Caribou	13	–19.1	+2.4	1.5	2.2	0.6	0.3	0.2	1.7	0.00	0.00	0.00	1.23	0.71
Muskox	32	–20.9	+3.0	1.2	2.2	0.5	0.1	0.1	1.7			0.00		0.72
Lagoon														
Caribou	5	–20.2	+3.7	2.0	3.3	1.2	0.7	0.7	0.9	0.00	0.00	0.00	0.03	0.03
Muskox	12	–21.0	+3.5	1.4	3.6	0.9	0.5	0.2	2.7			0.00		0.01
Early Thule														
Caribou	9	–19.8	+3.5	3.1	3.3	1.4	0.7	0.4	5.4	0.46	2.51	0.46	0.87	0.16
Muskox	20	–20.6	+3.8	1.5	4.7	1.0	0.3	0.4	4.1			0.62		0.21
Classic Thule														
Caribou	16	–19.4	+3.0	2.2	2.2	0.6	0.3	0.3	2.9	0.00	0.00	0.00	0.47	0.16
Muskox	7	–21.4	+4.5	0.6	1.9	0.7	0.4	0.2	0.6			0.00		0.81
Inuit														
Caribou	12	–19.9	+3.1	1.5	2.9	0.7	0.3	0.1	1.6	0.00	0.00	0.00	0.55	0.35
Muskox	28	–21.6	+4.7	1.4	3.2	0.8	0.2	0.2	2.9			0.00		0.19
Modern														
Caribou	15	–20.3	+3.7	1.2	2.6	0.6	0.3	0.2	1.8	0.32	0.58	0.32	0.00	0.00
Muskox	15	–20.9	+4.3	1.3	1.7	0.5	0.3	0.2	1.4			0.42		0.00

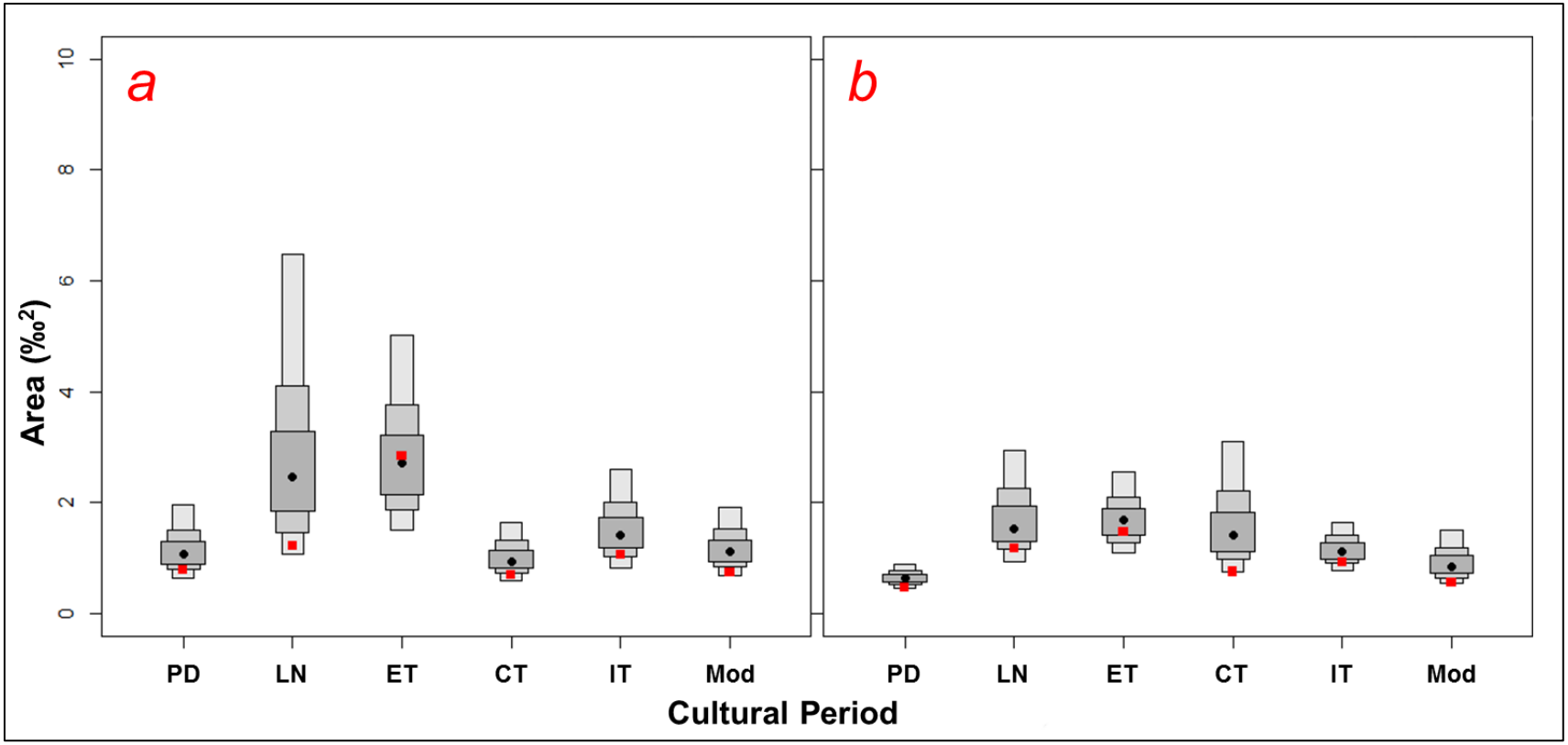


Figure 3.11. Credible intervals (at 10^4 iterations) for posterior probability distributions of (*a*) caribou and (*b*) muskox SEA_B from each cultural period. Thinnest boxes = 95% CI; medium-thick boxes = 75% CI; thickest boxes = 50% CI. "PD" = Pre-Dorset; "LN" = Lagoon; "ET" = Early Thule; "CT" = Classic Thule; "IT" = Inuit; "Mod" = modern. Red squares denote SEA*c* ellipse area estimates. Black circles denote the modal value of each SEA_B ellipse area estimate.

3.4.3 Caribou and Muskox Layman and Ellipse Metrics

Although we provide the full suite of common Layman metrics in Figures 3.12 and 3.13, and Table 3.7, some are too strongly influenced by sample size to produce useful interpretations of isotopic niche variation over time. For instance, it might be useful to compare the densities of isotopic data in different cultural periods using mean nearest neighbor distance (MNND) to make inferences about niche specialization. MNND, however, should always be strongly negatively correlated with sample size because the distance between δ-values in a dataset will necessarily decrease as more data are added. Simple linear regression modeling suggests that there are indeed strong negative correlations between sample size and MNND in our datasets: $MNND_{caribou}$ = -0.0(sample size) +0.9, adjusted R^2 = 0.7 (Figure 3.12d); and $MNND_{muskox}$ = -0.0(sample size) + 0.5, R^2 = 0.7 (Figure 3.13d). Consequently, MNND is not useful for making inferences about the density of caribou and muskox isotopic compositions in δ-space across time.

All variables being equal, convex hull area (CHA), carbon isotope range (CR), and nitrogen isotope range (NR) should have positive linear relationships with sample size, again because these metrics can only increase or remain the same, but not decrease, with sample size (Jackson et al. 2011). Likewise, distance-to-centroid (CD) should decrease, then plateau, with the addition of more data (Anderson and Santana-Garcon 2015). Caribou CR is weakly negatively correlated, and caribou NR is moderately-to-strongly negatively correlated with sample size (Figure 3.12a, b). Only caribou CHA has a positive correlation with sample size, but this correlation is weak (Figure 3.12f). Conversely, for the muskox dataset, CHA, CR, and NR all have non-significant correlations with sample size, as expected (Figure 3.13). In short, Layman metrics suggests that there are variations in caribou, but not necessarily muskox, isotopic niche over time that are strong enough to escape sample size dependence.

Caribou and muskox CHA values are both highest during the Early Thule period (CHA = 5.4‰^{2} and 4.1‰^{2}, respectively) (Table 3.7), and the sample sizes for both species during this period are neither the largest nor the smallest of all datasets (n = 9 and 20, respectively). This suggests that some significant change in isotopic niche width, independent of sample

size, occurred during this period. Caribou CR gradually increases over time until the Early Thule period, then gradually returns to Pre-Dorset levels during the Inuit and modern periods. Muskox CR remains between 1.0‰ and 1.5‰ across time except during the Classic Thule period, when it decreases to 0.6‰, but this is probably an artifact of small sample size.

Nitrogen range metrics are more equivocal: caribou NR exhibits no clear pattern except that it is highest during the Lagoon and Early Thule periods (3.3‰ and 3.3‰, respectively), and nearly as high (2.9‰) during the Inuit period. Muskox NR increases to 4.7‰ during the Early Thule period, but this NR value is skewed by a single sample with a $\delta^{15}N_{bc}$ of +6.7‰. If this sample is omitted, Early Thule NR decreases to 3.0‰[16], which is in line with the NR values of all other periods except the Classic Thule and modern periods. The pattern of caribou NR over time mimics the pattern of muskox CR over time. Caribou CD increases from 0.6‰^{2} in the Pre-Dorset period, to 1.4‰^{2} in the Early Thule period, then returns to Pre-Dorset levels during the Classic Thule period and remains near this value up to the present. Muskox CD follows the same pattern, although the variations in CD are much smaller across time periods than they are for caribou.

As presented in Table 3.6, increasing the number of posterior draws from 10^4 to 10^5 or 10^6 changes SEA_B estimates shown in Figure 3.11 very little, if at all, even at very small sample sizes (e.g. Lagoon period caribou and Classic Thule period muskoxen). We therefore refer to SEA_B estimates utilizing 10^4 posterior draws in the following sections.

The degree of similarity in caribou and muskox SEA_B estimates is given by $SEA_{B(C>M)}$, which is calculated in this case by comparing the proportion of SEA_B estimates for caribou that are greater than those of muskoxen (Jackson 2017). $SEA_{B(C>M)}$ values closer to 0 or 1 indicate greater dissimilarity in ellipse areas, while an $SEA_{B(C>M)}$ value of 0.5 indicates complete similarity (Szpak et al. 2014:120; Jackson 2017). Table 3.6 demonstrates that

[16]The inclusion or exclusion of this same data point does not significantly change the size or position of the Early Thule muskox ellipse, or its degree of overlap with the Early Thule caribou ellipse. For this reason, it is included in ellipse estimations.

$SEA_{B(C>M)}$ values in all periods are closer to 0 or 1 than to 0.5, which suggests that Bayesian-estimated caribou and muskox isotopic niche areas are different from one another throughout time.

Sample size notwithstanding, there are significant intra-specific variations in SEA_B values, which should be the most conservative estimate of fundamental isotopic niche area, across cultural periods (Table 3.6). Muskox SEA_B doubles from 0.7‰^{2} during the Pre-Dorset to 1.6‰^{2} during the Lagoon period, and remains above 1.0‰^{2} until the modern period. Similarly, caribou SEA_B values double from 1.1‰^{2} during the Pre-Dorset to 2.4‰^{2} during the Lagoon period and 2.7‰^{2} during the Early Thule period. Caribou SEA_B values then decrease to near-Pre-Dorset levels during the Classic Thule period and remain low until present.

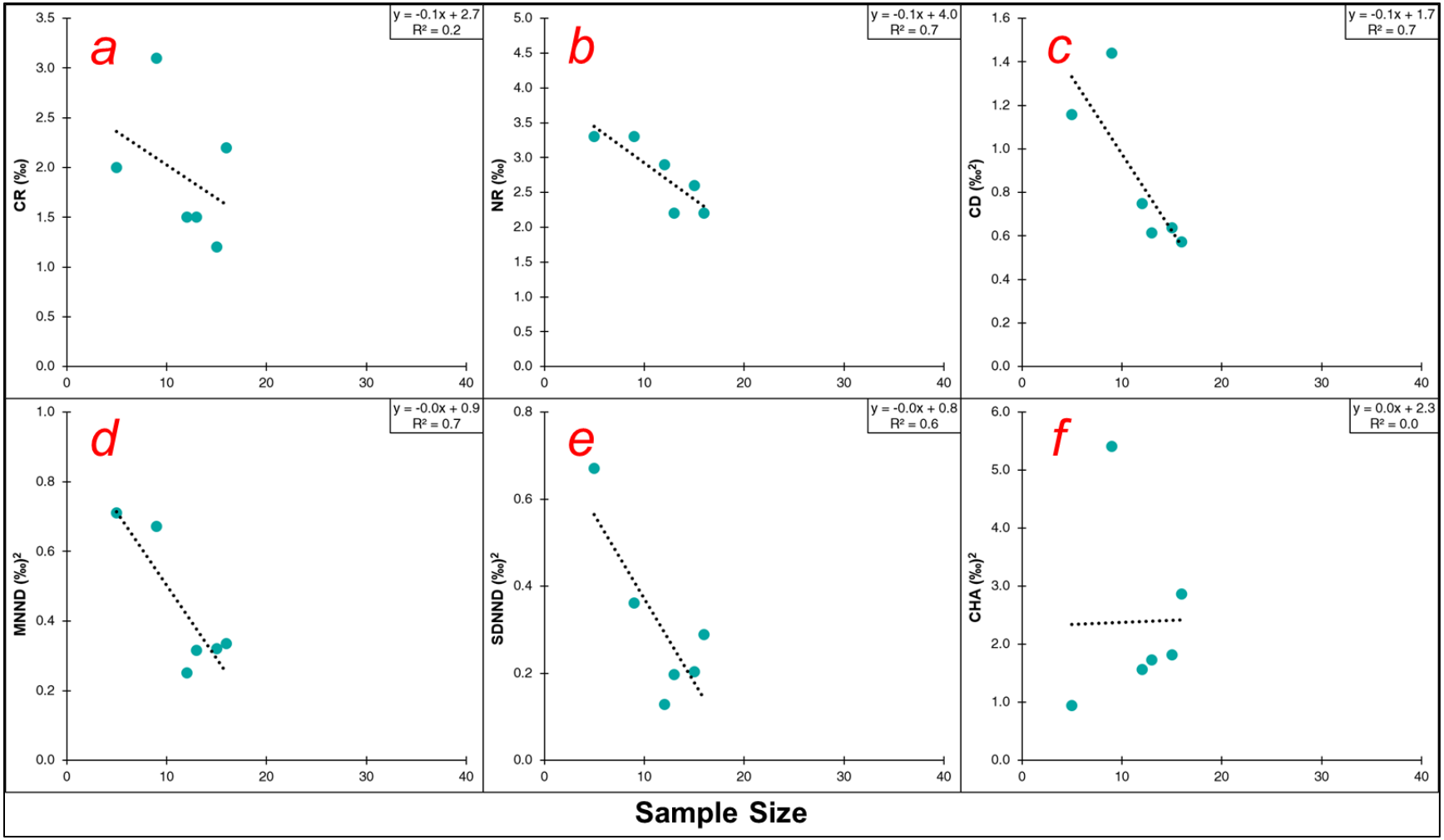


Figure 3.12. Layman metrics for caribou bone collagen plotted against sample size. **(*a*)** carbon range; **(*b*)** nitrogen range; **(*c*)** distance to centroid; **(*d*)** mean nearest neighbor distance; **(*e*)** standard deviation of nearest neighbor distance; **(*f*)** convex hull area.

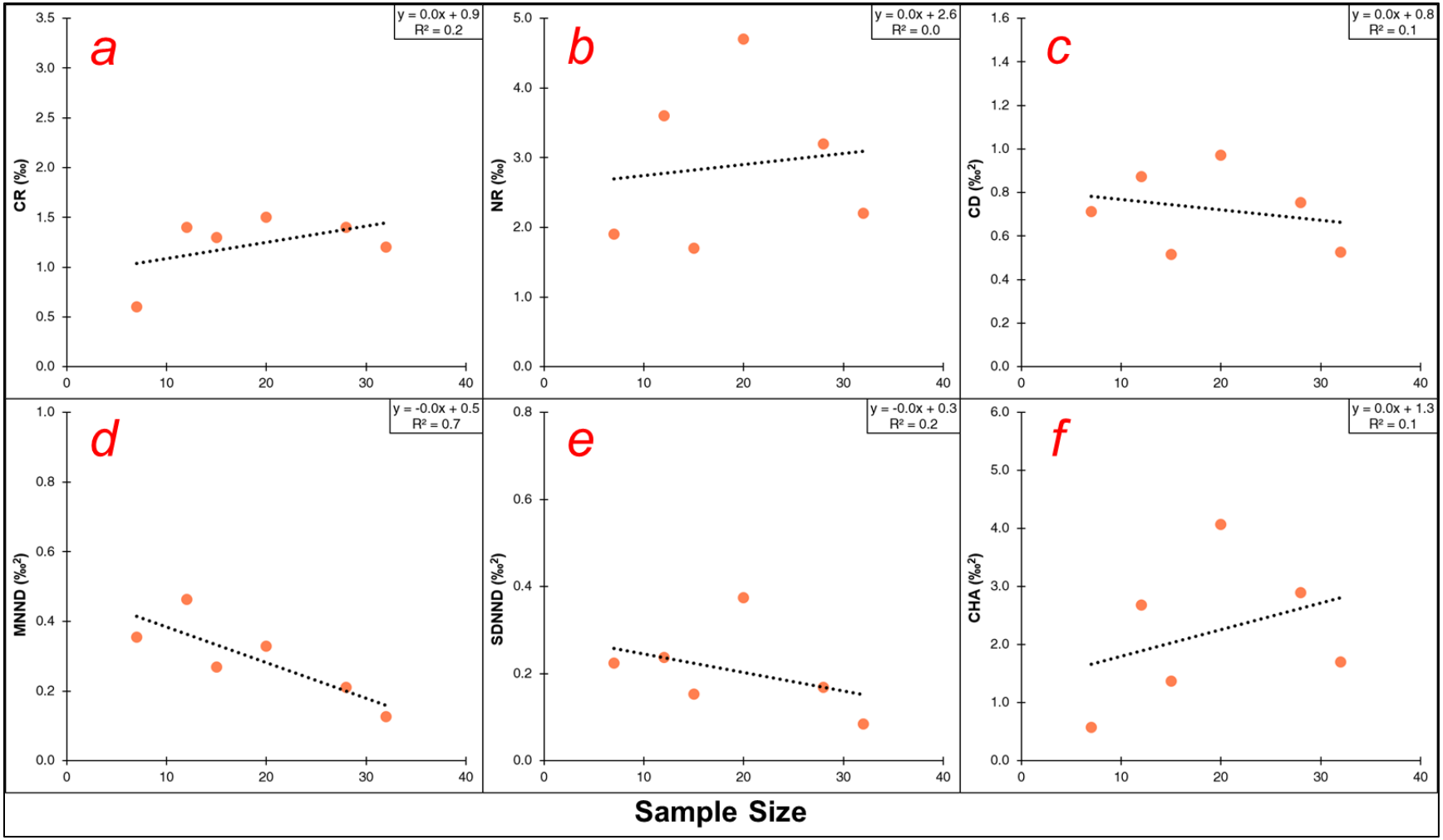


Figure 3.13. Layman metrics for muskox bone collagen plotted against sample size. **(*a*)** carbon range; **(*b*)** nitrogen range; **(*c*)** distance to centroid; **(*d*)** mean nearest neighbor distance; **(*e*)** standard deviation of nearest neighbor distance; **(*f*)** convex hull area.

3.4.4 Overlap in Caribou and Muskox Ellipses Across Cultural Periods

The area of overlap in non-transposed caribou and muskox SEA_c ellipses (in ‰^{2}) is given by $SEA_{c(O)}$ in Table 3.6. A more intuitive metric for our purposes, however, is the percentage of ellipse overlap, which we call $\%SEA_{c(O)}$. As an example, it is clear in Figure 3.9 that there is total separation of caribou and muskox SEA_c ellipses in δ-space during the Pre-Dorset, Classic Thule, and Inuit periods, while there is significant overlap during the Early Thule period. The area of overlap in Early Thule SEA_c ellipses is 1.05‰^{2}, which is not especially informative, but Table 3.6 demonstrates that in the Early Thule period, the muskox SEA_c ellipse overlaps 30% of the caribou SEA_c ellipse, while the caribou SEA_c ellipse overlaps 66% of the muskox SEA_c ellipse. Based on Schoener's (1968) criterion for dietary overlap, Matley et al. (2017) consider ellipse overlap greater than 60% to be significant. The proximity of the SEA_c ellipses during the Lagoon period, in addition to the small caribou sample size, suggests that with additional data, isotopic overlap during this period is likely. Although we establish in the section above that CHA is not a reliable metric of fundamental isotopic niche, even with the bias toward outlying isotopic compositions, overlap in convex hulls ($CHA_{(o)}$) (Table 3.7) only occurs in the Early Thule and modern datasets.

When the different carbon and nitrogen TDFs for caribou and muskoxen are applied, the relative positions of their SEA_c ellipses change dramatically. Transposed $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ and associated convex hulls and ellipses are presented in Figure 3.10. $SEA_{c(O)}$ and $\%SEA_{c(O)}$ values for transposed isotopic data are also presented in Table 3.6. When transposed, only the $\%SEA_{c(O)}$ values for Pre-Dorset period is significant (66% of the muskox ellipse is overlapped by the caribou ellipse), while there is only minor ellipse overlap during the Early Thule, Classic Thule, and Inuit periods. As we argue in our discussion, transposed $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ and associated convex hulls and ellipses presented in Figure 3.10 are likely more useful for making interpretations about ecological niche overlap.

3.4.5 Dentin Collagen $\delta^{13}C$ and $\delta^{15}N$ Results

Modern and archaeological dentin collagen samples were analyzed together in two analytical sessions. Again, an internal keratin standard (MP Biomedicals Inc., Cat No. 90211, Lot No. 9966H), and an international standard (IAEA-CH-6) were used to measure instrument analytical drift throughout the analytical sessions. Across 29 analyses of the internal keratin standard (accepted $\delta^{13}C$ and $\delta^{15}N$ = –24.04‰ and +6.36‰, respectively) $\delta^{13}C$ was –24.03±0.3‰ and $\delta^{15}N$ was 6.37±0.1‰. Across eight analyses of IAEA-CH-6 (accepted $\delta^{13}C$ = –10.45‰; Hut 1987), $\delta^{13}C$ was –10.88±0.4‰. The standard deviation of archaeological dentin collagen samples analyzed as instrumental duplicates (n = 6) is $\delta^{13}C$ = ±0.2‰, $\delta^{15}N$ = ±0.4‰, C% = ±0.3, and N% = ±0.2. The standard deviation of dentin collagen samples analyzed as method duplicates (n = 4) is $\delta^{13}C$ = ±0.0‰, $\delta^{15}N$ = ±0.7‰, C% = ±1.1, and N% = ±0.4.

Percent collagen content for archaeological dentin averages 12.5% (min = 5.2%; max = 18.9%), with no significant differences across time periods. As in Chapter 2, we attribute the generally low and variable collagen percentages in microbulk dentin samples to the presence of epoxy and enamel in the dentin samples when they were initially weighed. All residual epoxy and enamel was subsequently removed during the demineralization process. Calculated percent carbon (C%) and nitrogen (N%) in archaeological dentin samples averages 44.2% (min = 38.1%, max = 46.2%) and 16.0% (min = 13.6%, max = 17.1%), respectively. Atomic C:N ratios average 3.2 (min = 3.1; max = 3.3), indicating that archaeological microbulk dentin samples and their original isotopic compositions are probably well-preserved.

The carbon and nitrogen isotope compositions of sequential microbulk dentin collagen samples from caribou tooth crowns are presented in Figures 3.14 and 3.15, respectively and Table 3.3. The carbon and nitrogen isotope compositions of sequential microbulk dentin collagen samples from muskox M1 tooth crowns are presented in Figures 3.16 and 3.17, respectively, and Table 3.4. As with non-transposed bone collagen, modern $\delta^{13}C_{dc}$ is corrected by +1.7‰ for comparability to archaeological samples. Sequential microbulk dentin sample numbers follow the major axis of crown development. Where dentin was sampled from multiple tooth crowns in a single individual, dentin collagen isotopic

compositions are arranged in order of gross tooth development (e.g. dp4, M1, M2, M3, P4). Intra-tooth isotopic patterns, however, are not necessarily continuous between teeth because of developmental overlap and occlusal wear. Teeth that were too small or too-worn occlusally to obtain a sequence of microbulk dentin samples are designated "bulk". As in Chapter 2, we note that the "true" isotopic signals recorded in dentin collagen, especially in caribou teeth, are likely attenuated by our dentin sampling technique.

In caribou, the average of all $\delta^{13}C_{dc}$ across the Classic Thule, Inuit, and modern cultural periods is –19.2‰ (min = –20.2‰, max = –18.0‰) and the mean of all $\delta^{15}N_{dc}$ across cultural periods is +5.4‰ (min = +4.0‰, max = +6.4‰). Because of the small size of caribou teeth, we were mostly limited to bulk dentin sampling, and caribou dentin collagen samples are therefore uninformative of seasonal variation in $\delta^{13}C$ or $\delta^{15}N$. Where we sampled multiple teeth from the same individual, inter-tooth $\delta^{13}C_{dc}$ shows some minor variation. In BIBS16-19, mean inter-tooth $\delta^{13}C_{dc}$ gradually decreases across the dp4, M1, and M2 (Figure 3.14a). In BIBS14-214, mean inter-tooth $\delta^{13}C_{dc}$ increases between the dp4 and M1, and then decreases across the M1, M2, and M3 (Figure 3.14b). In BIBS14-298, mean inter-tooth $\delta^{13}C_{dc}$ increases across the M1, M2, and M3 (Figure 3.14c). Likewise, mean inter-tooth $\delta^{15}N_{dc}$ in BIBS16-19 is the same (+6.2‰) in the dp4 and M1, and then decreases slightly to +5.8‰ (Figure 3.15a). In BIBS14-214, mean inter-tooth $\delta^{15}N_{dc}$ increases between the dp4 and M1, decreases between the M1 and M2, and then remains the same between the M2 and M3 (Figure 3.15b). In BIBS14-298, inter-tooth $\delta^{15}N_{dc}$ decreases from +5.7 to +4.4‰ across the M1, M2 and M3 (Figure 3.15c).

As we establish in Chapter 2, the spacing or offset between dentin and bulk bone collagen $\delta^{13}C$ and $\delta^{15}N$ ($\Delta^{13}C_{dc\text{-}bc}$ and $\Delta^{15}N_{dc\text{-}bc}$, respectively) is useful for making inferences about the duration of nursing. As we argue in that chapter, tooth-averaged $\delta^{13}C_{dc}$ and $\delta^{15}N_{dc}$ should reflect average dietary inputs during the period when the tooth developed, while bulk bone collagen $\delta^{13}C$ and $\delta^{15}N$ reflect average dietary inputs over the last decade or so of life. Again, we expect, based on observational data and tooth eruption schedules that caribou and muskoxen both normally complete the weaning process within the first-year *post-partum*. If this is the case, then enrichments in ^{13}C and ^{15}N associated with nursing, and their associated dentin collagen-bone collagen isotopic offsets, should be greatest in

the M1s of both species, and then decline rapidly across M2s and M3s. Where sampled, fourth deciduous premolars (dp4s), which develop during the *peripartum* period (Banfield 1954; Kelsall 1968; Miller 1974), should have carbon and nitrogen isotope compositions similar to M1s, depending on the duration of the weaning process.

Caribou $\Delta^{13}C_{dc\text{-}bc}$ and $\Delta^{15}N_{dc\text{-}bc}$ offsets are listed in Tables 3.8 and 3.9, respectively. M1s, which are our primary focus in caribou, all display positive $\Delta^{13}C_{dc\text{-}bc}$ and $\Delta^{15}N_{dc\text{-}bc}$ offsets that range between +0.1 and +0.7‰ for carbon, and +1.7 and +3.0‰ for nitrogen. Of the three caribou in which multiple teeth were sampled, BIBS16-19 and BIBS14-214 display the expected patterns of decreasing $\Delta^{13}C_{dc\text{-}bc}$ and $\Delta^{15}N_{dc\text{-}bc}$ across teeth. In BIBS14-298, the $\Delta^{13}C_{dc\text{-}bc}$ offset is negligible in the M1 and M2 (+0.1‰ and +0.2‰, respectively) but increases to 0.9‰ in the M3. Conversely, the $\Delta^{15}N_{dc\text{-}bc}$ in the M1 of BIBS14-298 is the highest for all teeth sampled (3.0‰) but decreases as we would expect in the M2 and M3.

In muskox tooth samples, the average of all $\delta^{13}C_{dc}$ across time periods is –21.0‰ (min = –22.1‰, max = –19.8‰) and the mean of all $\delta^{15}N_{dc}$ across time periods is +7.0‰ (min = +4.8‰, max = +8.0‰). Because muskox teeth are much larger than caribou teeth, it was possible to obtain at least four sequential dentin samples in all but two teeth, BIBS14-474 M1 and BIBS14-162 M1, where occlusal wear was considerable. The M1s of BIBS14-407, -409, -209, -456, -169, and -445 and BIBS16-30 all exhibit a similar skewed, sawtooth pattern in their intra-tooth $\delta^{13}C_{dc}$ (but do not necessarily have similar values of $\delta^{13}C_{dc}$). This pattern is best exemplified in the intra-tooth $\delta^{13}C_{dc}$ of BIBS14-445 M1 (Figure 3.16a). The two M1s in which this pattern is absent are BIBS14-162, which is a single bulk dentin sample, and BIBS14-474. Although BIBS14-474 M1 only produced three sequential samples, the pattern of intra-tooth $\delta^{13}C_{dc}$ is distinct. While intra-tooth variation in $\delta^{13}C_{dc}$ is no greater than 0.7‰ in all other teeth, there is a +1.4‰ difference in the $\delta^{13}C_{dc}$ of the first two sequential samples of BIBS14-474 (Figure 3.16c). In contrast, intra-tooth patterns in $\delta^{15}N_{dc}$ vary considerably between M1s, though again, in no case does intra-tooth variation in $\delta^{15}N_{dc}$ exceed 0.7‰ (Figure 3.17).

As in caribou teeth, there are $\Delta^{13}C_{dc\text{-}bc}$ and $\Delta^{15}N_{dc\text{-}bc}$ offsets in nearly every muskox tooth sampled (Tables 3.10 and 3.11, respectively). In M1s, $\Delta^{13}C_{dc\text{-}bc}$ is highest (+0.6‰ or

+0.7‰) in samples from during the Early Thule, Classic Thule, and modern periods, and are otherwise relatively small (0.0‰, +0.1‰, or +0.4‰). Conversely, $\Delta^{15}N_{dc\text{-}bc}$ offsets are highest in BIBS16-30 (+4.6‰), from the Early Thule period, and BIBS14-169 (+3.9‰) from the modern period. The lowest $\Delta^{15}N_{dc\text{-}bc}$ (+1.8‰) is measured for BIBS14-474, from the Classic Thule period, and all other M1s have $\Delta^{15}N_{dc\text{-}bc}$ offsets between +2.5 and +3.2‰.

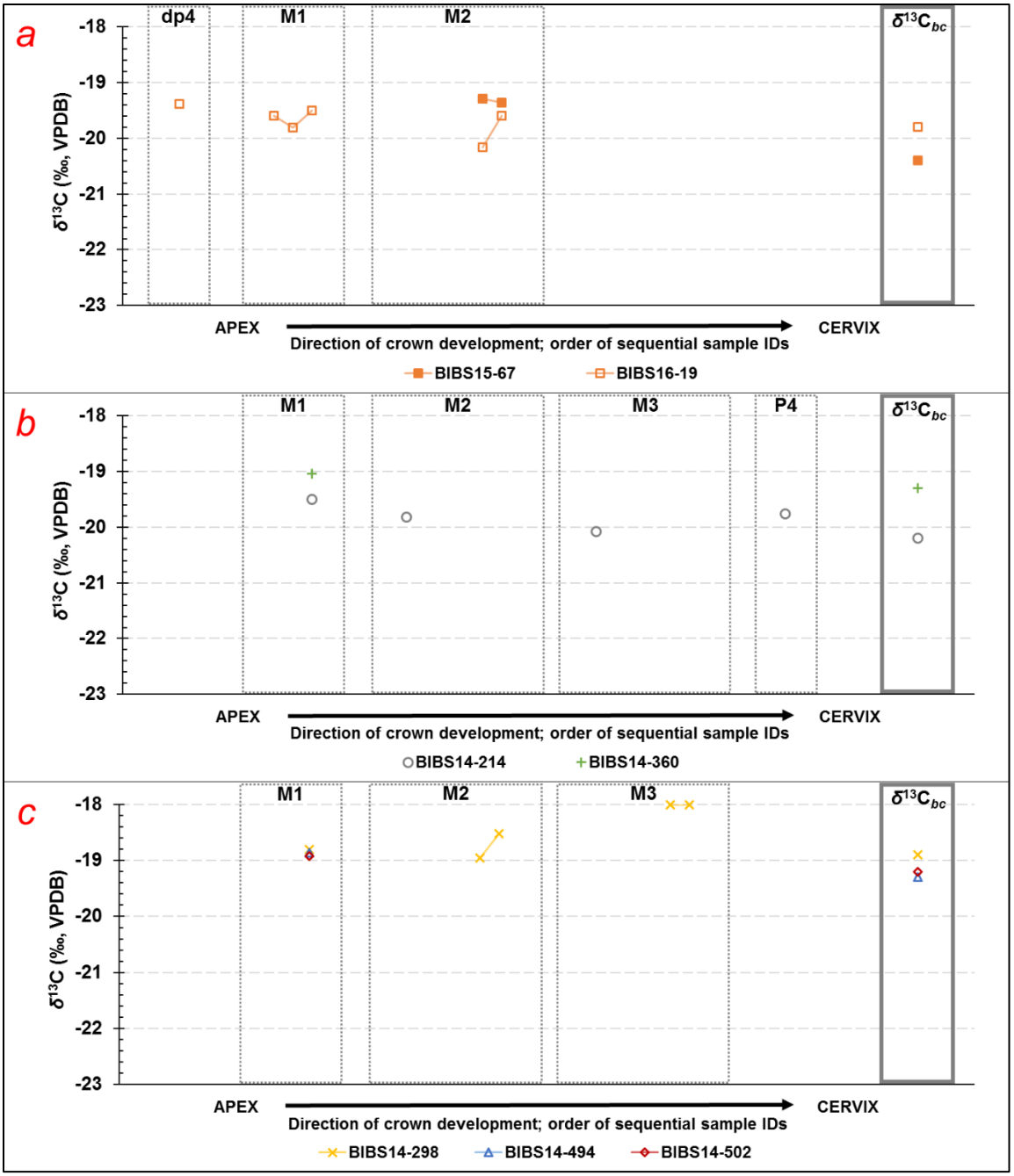


Figure 3.14. The $\delta^{13}C_{dc}$ of caribou tooth crowns from the: **(*a*)** modern period; **(*b*)** Inuit period; and **(*c*)** Classic Thule period. Data are displayed in approximate order of tooth development (dp4, M1, M2, M3, P4). The last sequential sample of each tooth is always taken from the ~ 5 mm of dentin closest to the root-enamel junction (REJ). The bulk bone collagen $\delta^{13}C$ of each caribou from which dentin is sampled is illustrated in the gray box at the far right. Modern dentin collagen carbon isotope compositions have been corrected by +1.7‰ for comparability with archaeological data.

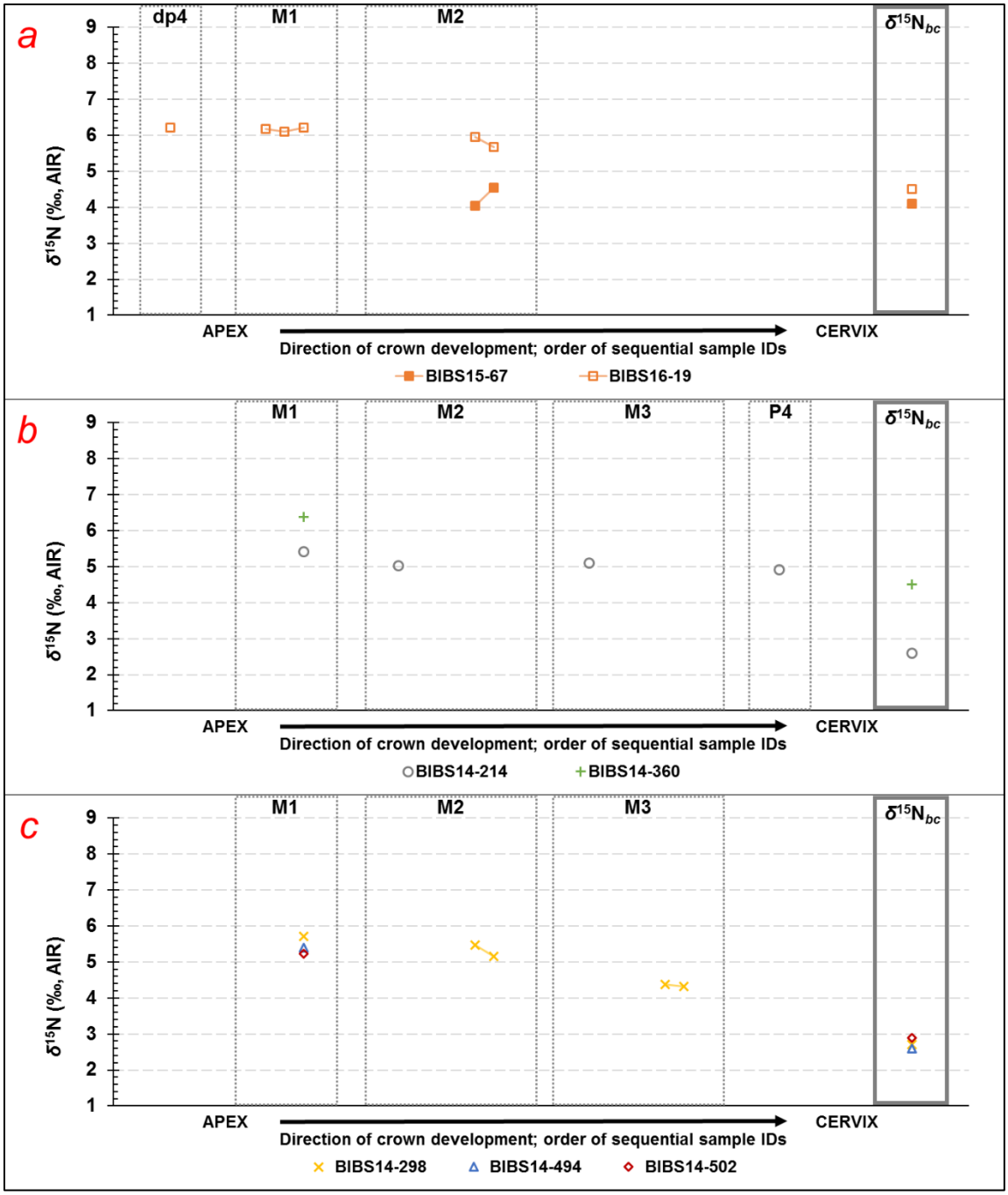


Figure 3.15. The $\delta^{15}N_{dc}$ of caribou tooth crowns from the: **(*a*)** modern period; **(*b*)** Inuit period; and **(*c*)** Classic Thule period. Data are displayed in approximate order of tooth development (dp4, M1, M2, M3, P4). The last sequential sample of each tooth is always taken from the ~ 5 mm of dentin closest to the root-enamel junction (REJ). The bulk bone collagen $\delta^{15}N$ of each caribou from which dentin collagen is sampled is illustrated in gray box at the far right.

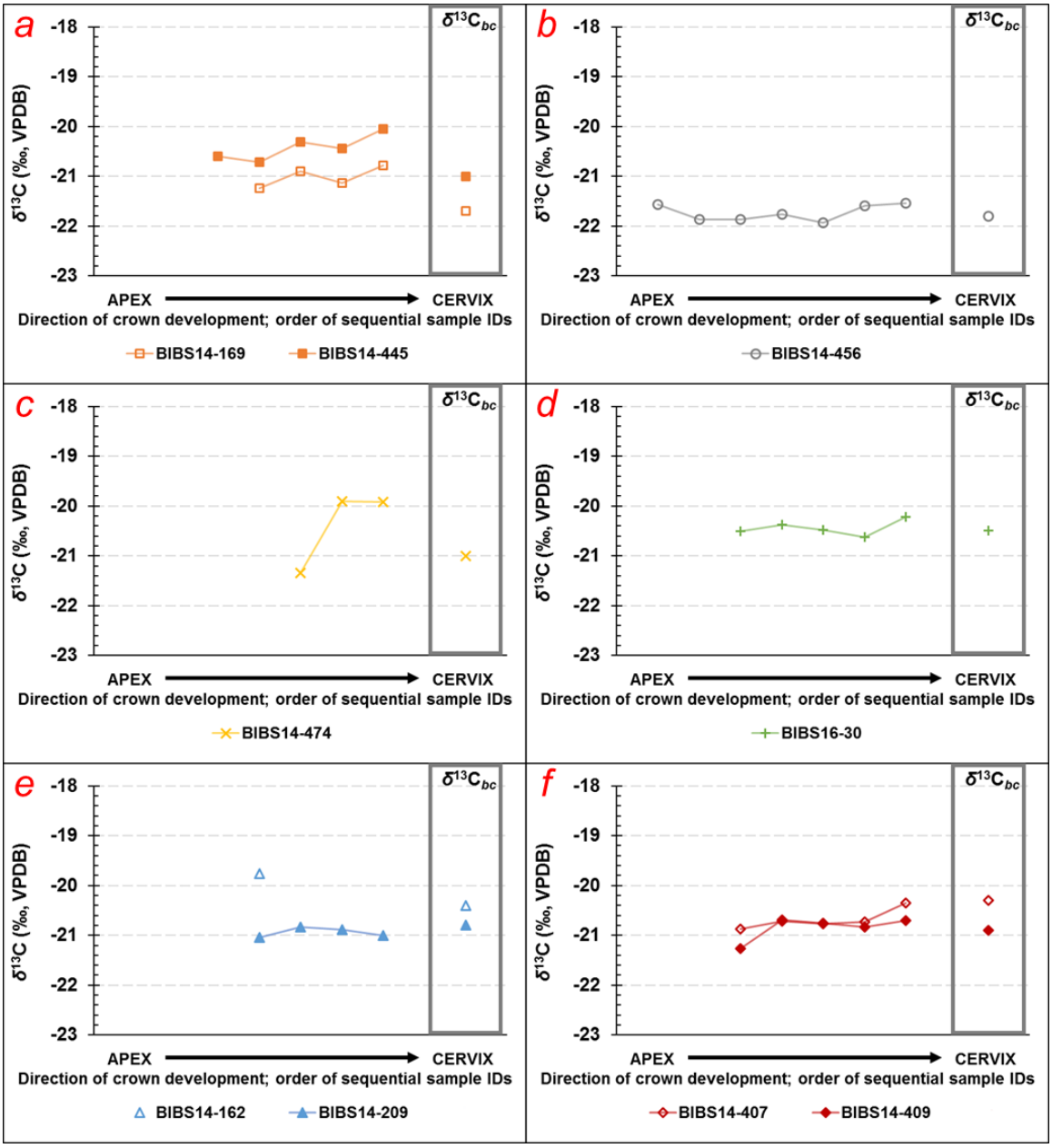


Figure 3.16. The $\delta^{13}C_{dc}$ of muskox tooth crowns from the: **(*a*)** modern period; **(*b*)** Inuit period; **(*c*)** Classic Thule period; **(*d*)** Early Thule period; **(*e*)** Lagoon Period; and **(*f*)** the Pre-Dorset period. The last sequential sample of each tooth is always taken from the ~ 5 mm of dentin closest to the root-enamel junction (REJ). The bulk bone collagen $\delta^{13}C$ of each muskox from which dentin is sampled is illustrated in the gray box at the far right. Modern dentin collagen carbon isotope compositions have been corrected by +1.7 for comparability with archaeological data.

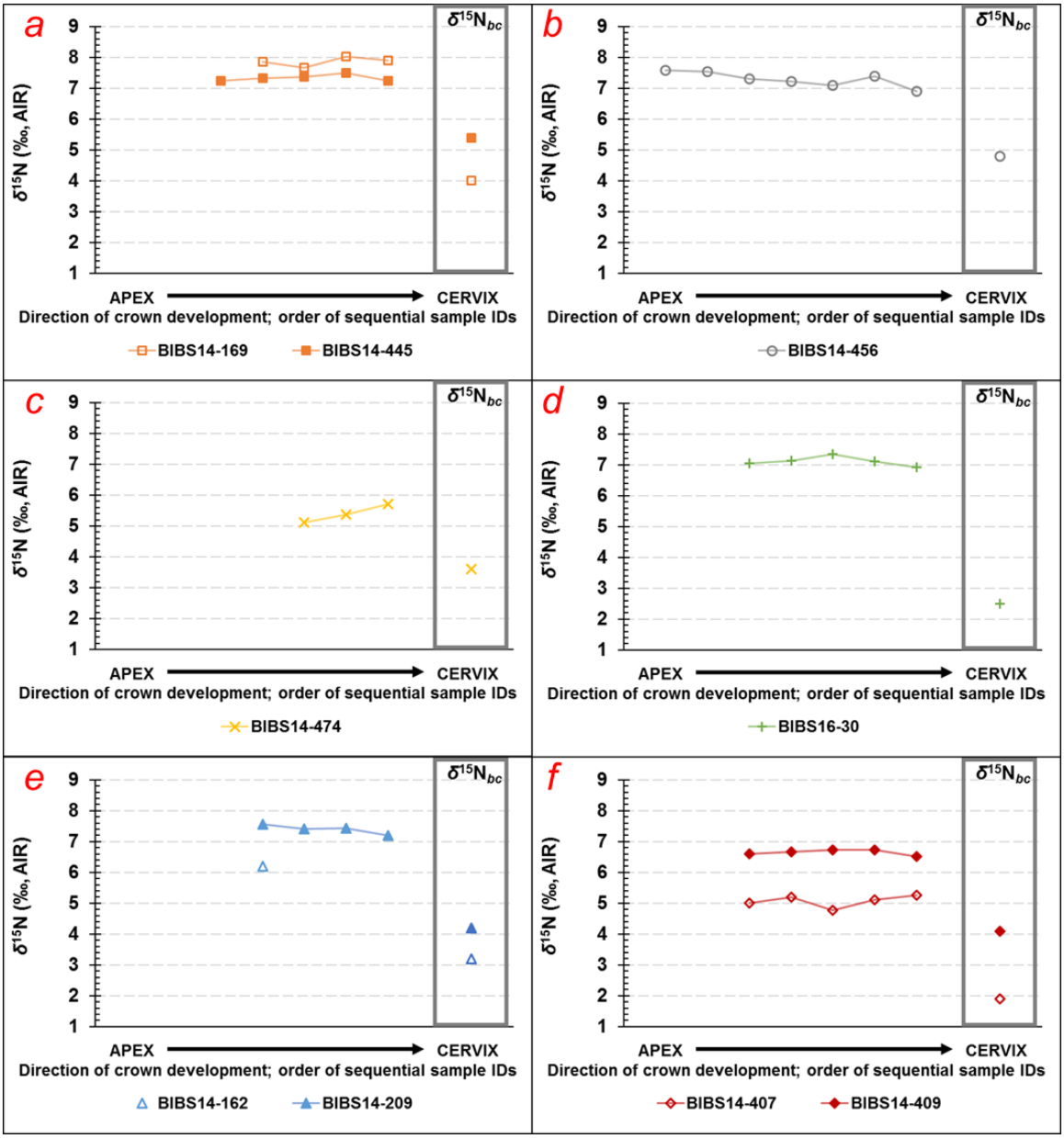


Figure 3.17. The $\delta^{15}N_{dc}$ of muskox tooth crowns from the: **(*a*)** modern period; **(*b*)** Inuit period; **(*c*)** Classic Thule period; **(*d*)** Early Thule period; **(*e*)** Lagoon Period; and **(*f*)** the Pre-Dorset period. The last sequential sample of each tooth is always taken from the ~ 5 mm of dentin closest to the root-enamel junction (REJ). The bulk bone collagen $\delta^{15}N$ of each caribou from which dentin collagen is sampled is illustrated in the gray box at the far right.

Table 3.8. Summary data for caribou dentin collagen $\delta^{13}C$, and dentin collagen-bone collagen $\delta^{13}C$ offsets. All modern carbon isotope compositions are adjusted by +1.7‰ for comparability with archaeological collagen data.

Sample ID	Taxon	Microbulk Sample	$\delta^{13}C_{dc}$ (‰, VPDB)	Intra-tooth Average $\delta^{13}C_{dc}$ (‰, VPDB)	$\delta^{13}C_{bc}$ (‰, VPDB)	$\Delta^{13}C_{dc\text{-}bc}$				
						dp4	M1	M2	M3	P4
Classic Thule										
BIBS14-298 M1	Caribou	BULK	–18.8	–18.8			+0.1			
BIBS14-298 M2	Caribou	DC1	–19.0	–18.7	–18.9			+0.2		
		DC2	–18.5							
BIBS14-298 M3	Caribou	DC1	–18.0	–18.0					+0.9	
		DC2	–18.0							
BIBS14-494 M1	Caribou	BULK	–18.9	–18.9	–19.3		+0.4			
BIBS14-502 M1	Caribou	BULK	–18.9	–18.9	–19.2		+0.3			
Inuit										
BIBS14-214 M1	Caribou	BULK	–19.5	–19.5			+0.7			
BIBS14-214 M2	Caribou	BULK	–19.8	–19.8	–20.2			+0.4		
BIBS14-214 M3	Caribou	BULK	–20.1	–20.1					+0.1	
BIBS14-214 P4	Caribou	BULK	–19.8	–19.8						+0.4
BIBS14-360 M1	Caribou	BULK	–19.0	–19.0	–19.3		+0.3			

Modern							
BIBS15-67 M2	Caribou	DC1 DC2	–19.3 –19.4	–19.3	–20.4		+1.1
BIBS16-19 dp4	Caribou	BULK	–19.4	–19.4		+0.4	
BIBS16-19 M1	Caribou	DC1 DC2 DC3	–19.6 –19.8 –19.5	–19.6	–19.8	+0.2	
BIBS16-19 M2	Caribou	DC1 DC2	–20.2 –19.6	–19.9			+0.1

Table 3.9. Summary data for caribou dentin collagen $\delta^{15}N$, and dentin collagen-bone collagen $\delta^{15}N$ offsets.

Sample ID	Taxon	Microbulk Sample	$\delta^{15}N_{dc}$ (‰, AIR)	Intra-tooth Average $\delta^{15}N_{dc}$ (‰, AIR)	$\delta^{15}N_{bc}$ (‰, AIR)	$\Delta^{15}N_{dc\text{-}bc}$ dp4	M1	M2	M3	P4
Classic Thule										
BIBS14-298 M1	Caribou	BULK	+5.7	+5.7			+3.0			
BIBS14-298 M2	Caribou	DC1	+5.5	+5.3	+2.7			+2.6		
		DC2	+5.1							
BIBS14-298 M3	Caribou	DC1	+4.4	+4.3					+1.6	
		DC2	+4.3							
BIBS14-494 M1	Caribou	BULK	+5.4	+5.4	+2.6		+2.8			
BIBS14-502 M1	Caribou	BULK	+5.2	+5.2	+2.9		+2.3			
Inuit										
BIBS14-214 M1	Caribou	BULK	+5.4	+5.4	+2.6		+2.8			
BIBS14-214 M2	Caribou	BULK	+5.0	+5.0				+2.4		
BIBS14-214 M3	Caribou	BULK	+5.1	+5.1					+2.5	
BIBS14-214 P4	Caribou	BULK	+4.9	+4.9						+2.3
BIBS14-360 M1	Caribou	BULK	+6.4	+6.4	+4.5		+1.9			

Modern							
BIBS15-67 M2	Caribou	DC1 DC2	+4.0 +4.5	+4.3	+4.1		+0.2
BIBS16-19 dp4	Caribou	BULK	+6.2	+6.2		+1.7	
BIBS16-19 M1	Caribou	DC1 DC2 DC3	+6.2 +6.1 +6.2	+6.2	+4.5	+1.7	
BIBS16-19 M2	Caribou	DC1 DC2	+6.0 +5.7	+5.8			+1.3

Table 3.10. Summary data for muskox dentin collagen $\delta^{13}C$, and dentin collagen-bone collagen $\delta^{13}C$ offsets. All modern carbon isotope compositions are adjusted by +1.7‰ for comparability with archaeological collagen data.

Sample ID	Taxon	Microbulk Sample	$\delta^{13}C_{dc}$ (‰, VPDB)	Intra-tooth Average $\delta^{13}C_{dc}$ (‰, VPDB)	$\delta^{13}C_{bc}$ (‰, VPDB)	$\Delta^{13}C_{dc\text{-}bc}$ M1
Pre-Dorset						
BIBS14-407 M1	Muskox	DC1	–20.9	–20.7	–20.3	+0.4
		DC2	–20.7			
		DC3	–20.8			
		DC4	–20.7			
		DC5	–20.4			
BIBS14-409 M1	Muskox	DC1	–21.3	–20.9	–20.9	0.0
		DC2	–20.7			
		DC3	–20.8			
		DC4	–20.8			
		DC5	–20.7			
Lagoon						
BIBS14-162 M1	Muskox	BULK	–19.8	–19.8	–20.4	+0.6
BIBS14-209 M1	Muskox	DC1	–21.0	–20.9	–20.8	+0.1
		DC2	–20.8			
		DC3	–20.9			
		DC4	–21.0			
Early Thule						
BIBS16-30 M1	Muskox	DC1	–20.5	–20.4	–20.5	+0.1
		DC2	–20.4			
		DC3	–20.5			
		DC4	–20.6			
		DC5	–20.2			
Classic Thule						
BIBS14-474 M1	Muskox	DC1	–21.3	–20.4	–21.0	+0.6
		DC2	–19.9			
		DC3	–19.9			

Inuit						
BIBS14-456 M1	Muskox	DC1	–21.6	–21.7	–21.8	+0.1
		DC2	–21.9			
		DC3	–21.9			
		DC4	–21.8			
		DC5	–21.9			
		DC6	–21.6			
		DC7	–21.5			
Modern						
BIBS14-169 M1	Muskox	DC1	–21.2	–21.0	–21.7	+0.7
		DC2	–20.9			
		DC3	–21.1			
		DC4	–20.8			
BIBS14-445 M1	Muskox	DC1	–20.6	–20.4	–21.0	+0.6
		DC2	–20.7			
		DC3	–20.3			
		DC4	–20.4			
		DC5	–20.0			

Table 3.11. Summary data for muskox dentin collagen $\delta^{15}N$, and dentin collagen-bone collagen $\delta^{15}N$ offsets.

Sample ID	Taxon	Microbulk Sample	$\delta^{15}N_{dc}$ (‰, AIR)	Intra-tooth Average $\delta^{15}N_{dc}$ (‰, AIR)	$\delta^{15}N_{bc}$ (‰, AIR)	$\Delta^{15}N_{dc\text{-}bc}$ M1
Pre-Dorset						
BIBS14-407 M1	Muskox	DC1	+5.0	+5.1	+1.9	+3.2
		DC2	+5.2			
		DC3	+4.8			
		DC4	+5.1			
		DC5	+5.3			
BIBS14-409 M1	Muskox	DC1	+6.6	+6.6	+4.1	+2.5
		DC2	+6.7			
		DC3	+6.7			
		DC4	+6.7			
		DC5	+6.5			
Lagoon						
BIBS14-162 M1	Muskox	BULK	+6.2	+6.2	+3.2	+3.0
BIBS14-209 M1	Muskox	DC1	+7.6	+7.4	+4.2	+3.2
		DC2	+7.4			
		DC3	+7.4			
		DC4	+7.2			
Early Thule						
BIBS16-30 M1	Muskox	DC1	+7.0	+7.1	+2.5	+4.6
		DC2	+7.1			
		DC3	+7.3			
		DC4	+7.1			
		DC5	+6.9			
Classic Thule						
BIBS14-474 M1	Muskox	DC1	+5.1	+5.4	+3.6	+1.8
		DC2	+5.4			
		DC3	+5.7			

Inuit						
BIBS14-456 M1	Muskox	DC1	+7.6	+7.3	+4.8	+2.5
		DC2	+7.5			
		DC3	+7.3			
		DC4	+7.2			
		DC5	+7.1			
		DC6	+7.4			
		DC7	+6.9			
Modern						
BIBS14-169 M1	Muskox	DC1	+7.9	+7.9	+4.0	+3.9
		DC2	+7.7			
		DC3	+8.0			
		DC4	+7.9			
BIBS14-445 M1	Muskox	DC1	+7.2	+7.3	+5.4	+1.9
		DC2	+7.3			
		DC3	+7.4			
		DC4	+7.5			
		DC5	+7.2			

3.4.6 Caribou versus Muskox Dentin Collagen $\delta^{13}C$ and $\delta^{15}N$

Because we were only able to obtain caribou teeth from Classic Thule and Inuit archaeological sites, we can only make comparisons between the $\delta^{13}C_{dc}$ and $\delta^{15}N_{dc}$ of caribou and muskoxen during these two periods. Additionally, because we were only able to sample bulk dentin from caribou teeth, we are limited to comparisons of tooth-averaged $\delta^{13}C_{dc}$ and $\delta^{15}N_{dc}$ between caribou and muskoxen. Although there is only a single muskox M1 from the Classic Thule period (BIBS14-474 M1), its tooth-averaged $\delta^{13}C_{dc}$ (–20.4‰) is ~ 1‰ lower than any of the tooth-averaged $\delta^{13}C_{dc}$ (~ –18.9‰) in the three caribou M1s from the Classic Thule period. A comparison of tooth-averaged $\delta^{15}N_{dc}$ between Classic Thule caribou (Table 3.9) and muskoxen (Table 3.11) demonstrates that the tooth-averaged $\delta^{15}N_{dc}$ of BIBS14-474 M1 (+5.4‰) is within the same range as the tooth-averaged $\delta^{15}N_{dc}$ from all three caribou. As we establish above, however, BIBS14-474 M1 appears to be an outlier in terms of its intra-tooth $\delta^{13}C_{dc}$ and $\delta^{15}N_{dc}$, and its bulk bone collagen $\delta^{15}N$ is one of the lowest of the Classic Thule muskoxen. In short, the differences between caribou and muskox dentin collagen isotopic compositions during the Classic Thule period mimic those of bone collagen isotopic compositions during the Classic Thule period (Figure 3.9d). The tooth-averaged $\delta^{13}C_{dc}$ from the single Inuit period muskox M1 (BIBS14-456 M1, –21.7‰) is ~ 2.5‰ lower than the tooth-averaged $\delta^{13}C_{dc}$ of the two caribou M1s from the Inuit period, while its tooth-averaged $\delta^{15}N_{dc}$ (+7.3‰) is about 2‰ higher. This pattern mimics that of non-transposed caribou and muskox bone collagen isotopic compositions during the Inuit period (Figure 3.9e).

3.5 Discussion

Metrics derived from bone collagen $\delta^{13}C$ and $\delta^{15}N$ indicate that the isotopic niches of caribou and muskoxen on Banks Island have varied considerably over the last 4000 years. The significance of this isotopic variation can be explored along two axes: niche dimensionality and niche proximity or overlap. Measures of niche dimensionality remain the same regardless of data transpositions and are themselves influenced by competition, while the niche proximity/overlap depends on parameters that are currently poorly-

constrained, like trophic discrimination factors and isotopic variability in forage sources over time.

3.5.1 Isotopic Niche Dimensionality Derived from $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$

SEA_B values (Table 3.6) suggest that caribou isotopic niche area tripled in size between the Pre-Dorset and Early Thule period, but decreased to Pre-Dorset levels during the Classic Thule period, and has remained at that low level into the present. Likewise, muskox SEA_B values nearly tripled between the Pre-Dorset and Early Thule periods. Unlike caribou SEA_B, which contracted rapidly to a small, stable value in the centuries following the Early Thule period, however, muskox SEA_B has only gradually decreased over the last several centuries. Although significantly influenced by sample size, CHA and CD values across cultural periods (Table 3.7) also point towards niche expansion in both species, followed by rapid niche contraction in caribou, and slower niche contraction in muskoxen.

Additionally, there are only weakly negative trends in caribou and muskox mean $\delta^{13}C_{bc}$ across cultural periods: $\delta^{13}C_{bc(caribou)} = -0.13(\text{cultural period}) - 19.3$, $R^2 = 0.3$; $\delta^{13}C_{bc(muskox)} = -0.07(\text{cultural period}) - 20.8$, $R^2 = 0.1$ (Figure 3.18). Conversely, there is a small but moderately-to-strongly significant positive trend in muskox, but not caribou, mean $\delta^{15}N_{bc}$ across cultural periods: $\delta^{15}N_{bc(caribou)} = 0.17(\text{cultural period}) + 2.8$, $R^2 = 0.2$; $\delta^{15}N_{bc(muskox)} = 0.31(\text{cultural period}) + 2.9$, $R^2 = 0.8$ (Figure 3.19). Taken together, the ellipse and Layman metrics suggest that: (1) caribou and muskoxen both experienced significant expansion of their isotopic niches on Banks Island during the Lagoon and Early Thule periods; (2) in both species, niche expansion in δ-space was largely along single, opposite axes; and (3) isotopic niche contraction after the Thule period occurred rapidly in caribou, but only gradually in muskoxen.

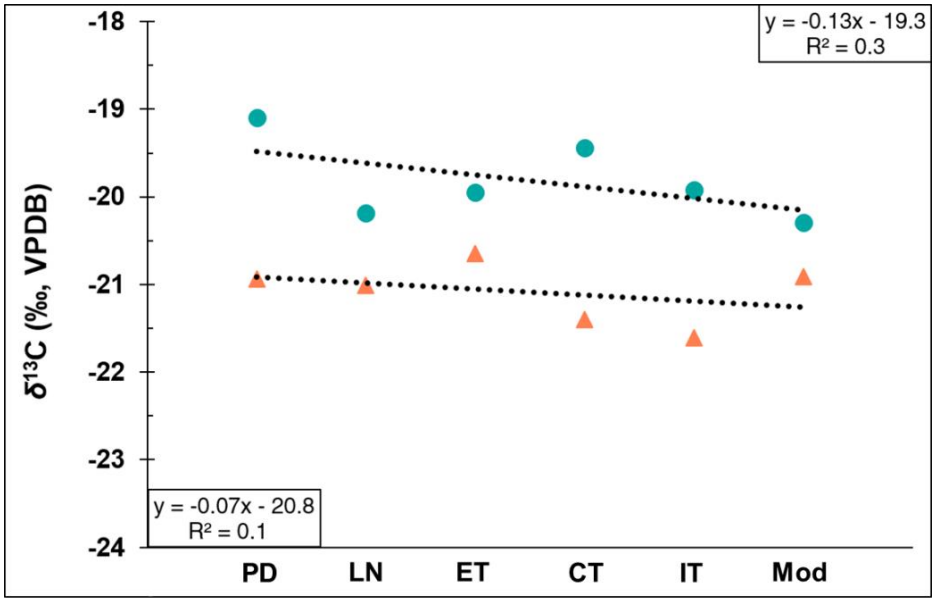


Figure 3.18. Mean $\delta^{13}C_{bc}$ for caribou (turquoise circles) and muskoxen (coral triangles) across cultural periods; linear regression equation and R^2 value for caribou mean $\delta^{13}C_{bc}$ values across time (top right corner), and linear regression equation and R^2 value for muskox mean $\delta^{13}C_{bc}$ across time (bottom left corner). "PD" = Pre-Dorset; "LN" = Lagoon; "ET" = Early Thule; "CT" = Classic Thule; "IT" = Inuit; "Mod" = modern.

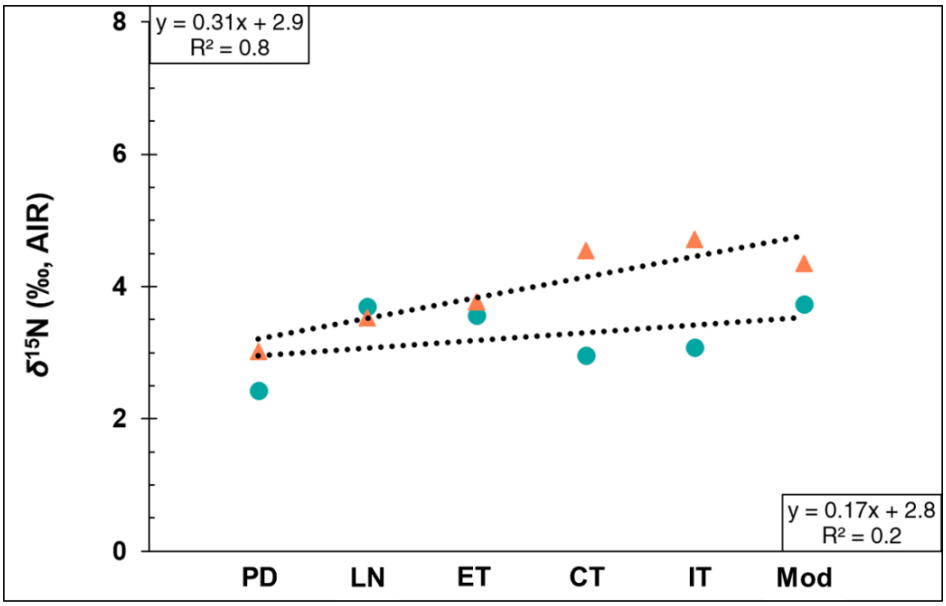


Figure 3.19. Mean $\delta^{15}N_{bc}$ for caribou (turquoise circles) and muskoxen (coral triangles) across cultural periods; linear regression equation and R^2 value for caribou mean $\delta^{15}N_{bc}$ values across time (bottom right corner), and linear regression equation and R^2 value for muskox mean $\delta^{15}N_{bc}$ across time (top left corner). "PD" = Pre-Dorset; "LN" = Lagoon; "ET" = Early Thule; "CT" = Classic Thule; "IT" = Inuit; "Mod" = modern.

3.5.2 Isotopic Niche Dimensionality and Models of Caribou and Muskox Niche Relationships

Evaluating only niche dimensionality, not relative niche position in δ-space, the classical framework of niche partitioning (Grinnell 1917; Gause 1936; Hutchinson 1957, 1978), would equate the small isotopic niche areas of Pre-Dorset caribou and muskoxen, given by their SEA_c and SEA_B values, with some degree of competitive niche specialization. Conversely, isotopic niche dimensionality during the Early Thule period – and with more data, probably the Lagoon period – suggests that radical changes occurred to the niche relationship between caribou and muskoxen. Again, the classical view of niche dimensionality suggests that a species' niche will expand as inter-specific competition decreases. Accordingly, the greater SEA_c and SEA_B values for caribou and muskoxen during the Lagoon and Early Thule periods would suggest that inter-specific forage competition was low, and the return to smaller isotopic niches areas in the Classic Thule, Inuit, and modern periods would indicate that competitive pressure to specialize resumed after the Early Thule period.

Within the ecological displacement model, variations in caribou and muskox isotopic niche dimensionality indicate a different pattern of potential competition across cultural periods. Again, within this framework, smaller niche area corresponds to lower intra-specific dietary variation, which in turn corresponds to decreased intra- or inter-specific dietary competition. Accordingly, small ellipse areas for Pre-Dorset caribou and muskoxen would suggest that niche competition between caribou and muskoxen during this cultural period was limited. The pattern of isotopic niche expansion during the Lagoon and Early Thule periods would also suggest that competitive niche diversification increased significantly during these two periods. The driving force for niche diversification could be either intra-specific or inter-specific forage competition, though at present, we have no independent methods for making inferences about past caribou and muskox population dynamics. Ancient DNA analysis of archaeological caribou and muskox bone samples used in this study (Rodrigues et al. forthcoming) will be useful for contextualizing this important aspect of caribou and muskox paleoecology on Banks Island. In any case, within the ecological

displacement model, a return to smaller isotopic niche areas in the Classic Thule, Inuit, and modern periods would equate with a decrease in forage competition.

3.5.3 Integrating Isotopic Niche Dimensionality and Proximity/Overlap to Evaluate Ecological Niche Models

With the assumption that Bayesian-derived TDFs are accurate, and that real TDFs varied only minimally across the last 4000 years, the transposition of $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ to quasi-IsoSpace should more accurately represent the actual spatial relationships of caribou and muskox isotopic niches than when presented in collagen δ-space. Accordingly, in this section, we evaluate niche dimensionality alongside niche proximity/overlap in quasi-IsoSpace, but not δ-space, in this section. We argue that caribou and muskox niche relationships conform to the expectations of the ecological displacement model until the Classic Thule period. During that period, changing forage conditions potentially altered the ecological relationship of caribou and muskoxen such that competitive specialization predicted by the Hutchinsonian niche framework developed.

The Pre-Dorset period on Banks Island occurred towards the end of the long, climatically-stable Holocene thermal maximum (HTM) (Figure 3.2b) (Overpeck et al. 1997; Fortin and Gajewski 2010; Peros 2010; Gajewski 2015b). In the Eastern Arctic, this period is characterized by high overall phytomass productivity and shrub/heath/forb-dominated tundra (Edlund 1986; Gajewski 1995; Gajewski et al. 2000; Gajewski 2015a). It is therefore reasonable to assume that forage conditions during this period were stable and likely optimal for both caribou and muskoxen. This assumption is supported by the large concentration of muskox and caribou skeletal remains at the Pre-Dorset Umingmak (PjRa-2) site on Banks Island (Müller-Beck 1977; Münzel 1987), and at ASTt sites spanning much of the Eastern Arctic during this time (Knuth 1967; Maxwell 1984, 1985; Bielawski 1988; Jensen 1998; Darwent 2004).

Radiocarbon dates (Figure 3.3, Table 3.1) demonstrate that the Pre-Dorset period on Banks Island lasted for at least 500 years, and so we might expect some climatic and ecological variability during these centuries. Because Pre-Dorset sites from which we sampled bone are relatively evenly-spaced across those 500 years, bone isotopic compositions should

index any significant ecological variability during the Pre-Dorset period. Instead, caribou and muskox isotopic niches from the Pre-Dorset period, measured by SEA_c and SEA_B values, are about as small as those from our modern dataset, which consists primarily of caribou and muskoxen harvested in a single year. In short, the intra-specific homogeneity of caribou and muskox $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ from the Pre-Dorset period strongly suggests a high degree of ecosystem and niche stability across the entire cultural period.

When considered inside a broader archaeological and paleoecological context, the classical framework of competition and niche partitioning cannot easily account for the small but considerably-overlapping SEA_c ellipses of Pre-Dorset caribou and muskoxen in quasi-IsoSpace (Figure 3.10a). The small isotopic niche areas for Pre-Dorset caribou and muskoxen, by themselves, would suggest greater inter-specific forage competition, but in the Hutchinsonian niche framework, the force driving sympatric species towards smaller niche areas is competitive specialization or exclusion (Grinnell 1917; Hardin 1960). Accordingly, niche segregation should always accompany small niche area, and this is clearly not the case when Pre-Dorset $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ are transposed to quasi-IsoSpace.

A possible explanation for the small but significantly overlapping isotopic niches of caribou and muskoxen during the Pre-Dorset period is that dietary overlap was offset by differences along other ecological niche axes. Pianka (1974) states that sympatric species avoid inter-specific dietary competition through any combination of three strategies: they use different forage, different activity intervals, and different foraging spaces. Relative to omnivores, carnivores, and herbivores in temperate regions, caribou and muskoxen on Banks Island are limited in their ability to diversify their diet while meeting seasonal metabolic and nutritional requirements. In addition, the isotopic data, when accounting for TDFs, suggest that the diets of Pre-Dorset caribou and muskoxen are nearly identical. Caribou and muskoxen also follow the same seasonal activity patterns, and there is no division of daily activity periods that might allow them to utilize the same range without competition, as in many other sympatric species (Kronfeld-Schor and Dayan 2003).

There is, however, evidence for an elevational partitioning of microhabitat between species, with caribou spending more time on hillsides and uplands, and muskoxen foraging

in lower wet sedge meadows and hummock tundra (Wilkinson and Shank 1975; Wilkinson et al. 1976; Ferguson 1991), though their ranges do overlap significantly. It is conceivable that the segregation of caribou and muskox micro- or macrohabitats during the Pre-Dorset period was great enough that, although they utilized the same forage sources, no inter-specific forage competition occurred. Caribou also travel more than muskoxen, and can therefore exploit forage resources across a greater area of the landscape than muskoxen. Additionally, the warm, stable climatic regime of the Pre-Dorset period probably permitted forage species on Banks Island to colonize greater portions of the landscape than in cooler periods. The differential use of landscape by caribou and muskoxen during the Pre-Dorset period is a testable hypothesis that would provide further insight into their unique niche relationship during this period. In Chapter 4, we explore the use of enamel oxygen isotope compositions from archaeological caribou and muskox teeth to reconstruct faunal movements on Banks Island across time. Our dataset, however, does not include any caribou teeth dated to the Pre-Dorset period, and we find in that chapter that tooth enamel $\delta^{18}O$ in both species is dominated by seasonal precipitation signals.

Contrary to the Hutchinsonian framework, an interpretation of Pre-Dorset isotopic niche based on the ecological displacement model is relatively straightforward. Because smaller niche areas are associated with less competition, the combination of small but significantly-overlapping ellipses during the Pre-Dorset period suggests that either the caribou and muskox populations were small enough that neither intra-specific nor inter-specific forage competition regulated niche size, or that preferred forage was so abundant that caribou and muskoxen could both maintain sizeable populations in a single ecological niche. The former explanation seems more likely since the carrying capacity of the tundra should increase with warmer temperatures and greater phytomass.

In Hutchinson's (1957, 1978) original conception, only a single species can occupy a fundamental ecological niche without competitive exclusion occurring (Soberón 2007). More recent work, however, suggests that species redundancy – that is, the existence of two species in the same niche, and which fulfill the same ecological functions – not only occurs in, but is an important aspect of some ecosystems (Lawton and Brown 1993; Naeem 1998; Rosenfeld 2002). Although it is possible that Pre-Dorset caribou and muskoxen

differed along other niche axes not indexed by $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ such as landscape use, the idea of species redundancy allows for the theoretical existence of multiples species in a single ecological niche. We argue that the warm, stable environmental conditions of the Pre-Dorset period permitted both caribou and muskoxen to persist in the same dietary – if not ecological – niche for the entirety of the Pre-Dorset period.

Larger but minimally-overlapping isotopic niches during the Lagoon and Early Thule periods (Figure 3.10b, c) closely follow the expectations for greater forage competition under the ecological displacement model. Because mean summer air temperatures in the Western Arctic were generally lower between ~ 3000 and ~ 1000 BP than today (Bradley 2000; Kaufman et al. 2004; Fortin and Gajewski 2010; Gajewski 2015b), overall phytomass productivity was depressed for much of the Lagoon phase. Dwarf willow (*Salix arctica*) appears to be an important spring and summer forage resource for modern caribou and muskoxen, although it either does not contribute largely to, or is not largely reflected in bulk bone collagen $\delta^{13}C$ and $\delta^{15}N$ (Chapter 2). Bayesian dietary mixing models in Chapter 2 also suggest that legumes (*Astragalus* spp., *Oxytropis* spp.) play a significant role in modern caribou diet on Banks Island. Neither dwarf willow nor legumes are cold-tolerant (Edlund 1986) and palynological evidence suggests that *Salix* productivity began declining in the Canadian Arctic between 3500 and 2500 years ago, and remained low until the 20th century (Gajewski 1995). Although dwarf birch (*Betula nana*) is poorly represented on Banks Island today (Edlund 1986; Dyke 2005), it is a staple of caribou and muskox diet elsewhere and palynological data also show that *Betula* pollen productivity on Banks Island was high until ~ 3000 years ago (Gajewski et al. 2000).

Bayesian dietary mixing models (Chapter 2) also suggest that yellow lichen (*Cetraria tilesii*) contributes significantly to modern caribou and muskox bone collagen isotopic compositions. We argue in Chapter 2 that *Cetraria* is an important source of carbohydrates and non-essential amino acids for both species during the winter. Assuming the $\delta^{13}C$ and $\delta^{15}N$ of lichens has remained the same across time, the pattern of high $\delta^{13}C_{bc}$ and low $\delta^{15}N_{bc}$ in Pre-Dorset caribou and muskoxen may also indicate that lichens were an important dietary resource during that period as well.

As cryptogams, lichens do not produce pollen, and so there are few direct indicators of lichen productivity in the Arctic prior to the late 20th century. It is possible that between the Pre-Dorset and Lagoon period, however, lichen phytomass was significantly reduced by the presence of multiyear snow cover. Several researchers (Locke and Locke 1977; Dyke 1978; Lévesque and Svoboda 1999) have posited that lichen-free zones in several Eastern Arctic locations are evidence that lichen phytomass was reduced by perpetual snowbanks during recent cold periods. Although lichens are more cold-tolerant than vascular plants, and can maintain photosynthetic and metabolic activity throughout the winter (Kappen 1993), they are slow-growing (Miller 1973; Henry and Gunn 1990; Klein 1987, 1992; Larter and Nagy 1997; Griller 2001; Joly et al. 2008). The dietary challenge presented to caribou and muskoxen by reduced lichen availability during winter might also explain why the SEA_c ellipses of Lagoon and Early Thule caribou and muskoxen exhibit greater eccentricity towards high $\delta^{15}N$.

The Early Thule period also coincides with the end of the Medieval Warm Period (MWP) which lasted from ~ 1100 cal. BP to ~ 900 cal. BP (McGhee 1983; Podritske and Gajewski 2007; Trouet et al. 2009; D'Andrea et al. 2011), and the large isotopic niches of caribou and muskoxen during this period may reflect ecological turmoil caused by relatively rapid oscillations from colder, to warmer, to colder climatic regimes preceding and following the MWP. Consequently, we expect the apparent niche diversification during the Lagoon and Early Thule periods to reflect competitive niche expansion due to the reduced availability of preferred forage types, potentially including shrubs, legumes, and lichens as a result of climatic instability.

As to alternative forage sources utilized by caribou and muskoxen during colder periods, the Lagoon and Early Thule periods both coincide with the beginning of an increase in graminoid productivity in the Western Canadian Arctic (Gajewski et al. 2000; Gajewski and MacDonald 2004; Peros and Gajewski 2009). Non-leguminous forbs, specifically *Saxifragaceae*, also briefly increased in productivity around the time of the Early Thule period (Gajewski and MacDonald 2004). Along with potentially lower lichen availability, the increase in both caribou and muskox $\delta^{15}N_{bc}$ during the Lagoon and Early Thule period

may reflect increasing utilization of non-leguminous forbs and sedges, respectively, by caribou and muskoxen.

Lagoon and Early Thule bone collagen isotopic compositions, transposed into quasi-IsoSpace, fail to meet the expectations of competitive niche specialization outlined by the classical ecological niche framework. A Hutchinsonian interpretation of the large isotopic niches of Lagoon and Early Thule caribou and muskoxen would suggest that competitive drive towards dietary specialization relaxed during these periods. Given the decline in average annual air temperature during these periods, this interpretation seems unlikely.

The apparent partition of caribou $\delta^{13}C_{bc}$ into two relatively distinct clusters during the Early Thule period (most apparent in Figure 3.10c) may have additional ecological significance. Though potentially an artifact of a relatively small sample size, this clustering may represent a resource polymorphism (Smith and Skúlason 1996; Matthews and Mazumder 2004), where members of a single species begin utilizing two distinct dietary resource pools. Intra-specific resource polymorphisms often occur with genetic divergence, but in this context, it may indicate that non-indigenous caribou herds with different forage bases, such as barren ground caribou, were present on Banks Island in greater numbers during the Early Thule period. It is also possible that forage conditions on Banks Island were so poor during the Early Thule period that greater numbers of Peary caribou from Banks Island foraged elsewhere before returning and being harvested by hunters. Again, oxygen isotopic analysis of tooth enamel is well-suited for testing these hypotheses, but we did not recover any caribou teeth from Early Thule sites on Banks Island.

Finally, it is possible that the two clusters of caribou bone collagen isotopic compositions represent a dietary transition between two distinct Early Thule occupational events. All but one of the Early Thule caribou bone samples originate from the OhRh-1 site at Nelson River on Banks Island (Figure 3.1), and current research (Arnold 1986; Friesen and Arnold 2008) suggests that the entire Nelson River site was only inhabited for a few decades. Still, given the probable ecological instability during the Early Thule period, caribou diets may have varied significantly from year-to-year.

The transition to smaller but minimally-overlapping isotopic niches during the Classic Thule and Inuit periods suggests that some fundamental decoupling of caribou and muskox niche dynamics occurred during these cultural periods. Most notably, caribou appear to return to the same approximate position in quasi-IsoSpace as during the Pre-Dorset period, while the mean $\delta^{15}N_{bc}$ for muskoxen continues to increase. This small but strongly linear increase in muskox mean $\delta^{15}N_{bc}$ (Figure 3.19) warrants consideration and has several potential causes.

A common explanation for increased tissue $\delta^{15}N$ is the catabolic utilization of body tissues due to increased dietary stress (Hobson et al. 1993; Fuller et al. 2005; Drucker et al. 2012). We argue in Chapter 2 that because of evolved physiological adaptations to the Arctic environment, catabolic enrichment of tissue $\delta^{15}N$ probably does not occur in muskoxen or caribou. Instead, the simplest explanation for higher $\delta^{15}N_{bc}$ during the Classic Thule, and especially Inuit period, is that muskoxen increasingly utilized forage resources with higher $\delta^{15}N$. Although we cannot currently quantify forage $\delta^{13}C$ and $\delta^{15}N$ in the past, isotopic analysis of modern forage samples from Banks Island (Chapter 2) demonstrates that graminoids, and specifically sedges, have higher $\delta^{15}N$ than other forage samples we collected. Palynological data (Gajewski et al. 2000; Gajewski and MacDonald 2004; Peros and Gajewski 2009) also suggest that grass and sedge productivity in the Western Canadian Arctic also began increasing after ~ 3000 BP. Given their general morphological and physiological adaptations towards the efficient digestion of low quality forage like grasses (Hofmann 2000), muskoxen may have capitalized on increasing graminoid availability during the colder centuries to avoid forage competition with caribou while still meeting their nutritional and metabolic needs.

3.5.4 Muskox Bone Collagen Isotopic Compositions as Indices of Ecological Change

The increase in the mean $\delta^{15}N_{bc}$ of muskoxen between the Pre-Dorset and Inuit periods may also indicate that muskoxen, due to their limited ranges and forage preferences, integrate signals from ecological changes like terrestrial nitrogen cycle "openness" (Austin and Vitousek 1998) more closely than caribou. Biotic factors that affect terrestrial nitrogen balance, and subsequently ecosystem $\delta^{15}N$, include increased or decreased trampling and

grazing by herbivores (Schlesinger et al. 1990; Smith 1996; Welker et al. 2004; Pajunen et al. 2008; Olofsson et al. 2009; Post 2013; Falk et al. 2015; Koch and Fox 2017), and increased or decreased nitrogenous input from animal waste (Ambrose 1991; Smith 1996; Frank and Evans 1997; Tozer et al. 2005). Given that the muskox population on Banks Island can expand to significant numbers, muskox grazing, trampling, and waste inputs have probably influenced the nitrogen cycling significantly during certain periods over the last 4000 years. At present, however, we can only speculate about muskox paleodemography on Banks Island, and it is unclear at what population density level these processes begin to impart significant effects on overall terrestrial nitrogen balance. The cycling of terrestrial and marine nitrogen sources by lesser snow geese (*Chen caerulescens*), which maintain large colonies on Banks Island (Kerbes et al. 1999; Samuel et al. 1999), and seabirds, respectively, is also probably significant to the nitrogen balance of Banks Island. Again, however, we know little about the paleodemography of different bird species on Banks Island, and so it is unclear whether avian nutrient inputs have increased or decreased over time.

In any case, abiotic factors that affect the openness of the terrestrial nitrogen system should be the most important in dictating long-term trends in ecosystem-wide nitrogen availability and δ^{15}N trends on the tundra. In a "closed" nitrogen system, nitrogen inputs and outputs are balanced, and little or no nitrogen is lost from the system. As a result, soil and plant δ^{15}N remains low over time (Handley et al. 1999; Stevens et al. 2008). In more "open" nitrogen systems, inputs and outputs are disproportionate from one another and soil and plant δ^{15}N will change depending on the input or output processes occurring (Austin and Vitousek 1998; Handley et al. 1999). Nitrogen cycle "openness" is typically associated with ecosystem ^{15}N-enrichment because ^{14}N is preferentially fractionated in "nearly all nitrogen transformation processes" (Austin Vitousek 1998:520). In reality, the terrestrial nitrogen cycles of few ecosystems are completely closed, given that outflow (i.e. demand) for nitrogen generally exceeds inputs (Amundson et al. 2003; Marshall et al. 2007). Consequently, at steady state over long periods of time, nitrogen losses will approach or exceed input rates and ecosystem-wide δ^{15}N will increase (Handley and Raven 1992; Austin Vitousek 1998; Amundson et al. 2003).

In general, plants can acquire nitrogen from three sources: (1) soil-bound ammonium (NH_4^+), nitrate (NO_3^-), and natural monomers (i.e. proteins and amino acids) via associations with fungal (mycorrhizal) symbionts (Read 1991; Jones et al. 2005; Hobbie and Hobbie 2006); (2) N_2-fixation via associations with root-borne bacterial (rhizobial) symbionts (Alexander et al. 1978; Zahran 1999; Vitousek et al. 2002); and (3) directly from soil-bound natural monomers (Schimel and Chapin 1996; Schimel and Bennett 2004; Farrell et al 2011). The availability of NH_4^+ and NO_3^- is generally limited in tundra ecosystems. Even at present, when average annual air temperatures in the Arctic are relatively high (Navarro et al. 2016; Lecavalier et al. 2017), the perennially cold, nearly anaerobic soils of the Arctic limit microbial decomposition of organic polymers and mineralization of nitrogen into ammonium and nitrate (Van Cleve and Alexander 1981; Kielland 1994; Hicks Pries et al. 2012). Consequently, soil concentrations of NH_4^+ and NO_3^- tend to be small, and most soil-bound nitrogen will occur in the form of labile proteins and amino acids (Kielland 1995; Lipson and Näsholm 2001), which are cycled continuously between living and dead organic pools (Stevens and Hedges 2004:983).

The major source of *new* nitrogen entering tundra ecosystems is N_2-fixation by free-living soil cyanobacteria (Alexander and Schell 1973; Stutz 1977; Henry and Svoboda 1986; Solheim et al. 1994; Chapin et al. 1991; Liengen and Olsen 1997; Vitousek et al. 2002). Since N_2-fixation by free-living soil cyanobacteria is inhibited by increased aridity and lower temperature (Alexander et al. 1978; Chapin 1991; Chapin and Bledsoe 1992), and the availability of inorganic nitrogen on the tundra is low in general, the demand for monomeric soil nitrogen sources by primary producers likely intensified during the cooler period from ~ 3000 BP to 1500 cal. BP. As the imbalance between nitrogen inputs and outputs increased, proteins and amino acids recycled back into the soil nitrogen pool would have increasingly higher $\delta^{15}N$.

Significantly, recent research demonstrates that the sedges from the genera *Carex* and *Eriophorum* are flexible in their nitrogen uptake strategies, and when necessitated by low inorganic nitrogen availability, can forgo symbiotic mycorrhizal associations and directly assimilate organic soil nitrogen sources like labile soil amino acids (Chapin et al. 1988, 1993; Kielland 1994; Schimel and Chapin 1996). The ability of sedges to directly

assimilate organic soil nitrogen sources allows them to "short-circuit" (Kielland 1994:2381) the inorganic mineralization process. Additionally, direct uptake of organic nitrogen sources by sedges reduces competition with plant genera like *Salix*, *Dryas*, and *Cassiope* (Michelsen et al. 1998), which may only obtain nitrogen from inorganic sources via mycorrhizal associations. We argue then, that sedges, because of their ability to uptake organic nitrogen directly from the soil, will track increasing ecosystem $\delta^{15}N$, while in mycorrhizally-associating plants, the ecosystem $\delta^{15}N$ signal is obscured by multiple fractionating processes involved with uptake of inorganic nitrogen (Högberg 1997; Evans 2001; Robinson 2001).

Along with studies of fecal (Oakes et al. 1992; Larter and Nagy 1997, 2004) and rumen (Thing et al. 1987) content, we demonstrate in Chapter 2 that sedges are a significant dietary resource for muskoxen. Although sedges also appear to be an important part of modern caribou diet on Banks Island, caribou SEA_c ellipses in Figure 3.9f suggest that mean caribou $\delta^{15}N_{bc}$ is higher today than at any time after the Early Thule period. This implies that the utilization of sedges by modern caribou is greater than that of caribou during the Classic Thule and Inuit periods. Dietary mixing models in Chapter 2 also demonstrate that legumes may be an important forage source for caribou. Because arctic legumes can utilize atmospheric N_2 via associations with root-borne bacterial (rhizobial) symbionts (Alexander et al. 1978; Prévost et al. 1987; Prévost et al. 1990), their $\delta^{15}N$ should remain close to 0‰ regardless of changes in the terrestrial nitrogen cycle. It is possible then, that the increase in mean muskox $\delta^{15}N_{bc}$, particularly during the Classic Thule and Inuit periods, represents increasing utilization of sedges, the $\delta^{15}N$ of which were steadily driven upwards by the opening of the terrestrial nitrogen cycle. In short, caribou $\delta^{15}N_{bc}$ from the Classic Thule and Inuit periods may not reflect increasing ecosystem $\delta^{15}N$ because of greater legume consumption, and lower sedge consumption, relative to muskoxen.

3.5.5 Caribou Dentin Collagen Isotopic Compositions and Seasonal Dietary Variation

Aside from the M1 of BIBS14-214, tooth-averaged $\delta^{13}C_{dc}$ in the M1s of Thule and Inuit caribou is about 0.5‰ higher than the $\delta^{13}C$-corrected, tooth-averaged $\delta^{13}C_{dc}$ of the modern caribou M1 (BIBS16-19 M1) (Table 3.8). Likewise, tooth-averaged $\delta^{15}N_{dc}$ in all

archaeological caribou M1s except for BIBS14-360 is ~ 0.5‰ lower than the tooth-averaged $\delta^{15}N_{dc}$ of BIBS16-19 M1 (Table 3.9). In terms of its bulk bone collagen $\delta^{15}N_{bc}$ (+4.5‰, Table 3.2), BIBS14-360 appears to be an outlier compared to other Inuit period caribou. Overall then, tooth-averaged $\delta^{13}C_{dc}$ and $\delta^{15}N_{dc}$ from caribou M1s reflects the same pattern as in bone collagen of decreasing $\delta^{13}C$ and increasing $\delta^{15}N$ across the Classic Thule, Inuit, and modern periods. Potential seasonal variation in $\delta^{13}C_{dc}$ and $\delta^{15}N_{dc}$ in caribou M1s is obscured by our bulk dentin sampling method. Still, the similarity of bone and dentin collagen isotopic signals suggests that changes in caribou isotopic niche over the last ~ 700 years are not due to seasonal dietary variation alone, but are also in part the result of change in overall diet.

Except for BIBS14-360, high $\Delta^{15}N_{dc\text{-}bc}$ offsets in most of the archaeological caribou M1s are explained by low bone collagen $\delta^{15}N$ (i.e. less than +3.0‰), rather than particularly high $\delta^{15}N_{dc}$. A pattern of higher $\Delta^{15}N_{dc\text{-}bc}$ offsets due to lower $\delta^{15}N_{bc}$ is what we would expect if calves were supplementing their diets by nursing while the diets of their cows consisted of forage with low $\delta^{15}N$. Accounting for the disparity between tooth formation and eruption, the 1‰ decrease in the $\Delta^{15}N_{dc\text{-}bc}$ offsets of BIBS14-298 M2 and M3 (Table 3.9) suggests that weaning began sometime within the second summer of life. Conversely, in BIBS14-214 the $\Delta^{15}N_{dc\text{-}bc}$ offset remains above 2‰ in all teeth. Based on our discussion of caribou tooth eruption times, nursing and dentin collagen isotopic compositions in Chapter 2, high $\Delta^{15}N_{dc\text{-}bc}$ offsets in multiple permanent teeth indicate that this caribou probably continued nursing into the third winter of life. Again, because of lactational anestrus in caribou, under normal conditions we should expect small or absent $\Delta^{15}N_{dc\text{-}bc}$ offsets in teeth developing after birth. Where $\Delta^{15}N_{dc\text{-}bc}$ offsets in caribou molars and permanent premolars are high, there is some indication that nutritional conditions were poor enough that caribou cows were compelled to sacrifice reproductive potential to ensure the survival of existing calves by continuing nursing.

The potential link between caribou $\Delta^{15}N_{dc\text{-}bc}$ and demographic variation provides additional insight into the overall niche dynamics of caribou and muskoxen during the Classic Thule, Inuit, and modern periods. Again, Bayesian dietary mixing models (Chapter 2) suggest that sedges contribute significantly to modern caribou bone collagen isotopic compositions. In

Chapter 2, we also suggest that the high proportional contribution of sedges to modern caribou bone collagen is the result of caribou moving into the muskox ecological niche after very recent declines in the muskox population (Kelvin 2016). The higher $\delta^{15}N_{bc}$ in modern caribou relative to caribou from the Classic Thule and Inuit periods also supports the idea of a recent shift towards greater sedge consumption. That the $\Delta^{15}N_{dc\text{-}bc}$ offset in the modern caribou M1 ($\Delta^{15}N_{dc\text{-}bc}$ = +1.7‰) is also lower than the $\Delta^{15}N_{dc\text{-}bc}$ offsets in caribou M1s from the Classic Thule ($\Delta^{15}N_{dc\text{-}bc}$ = +3.0‰, +2.8‰, and +2.3‰) and one of the two caribou M1s from the Inuit period ($\Delta^{15}N_{dc\text{-}bc}$ = +2.8‰) (Table 3.9) also suggest a causal relationship between access to sedges, shorter weaning times, and increases in the caribou population size.

3.5.6 Muskox Dentin Collagen Isotopic Compositions and Seasonal Dietary Variation

As with caribou, $\delta^{13}C_{dc}$ and $\delta^{15}N_{dc}$ in muskox M1s largely mirrors changes in bone collagen $\delta^{13}C$ and $\delta^{15}N$ across cultural periods. For instance, Figure 3.18 demonstrates that mean $\delta^{13}C_{bc}$ for muskoxen is lowest during the Inuit and Classic Thule periods, respectively. In Figure 3.16a, the intra-tooth $\delta^{13}C_{dc}$ of BIBS14-456 M1, which is directly dated to the Inuit period (302-147 cal. BP, Figure 3.3, Table 3.1), is noticeably lower than those of other muskox M1s. BIBS14-474 M1, which dates to the Classic Thule period, should also have low intra-tooth $\delta^{13}C_{dc}$, but Figure 3.16c demonstrates that this not the case. Instead, the $\delta^{13}C_{dc}$ of the first microbulk dentin sample from BIB14-474 M1 is relatively low compared to other dentin collagen samples, but in the next microbulk dentin sample, $\delta^{13}C_{dc}$ increases by more than 1‰. Following the argument that occlusally-worn muskox M1s largely track dietary shifts between the middle of the first summer and first winter of life, the intra-tooth $\delta^{13}C_{dc}$ from the M1 of BIBS14-474 suggests that this muskox switched relatively rapidly from a lower-$\delta^{13}C$ diet in summer to a higher-$\delta^{13}C$ diet during winter. Based on modern forage isotopic compositions, and patterns in modern muskox crown dentin collagen (Chapter 2), however, we expect an increase in intra-tooth $\delta^{13}C_{dc}$ to correspond with a decrease in intra-tooth $\delta^{15}N_{dc}$. Instead, $\delta^{15}N$ increases across sequential microbulk dentin samples from the M1 of BIBS14-474 (Figure 3.17c), and this pattern is only observed in one other muskox M1 (BIBS14-407). Given that the M1 from BIBS14-474 has the lowest

tooth-averaged $\Delta^{15}N_{dc\text{-}bc}$ offset of all M1s (1.8‰), it may be that this muskox was weaned earlier than most of the other muskoxen from which we sampled teeth. Consequently, the intra-tooth $\delta^{13}C_{dc}$ of BIBS14-474 M1 tracks changes in forage $\delta^{13}C$, while its $\delta^{15}N_{dc}$ integrates a rapid seasonal shift in climatic conditions, such as aridity. Additionally, the bones and teeth of BIBS14-474 were collected at QbPu-3, at the northern edge of Mercy Bay (Figure 3.1), and it is possible that this muskox migrated across sea ice from another island such as Melville Island or the northern part of Victoria Island, during its first winter of life. The unique dentin collagen isotopic compositions from BIBS14-474 may therefore reflect geographic variation in forage $\delta^{13}C$ and $\delta^{15}N$.

Based on published accounts of weaning times (Tener 1965; Parker et al. 1990; Adamczewski et al. 1997) and tooth eruption patterns (Tener 1965; Henrichsen and Grue 1980) in muskoxen, we hypothesize in Chapter 2 that the isotopic compositions of crown dentin collagen in muskox M1s should capture the transition from nursing to full herbivory in muskoxen during the first year or so of life. Accordingly, we expected to observe significant decreases in $\delta^{15}N$ across sequential crown dentin samples in each archaeological muskox M1. Such a pattern would have reflected a decrease in milk supplementation as the tooth developed, particularly in warmer periods when phytomass productivity was higher. Instead, the absence of major decreases in $\delta^{15}N_{dc}$ in each tooth, and relatively large $\Delta^{15}N_{dc\text{-}bc}$ offsets (i.e. greater than 2‰) in all but one M1 (BIBS14-474 M1), suggest that none of the muskoxen from which we sampled teeth weaned during the time when the crowns of their M1s developed. That the two Pre-Dorset muskoxen (BIBS14-407 and -409) have relatively high $\Delta^{15}N_{dc\text{-}bc}$ offsets (3.2‰ and 2.5‰, respectively) is especially surprising, given the higher average annual air temperature, and presumably greater phytomass productivity during this period. The relatively homogenous intra-tooth $\delta^{15}N_{dc}$ of BIBS14-409 M1 suggests that this muskox was still nursing during most of the time that the M1 was developing. Conversely, the intra-tooth variability in $\delta^{15}N_{dc}$ in the M1 of BIBS14-407 would suggest that this muskox was weaned early, and hence that the intra-tooth $\delta^{15}N_{dc}$ of its M1 reflects forage $\delta^{15}N$ variation. The $\Delta^{15}N_{dc\text{-}bc}$ offset is greater in the M1 of BIBS14-407 than in the M1 of BIBS14-409, however, in part because the inter-tooth averaged $\delta^{15}N_{dc}$ for BIBS14-409 M1 (+6.6‰) is 1.5‰ greater than the inter-tooth averaged $\delta^{15}N_{dc}$ for BIBS14-407 M1 (+5.1‰), and in part because the bone collagen $\delta^{15}N$ of

BIBS14-409 (+4.1‰) is 2.2‰ higher than the bone collagen $\delta^{15}N$ of BIBS14-407 (+1.9‰). The bone collagen $\delta^{15}N$ of BIBS14-407 and BIBS14-409 are the lowest and highest, respectively, of the thirty-six Pre-Dorset muskox bone collagen samples we analyzed, though they are not necessarily outliers.

In Chapter 2, we discuss other potential explanations for large $\Delta^{15}N_{dc\text{-}bc}$ offsets in modern muskox teeth, including seasonal catabolism and the assimilation of dead gut microflora. Neither of these explanations are satisfactory, since both processes should recur throughout life and should therefore affect the $\delta^{15}N$ of bone collagen as well. We also considered whether persistent $\Delta^{15}N_{dc\text{-}bc}$ offsets in the muskox M1s are due to dietary differences between earlier and later life. Oakes et al. (1992) suggest that in spring and summer, muskox calves consume more sedges, rushes and forbs, yearlings consume more forbs and grasses, and adult muskoxen mostly sedges, rushes and grasses. Even though we have no isotopic data for rushes, a lack of isotopic data from rushes still fails to explain the $\Delta^{15}N_{dc\text{-}bc}$ offsets because modern forbs have lower $\delta^{15}N$ than modern sedges or grasses. If forb consumption declined significantly in adulthood, we would expect bone collagen to be enriched in ^{15}N relative to crown dentin collagen. Instead, we observe the opposite in both modern and archaeological muskox teeth. Consequently, we suggest that: (1) either our model of muskox tooth development, which is based only on eruption schedules, is incorrect and M1s begin to develop well before parturition, or (2) muskox cows nurse into at least the second spring or summer of life as a matter of course. Henrichsen and Grue (1980:9) report that at birth, the muskox M1 is found "as loose parts in the alveolus" and from personal observations, these "loose parts" are the small (~ 10 mm), apical-most portions of the cusps. The $\delta^{13}C_{dc}$ and $\delta^{15}N_{dc}$ of these portions of the tooth cusps should capture prenatal, maternal dietary signals. Since significant portions of the tooth crown, including the entire cusp, are obliterated by occlusal wear in adulthood, however, the remaining portions of the M1 must have developed sometime between birth and the second summer of life. If muskoxen nurse into the second year of life in general, this also suggests that, contrary to traditional knowledge (Nagy 1999) and some observational data (Latour 1987; Gunn et al. 1991), muskoxen are historically more likely to calve every other year than on a yearly basis.

3.5.7 The Archaeological Significance of Caribou and Muskox Niche Relationships on Banks Island

The intra- and inter-specific homogeneity of Pre-Dorset caribou and muskox $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$, when transformed into quasi-IsoSpace, suggests that the Pre-Dorset occupation on Banks Island ended abruptly. If the utilization of caribou and muskoxen during the Pre-Dorset decreased gradually as temperatures slowly declined and ecological conditions deteriorated, we might expect relatively large ellipses, that if theoretically subdivided in time, would resolve into multiple niche positions. That is, if there were enough bone samples and radiocarbon dates to arrange Pre-Dorset caribou and muskox $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ into a temporal sequence, we might expect to see a gradual expansion of niche widths, reflecting decreasing forage availability and greater intra-specific dietary variability.

The Pre-Dorset bone collagen dataset is not large enough to formally test this hypothesis, but available radiocarbon dates (Figure 3.3, Table 3.1) suggest that the Shoran Lake site (PjRa-1) may have been used several hundred years earlier in the Pre-Dorset period than Umingmak (PjRa-2). Radiocarbon dates from the Twin Lakes site (PjPx-10) seem to span the entire Pre-Dorset period. Arnold (1983), however, suggests that Shoran Lake and Umingmak were inhabited simultaneously. Consequently, the apparent temporal stratification of Pre-Dorset sites may be the result of a small radiocarbon dataset.

Nevertheless, Figure 3.20 demonstrates no obvious variation in Pre-Dorset caribou and muskox $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ by site. The seemingly tighter "packing" of the muskox isotopic data from PjRa-2, relative to those of PjRa-1, which could be construed as a change in dietary specialization related to increased competition later in the Pre-Dorset period, is probably related to the smaller muskox sample size from PjRa-1 relative to PjRa-2. In short, even if the Pre-Dorset can be sub-divided temporally by archaeological site, the homogeneity of isotopic compositions at all three sites emphasizes the overall low dietary variation across the entire period.

It therefore seems unlikely that a combination of declining ecological conditions and overexploitation by humans drove caribou or muskoxen to the point of extirpation at the end of the Pre-Dorset period. Given the evidence for the relatively swift onset of cooler

temperatures across the North American Arctic around 3500 cal. BP (Kaufman et al. 2004; D'Andrea et al. 2011; Gajewski 2015b), groups on Banks Island who were culturally adapted towards terrestrial resource utilization probably rapidly abandoned the Shoran Lake complex (i.e. the PjRa-1 and PjRa-2 sites) and PjPx-10 because of new challenges to the ASTt lifeway brought on by declining temperatures.

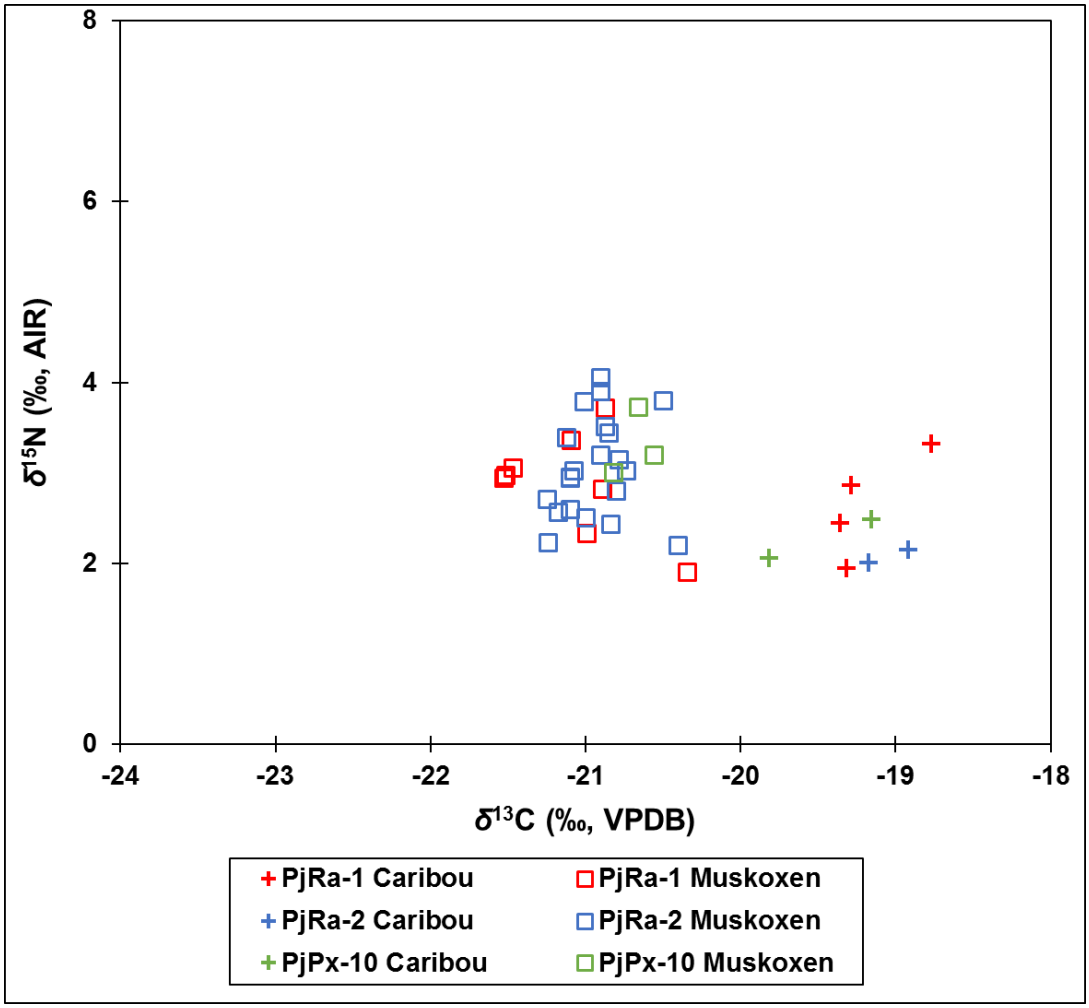


Figure 3.20. Non-transposed caribou and muskox bone collagen $\delta^{13}C$ and $\delta^{15}N$ values from the Pre-Dorset period, divided by archaeological site, demonstrating the relative homogeneity of isotopic values across the entire Pre-Dorset period.

Given the seasonal nutritional and metabolic challenges caribou and muskoxen face in general, the competitive expansion of caribou niche during the Lagoon and Early Thule periods was likely fitness-reducing, and may be responsible for the generally poorer representation of caribou relative to muskoxen at Lagoon and Early Thule period sites on Banks Island. Although cultural factors may also have been at play, if larger isotopic niche areas during the Lagoon and Early Thule periods do correspond to poorer forage conditions and lower calf productivity, it could be that people encountered fewer caribou or muskoxen, in poorer body condition, less often during the season(s) in which sites were inhabited. Consequently, hunting them for food may not have been "worth the effort": Lent (1999) notes that caribou and muskoxen in poor physical condition often have unpalatable meat. Since bowhead whales and ringed seal utilize marine resources, and geese migrate, these species were probably unaffected by terrestrial ecological changes on Banks Island, and were presumably abundant. Additionally, geese and ringed seal are relatively easy to hunt, provide high caloric returns. the amount of meat and fat provided by bowhead whales relative to the effort required to harvest them is also significant. Consequently, caribou and muskox hunting may have only occurred on a supplemental basis, or when animals were passively encountered during these periods.

The abundance of Inuit period sites on Banks Island, and the high representation of muskoxen in particular at those sites, suggest that muskoxen were abundant during this time. As we argue above, this productivity may be the result of increased graminoid availability, reflected in part by high $\delta^{15}N_{bc}$. The generally poor representation of caribou at Inuit period sites, and limited evidence of prolonged nursing given by the intra-tooth $\delta^{15}N_{dc}$ of a single caribou (BIBS14-214) may indicate that caribou were not as productive as muskoxen during the Inuit period. A hypothesis for future research is whether Inuit period groups actively managed the muskox population on Banks Island. In particular, the Head Hill (PlPx-1) site contains the skeletal remains of more than 500 muskoxen, many of which are still articulated (Wilkinson and Shank 1975; Hickey 1982; Shank et al. 1994). Radiocarbon dates (Figure 3.3, Table 3.1; Shank et al. (1994) also suggest that Head Hill was probably used for more than a century around 250 cal. BP. Elders from Sachs Harbour who visited Head Hill have described the abundance of muskox remains as "wasteful"

(Lisa Hodgetts, personal communication, 2016). People on Banks Island historically preferred the taste of caribou to muskoxen (Nagy 1999; Kelvin 2016), and traditional ecological knowledge records that the muskox population, left unchecked, will increase rapidly (Nagy 1999). As we discuss in Chapter 2, some people on Banks Island also believe that the behavior or odor of muskoxen drives caribou away (Nagy 1999; Kelvin 2016). Collected oral accounts (Nagy 1999) document that prior to the mid-twentieth century, people on Banks Island did cull muskoxen to keep them from driving the caribou away. Sachs Harbour resident Sam Lennie, recorded by Muriel Nagy in the 1990s recalls that in the past, "[Elder] Susie Tiktalik told hunters and trappers, "if anyway you fellows could destroy all them muskox, do it" (Nagy 1999:154)[17]. Given the probable cultural continuity across the Inuit period on Banks Island, it is conceivable that muskox culling was also practiced, or started, during this period as a response to a rapid population boom.

That the transposed SEA_c ellipses of modern caribou and muskoxen do not overlap, despite mean summer temperatures being comparable to those of the Pre-Dorset period, suggests that changes to phytomass composition on Banks Island during cooler periods fundamentally altered the niche dynamics of caribou and muskoxen, such that they now utilize distinct ecological niches. It is also possible that the modern caribou and muskox isotopic datasets, drawing largely from a single year of harvests, capture only transitory niche conditions associated with the recent decline of the muskox population, and the increase in the caribou population (Kelvin 2016).

3.6 Conclusion

Isotopic approaches to ecological niche estimation have developed rapidly over the past decade. Statistical packages like SIBER now permit researchers to quantify the niche metrics of individuals in ecological communities, while mixing models can be used to estimate the proportional contributions of different source data to consumer tissues. The

[17]The ecological rationale behind this management strategy, and the negative consequences of a muskox hunting ban imposed by the Canadian government from 1917 to 1971, are discussed by Barr (1991) and Nagy (1999).

thread linking these methods is the trophic discrimination factor, and until recently, TDFs have been sufficiently poorly-constrained that researchers have used the same TDFs across a single trophic level. As empirical data from controlled feeding studies and alternative approaches to TDF estimation like SIDER advance our understanding of TDF variation within trophic levels, we predict that the concept of "isotopic niche" will increasingly be called into question, and with it, some existing interpretations of sympatric niche relationships. We agree with Newsome et al. (2007, 2012) that researchers should present consumer isotopic data in "IsoSpace" or "DietSpace" whenever possible to more accurately describe dietary relationships. This presents serious problems for workers in paleoecology, however, where trophic discrimination factors and source isotopic compositions are unknown and perhaps unknowable. Bayesian approaches to TDF estimation present a partial solution to this problem by allowing researchers to transform consumer isotopic compositions into what we call "quasi-IsoSpace". This transformation of the isotopic data is particularly important when investigating potential niche competition between sympatric species with strict seasonal nutritional and metabolic requirements like caribou and muskoxen. Because there may be differences in trophic discrimination factors between species, the comparison of their tissue isotopic compositions can provide a misleading picture of niche overlap. Finally, we suggest that researchers wishing to explore seasonal variation in muskox diet should focus on M2s or M3s, since the $\delta^{13}C_{dc}$ and $\delta^{15}N_{dc}$ of these teeth is more likely to capture the weaning process. Likewise, our understanding of nursing in archaeological caribou would benefit significantly from the isotopic analysis of crown dentin collagen from additional M2s and M3s, since nursing potentially continues after the development of the M1.

This chapter demonstrates that when different TDFs are applied to sympatric species, their apparent isotopic niche relationships can change dramatically. Transposed $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$ from archaeological caribou and muskoxen suggests that caribou and muskoxen on Banks Island do not necessarily exert competitive pressure on one another. Instead, both species have persisted on Banks Island at different times and under variable ecological conditions by capitalizing on their relative dietary flexibility to avoid forage competition. Still, nutritional stress related to decreased phytomass during the Lagoon and Early Thule periods probably coincided with greater mortality and lower productivity in both species.

Given the abundance of other faunal resources, human hunters during these periods may have only harvested caribou or muskoxen opportunistically. The morphological and physiological adaptations of muskoxen, which allow them to extract the maximum amount of nutritive value from lower-quality forage like grass, and the ability of muskox cows to remain fertile while nursing yearlings, may have also provided demographic advantages over caribou during the Inuit period.

3.7 References

Adamczewski JZ, Fargey PJ, Laarveld B, Gunn A, Flood PF. 1997. The Influence of Fatness on the Likelihood of Early-Winter Pregnancy in Muskoxen (*Ovibos moschatus*). Theriogenology 50: 605-614.

Alexander VM, Schell DM. 1973. Seasonal and Spatial Variation of Nitrogen Fixation in the Barrow, Alaska, Tundra. Arctic and Alpine Research 5: 77-88.

Alexander VM, Billington M, Schell DM. 1978. Nitrogen Fixation in Arctic and Alpine Tundra. In: Tieszen LL, editor. Vegetation and Production Ecology of an Alaskan Arctic Tundra. Ecological Studies Series 29. New York: Springer-Verlag. Pp. 539-558.

Ambrose SH. 1990. Preparation and Characterization of Bone and Tooth Collagen for Isotopic Analysis. Journal of Archaeological Science 17: 431-451.

Ambrose SH. 1991. Effects of Diet, Climate and Physiology on Nitrogen Isotope Abundances in Terrestrial Foodwebs. Journal of Archaeological Science 18: 293-317.

Ambrose SH, Norr L. 1993. Experimental Evidence for the Relationship of the Carbon Isotope Ratios of Whole Diet and Dietary Protein to Those of Bone Collagen and Carbonate. In: Lambert JB, Grupe G, editors. Prehistoric Human Bone: Archaeology at the Molecular Level. Berlin: Springer-Verlag. Pp. 1-38.

Amundson R, Austin AT, Schuur G, Yoo K, Matzek V, Kendall C, Uebersax A, Brenner D, Baisden WT. 2003. Global Patterns of the Isotopic Composition of Soil and Plant Nitrogen. Global Biogeochemical Cycles 17(1): 31-42.

Anderson MJ, Santana-Garcon J. 2015. Measures of Precision for Dissimilarity-based Multivariate Analysis of Ecological Communities. Ecology Letters 18: 66-73.

Arnold CD. 1980. A Paleoeskimo Occupation on Southern Banks Island, N.W.T. Arctic 33(3): 400-426.

Arnold 1983. A Summary of the Prehistory of the Western Canadian Arctic. Arctic Archaeology 33: 10-20.

Arnold CD. 1986. In Search of the Thule Pioneers. In: Bielawski E, Kobelka C, Janes RR, editors. Thule Pioneers: Occasional Papers of the Prince of Whales Northern Heritage Centre Number 2. Pp. 1-93.

Arundale WH. 1981. Radiocarbon Dating in Eastern Arctic Archaeology: A Flexible Approach. American Antiquity 46(2): 244-271.

Atasoglu C, Guliye AY, Wallace RJ. 2004. Use of Stable Isotopes to Measure *de novo* Synthesis and Turnover of Amino Acid-C and -N in Mixed Micro-Organisms from the Sheep rumen *in vitro*. British Journal of Nutrition 91: 253-261.

Austin AT, Vitousek PM. 1998. Nutrient Dynamics on a Precipitation Gradient in Hawai'i. Oecologia 113(4): 519-529.

Balasse M, Tresset A. 2002. Early Weaning of Neolithic Domestic Cattle (Bercy, France) Revealed by Intra-tooth Variation in Nitrogen Isotope Ratios. Journal of Archaeological Science 29: 853-859.

Balasse M. 2003. Potential Biases in Sampling Design and Interpretation of Intra-tooth Isotope Analysis. International Journal of Osteoarchaeology 13: 3-10.

Banfield AWF. 1954. Preliminary Investigation of the Barren-ground Caribou. Canadian Wildlife Service Wildlife Management Bulletin Series 1, Numbers 10A and 10B.

Barr W. 1991. Back from the Brink: The Road to Muskox Conservation in the Northwest Territories. Komatik Series 3. Calgary: The Arctic Institute of North America.

Batschelet E. 1981. Circular Statistics in Biology. London: Academic Press.

Bearhop S, Thompson DR, Waldron S, Russell IC, Alexander G, Furness RW. 1999. Stable Isotopes Indicate the Extent of Freshwater Feeding by Cormorants *Phalacrocorax carbo* Shot at Inland Fisheries in England. Journal of Applied Ecology 36: 75-84.

Ben-David M, Shochat E, Adams LG. 2001. Utility of Stable Isotope Analysis in Studying Foraging Ecology of Herbivores: Examples from Moose and Caribou. Alces 37(2): 421-434.

Bielawski E. 1988. Paleoeskimo Variability: The Early Arctic Small-Tool Tradition in the Central Canadian Arctic. American Antiquity 53(1): 52-74.

Bocherens H, Drucker D. 2003. Trophic Level Isotopic Enrichment of Carbon and Nitrogen in Bone Collagen: Case Studies from Recent and Ancient Terrestrial Ecosystems. International Journal of Osteoarchaeology 13: 46-53.

Bocherens H, Drucker DG, Germonpré M, Lázničková-Galetová M, Naito YI, Wissing C, Brůžek J, Oliva M. 2015. Reconstruction of the Gravettian Food-web at Předmostí I Using Multi-isotopic Tracking (^{13}C, ^{15}N, ^{34}S) of Bone Collagen. Quaternary International 359/360: 211-228.

Bocherens H, Hofman-Kamińska E, Drucker DG, Schmölcke U, Kowalczyk R. 2015. European Bison as a Refugee Species? Evidence from Isotopic Data on Early Holocene Bison and Other Large Herbivores in Northern Europe. PLoS ONE 10(2): e0115090.

Bocherens H, Drucker DG, Haidle MN, Müller-Beck H, Münzel SC, Naito YI. 2016. Isotopic Evidence (C, N, S) for a High Aquatic Dietary Contribution for a Pre-Dorset Muskox Hunter from Umingmak (Banks Island, Canada). Journal of Archaeological Science: Reports 6: 700-708.

Bolnick DI. 2001. Intraspecific Competition Favours Niche Width Expansion in *Drosophila melanogaster*. Nature 410: 463-466.

Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML. 2003. The Ecology of Individuals: Incidence and Implications of Individual Specialization. The American Naturalist 161(1): 2-28.

Bradley RS. 2000. Past Global Changes and Their Significance for the Future. Quaternary Science Reviews 19: 391-402.

Carlson SJ. 1990. Vertebrate Dental Structures. In: Carter JG, editor. Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends, Volume 1. New York: Van Nostrand Reinhold.

Caut S, Angulo E, Courchamp F. 2009. Variation in Discrimination Factors (δ^{15}N and δ^{13}C): The Effect of Diet Isotopic Values and Applications for Diet Reconstruction. Journal of Applied Ecology 46: 443-453.

Chapin FS, III, Fetcher N, Kielland K, Everett KR, Linkins AE. 1988. Productivity and Nutrient Cycling of Alaskan Tundra: Enhancement by Flowing Soil Water. Ecology 69(3): 693-702.

Chapin DM, Bliss LC, Bledsoe LJ. 1991. Environmental Regulation of Nitrogen Fixation in a High Arctic Lowland Ecosystem. Canadian Journal of Botany 69: 2744-2755.

Chapin DM, Bledsoe C. 1992. Nitrogen Fixation in Arctic Plant Communities. In: Chapin FS, III, Jeffries RL, Reynolds JF, Shaver GR, Svoboda J, editors. Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective. San Diego: Academic Press. Pp. 301-319.

Chapin FS, III, Moilanen L, Kielland K. 1993. Preferential Use of Organic Nitrogen for Growth by a Non-mycorrhizal Arctic Sedge. Nature 361: 150-153.

Collignon B, Weber Müller-Wille L. 2006. Knowing Place: the Inuinnait, Landscapes, and the Environment. Edmonton: Canadian Circumpolar Institute Press.

Collins HB. 1953. Radiocarbon Dating in the Arctic. American Antiquity 18(3): 197-203. Coombs P, Barber K. 2005. Environmental Determinism in Holocene Research: Causality of Coincidence? Area 37(3): 303-311.

COSEWIC. 2004. COSEWIC Assessment and Update Status Report in the Peary caribou *Rangifer tarandus Pearyi* and the barren-ground caribou *Rangifer tarandus groenlandicus* (Dolphin and Union Population) in Canada. Ottawa: Committee on the Status of Endangered Wildlife in Canada.

Cox G, Sealy J. 1997. Investigating Identity and Life Histories: Isotopic Analysis and Historical Documentation of Slave Skeletons Found on the Cape Town Foreshore, South Africa. International Journal of Historical Archaeology 1(3): 207-224.

D'Andrea WJ, Huang Y, Fritz SC, Anderson NJ. 2011. Abrupt Holocene Climate Change as an Important Factor for Human Migration in West Greenland. Proceedings of the National Academy of Sciences 108(24): 9765-9769.

Darwent CM. 2004. The Highs and Lows of High Arctic Mammals: Temporal Change and Regional Variability in Paleoeskimo Subsistence. In: Mondini M, Muñoz S, Wickler S, editors. Colonisation, Migration, and Marginal Areas: A Zooarchaeological Approach. Oxford: Oxbow Books. Pp. 62-73.

Dayan T, Simberloff D. 2005. Ecological and Community-wide Character Displacement: The Next Generation. Ecological Letters 8: 875-894.

DeNiro MJ. 1985. Postmortem Preservation and Alteration of *In Vivo* Bone Collagen Isotope Ratios in Relation to Palaeodietary Reconstruction. Nature 317: 806-809.

Derbridge JJ, Merkle JA, Bucci ME, Callahan P, Koprowski JL, Polfus JL, Krausman PR. 2015. Experimentally Derived δ^{13}C and δ^{15}N Discrimination Factors for Gray Wolves and the Impact of Prior Information in Bayesian Mixing Models. PLoS ONE 10(3): e0119940.

Dewhurst RJ, Davies DR, Merry RJ. 2000. Microbial Protein Supply from the Rumen. Animal Feed Science and Technology 85: 1-21.

Dionne K, Dufresne F, Nozais C. 2016. Variation in δ^{13}C and δ^{15}N Trophic Enrichment Factors Among *Hyalella azteca* Amphipods from Different Lakes. Hydrobiologia 781: 217-230.

Drucker DG, Bocherens H, Billiou D. 2003. Evidence for Shifting Environmental Conditions in Southwestern France from 33 000 to 15 000 Years Ago Derived from Carbon-13 and Nitrogen-15 Natural Abundances in Collagen of Large Herbivores. Earth and Planetary Science Letters 216: 163-173.

Drucker DG, Hobson KA, Münzel SC, Pike-Tay A. 2012. Intra-Individual Variation in Stable Carbon (δ13C) and Nitrogen (δ15N) Isotopes in Mandibles of Modern Caribou of Qamanirjuaq (*Rangifer tarandus groenlandicus*) and Banks Island (*Rangifer tarandus pearyi*): Implications for Tracing Seasonal and Temporal Changes in Diet. International Journal of Osteoarchaeology 22: 494-504.

Dyke AS. 1978. Indications of Neoglacierization on Somerset Island, District of Franklin. Geological Survey of Canada Current Research Papers 78(1-B): 215-217.

Dyke AS. 2005. Late Quaternary Vegetation History of Northern North America Based on Pollen, Macrofossil, and Faunal Remains. Géographie Physique et Quaternaire 59(2-3): 211-262.

Dyke AS, Savelle JM. 2009. Paleoeskimo Demography and Sea-level History, Kent Peninsula and King William Island, Central Northwest Passage, Arctic Canada. Arctic 62: 371-392.

Dyke AS, Savelle JM, Johnson DS. 2011. Paleoeskimo Demography and Holocene Sea-level History, Gulf of Boothia, Arctic Canada. Arctic 64: 151-168.

Edlund SA. 1986. Modern Arctic Vegetation Distribution and Its Congruence with Summer Climate Patterns. In: French HM, editor. Climate Change Impacts in the Canadian Arctic, Proceedings of a Canadian Climate Program Workshop, March 3-5, 1986, Geneva Park, Ontario.

Ervynck A. 1999. Possibilities and Limitations of the Use of Archaeozoological Data in Biogeographical Analysis: A Review with Examples from the Benelux Region. Belgian Journal of Zoology 129: 125-138.

Evans RD. 2001. Physiological Mechanisms Influencing Plant Nitrogen Isotope Composition. TRENDS in Plant Science 6(3): 121-126.

Falk JM, Schmidt NM, Christensen TR, Ström L. 2015. Large Herbivore Grazing Affects the Vegetation Structure and Greenhouse Gas Balance in a High Arctic Mire. Environmental Research Letters 10: 045001.

Fantle MS, Dittel AI, Schwalm SM, Epifanio CE, Fogel ML. 1999. A Food Web Analysis of the Juvenile Blue Crab, *Callinectes sapidus*, Using Stable Isotopes in Whole Animals and Individual Amino Acids. Oecologia 120: 416-426.

Farrell M, Hill PW, Wanniarachchi SD, Farrar J, Bardgett RD, Jones DL. 2011. Rapid Peptide Metabolism: A Major Component of Soil Nitrogen Cycling? Global Biogeochemical Cycles 25: GB3014.

Feranec RS, MacFadden BJ. 2006. Isotopic Discrimination of Resource Partitioning Among Ungulates in C_3-dominated Communities from the Miocene of Florida and California. Paleobiology 32(2): 191-205.

Feranec RS. 2007. Stable Carbon Isotope Values Reveal Evidence of Resource Partitioning Among Ungulates from Modern C_3-dominated Ecosystems in North America. Palaeogeography, Palaeoclimatology, Palaeoecology 252: 575-585.

Ferguson RS. 1991. Detection and Classification of Muskox Habitat on Banks Island, Northwest Territories, Canada, Using Landsat Thematic Mapper Data. Arctic 44(S1): 66-74.

Fogel ML, Tuross N, Owsley DW. 1989. Nitrogen Isotope Tracers of Human Lactation in Modern and Archaeological Populations. Annual Report of the Director Geophysical Laboratory, Carnegie Institution, Washington, 1988-1989. Pp. 111-117.

Fortin M-C, Gajewski K. 2010. Holocene Climate Change and Its Effect on Lake Ecosystem Production on Northern Victoria Island, Canadian Arctic. Journal of Paleolimnology 43: 219-234.

Fox-Dobbs K, Leonard JA, Koch PL. 2008. Pleistocene Megafauna from Eastern Beringia: Paleoecological and Paleoenvironmental Interpretations of Stable Carbon and Nitrogen Isotope and Radiocarbon Records. Palaeogeography, Palaeoclimatology, Palaeoecology 261: 30-46.

France CAM, Zelanko PM, Kaufman AJ, Holtz TR. 2007. Carbon and Nitrogen Isotopic Analysis of Pleistocene Mammals from the Saltville Quarry (Virginia, USA): Implications for Trophic Relationships. Palaeogeography, Palaeoclimatology, Palaeoecology 249: 271-282.

Frank DA, Evans RD. 1997. Effects of Native Grazers on Grassland N Cycling in Yellowstone National Park. Ecology 78(7): 2238-2248.

Friedli H, Lötscher H, Oeschger H, Siegenthaler U, Stauffer B. 1986. Ice Core Record of the $^{13}C/^{12}C$ Ratio of Atmospheric CO_2 of the Past Two Centuries. Nature 324: 237-238.

Friesen TM, Arnold CD. 2008. The Timing of the Thule Migration: New Dates from the Western Canadian Arctic. American Antiquity 73(3): 527-538.

Fuller BT, Fuller JL, Sage NE, Harris DA, O'Connell TC, Hedges REM. 2005. Nitrogen Balance and $\delta^{15}N$: Why You're Not What You Eat During Nutritional Stress. Rapid Communications in Mass Spectrometry 19: 2497-2506.

Gage JP, Francis MJO, Triffitt JT. 1989. Collagen and Dental Matrices. London: Wright Press.

Gajewski K. 1995. Modern and Holocene Pollen Assemblages from Some Small Arctic Lakes on Somerset Island, NWT, Canada. Quaternary Research 44: 228-236.

Gajewski K, Mott RJ, Ritchie JC, Hadden K. 2000. Holocene Vegetation History of Banks Island, Northwest Territories, Canada. Canadian Journal of Botany 78: 430-436.

Gajewski K, MacDonald GM. 2004. Palynology of North American Arctic Lakes. In: Pienitz R, Douglas MSV, Smol JP, editors. Long-term Environmental Change in Arctic and Antarctic Lakes. Dordrecht: Springer. Pp. 89-116.

Gajewski K. 2015a. Impact of Holocene Climate Variability on Arctic Vegetation. Global and Planetary Change 133: 272-287.

Gajewski K. 2015b. Quantitative Reconstruction of Holocene Temperatures Across the Canadian Arctic and Greenland. Global and Planetary Change 128: 14-23.

Gause GF. 1936. The Struggle for Existence. Baltimore: Williams and Wilkins.

Giddings JL. 1964. The Archaeology of Cape Denbigh. Rhode Island: Brown University Press.

Grant PR. 1972. Convergent and Divergent Character Displacement. Biological Journal of the Linnean Society 4: 39-69.

Grayson DK. 1981. A Critical View of the Use of Archaeological Vertebrates in Paleoenvironmental Reconstruction. Journal of Ethnobiology 1: 28-38.

Greer AL, Horton TW, Nelson XJ. 2015. Simple Ways to Calculate Stable Isotope Discrimination Factors and Convert Between Tissues. Methods in Ecology and Evolution 6: 1341-1348.

Griller N. 2001. Short and Long Term Recovery of Plant Communities Following Intensive Grazing by Caribou (*Rangifer tarandus*) and Muskoxen (*Ovibos moschatus*) in the Low Arctic of Nunavut, Canada. [Dissertation]. [Vancouver (*BC*)]: University of British Columbia.

Grinnell J. 1917. The Niche-relationships of the California Thrasher. Auk 34: 427-433.

Gunn A, Shank C, McLean B. 1991. The History and Management of Muskoxen on Banks Island. Arctic 44(3): 188-195.

Halley DJ, Minagawa M, Nieminen M, Gaare E. 2010. Diet: Tissue Stable Isotope Fractionation of Carbon and Nitrogen in Blood Plasma and Whole Blood of Male Reindeer *Rangifer tarandus*. Polar Biology 33: 1303-1309.

Handley LL, Raven JA. 1992. The Use of Natural Abundance of Nitrogen Isotopes in Plant Physiology and Ecology. Plant, Cell and Environment 15: 965-985.

Handley L, Austin A, Robinson D, Scrimgeour C, Raven J, Heaton T, Schmidt S, Stewart G. 1999. The 15-N Natural Abundance (δ^{15}N) of Ecosystem Samples Reflects Measures of Water Availability. Australian Journal of Plant Physiology 26: 185-199.

Hardin G. 1960. The Competitive Exclusion Principle. Science 131(3409): 1292-1297.

Hare PE, Fogel ML, Stafford TW Jr., Mitchell AD, Hoering TC. 1991. The Isotopic Composition of Carbon and Nitrogen in Individual Amino Acids Isolated from Modern and Fossil Proteins. Journal of Archaeological Science 18: 277-292.

Harp E. Jr. 1958. Prehistory in the Dismal Lake Area, N. W. T., Canada. Arctic 11(4): 219-249.

Healy K, Kelly SBA, Guillerme T, Inger R, Bearhop S, Jackson AL. 2016. Predicting Trophic Discrimination Factor Using Bayesian Inference and Phylogenetic, Ecological and Physiological Data. DEsIR: Discrimination Estimation in R. PeerJ Preprints 4: e1950v1.

Hedges REM, Clement JG, Thomas CDL, O'Connell TC. 2007. Collagen Turnover in the Adult Femoral Mid-Shaft: Modeled from Anthropogenic Radiocarbon Tracer Measurements. American Journal of Physical Anthropology 133: 808-816.

Helmer JW. 1994. Resurrecting the Spirit(s) of Taylor's "Carlsberg Culture": Cultural Traditions and Cultural Horizons in Eastern Arctic Prehistory. In: Morrison D, Pilon J-L, editors. Threads of Arctic Prehistory: Papers in Honour of William E. Taylor, Jr. Mercury Series, Archaeological Survey of Canada Paper 149. Quebec: Canadian Museum of Civilization. Pp. 15-34.

Henrichsen P, Grue H. 1980. Age Criteria in the Muskox (*Ovibos moschatus*) from Greenland. Danish Review of Game Biology 11(4): 1-18.

Henry GHR, Svoboda J. 1986. Dinitrogen Fixation (Acetylene Reduction) in High Arctic Sedge Meadow Communities. Arctic and Alpine Research 18(2): 181-187.

Henry GHR, Gunn A. 1990. Recovery of Tundra Vegetation After Overgrazing by Caribou in Arctic Canada. Arctic 44(1): 38-42.

Hickey CG. 1982. Archaeological and Historical Investigations of Nineteenth Century Copper Inuit Culture. Preliminary report on file at the Canadian Museum of Civilization, Ottawa, Ontario.

Hicks Pries CE, Schuur EAG, Crummer KG. 2012. Holocene Carbon Stocks and Carbon Accumulation Rates Altered in Soils Undergoing Permafrost Thaws. Ecosystems 15(1): 162-173.

Hill PA, Orth M. 1998. Bone Remodelling. British Journal of Orthodontics 25: 101-107.

Hillson S. 2000. Teeth. Cambridge: Cambridge University Press.

Hobbie JE, Hobbie EA. 2006. ^{15}N in Symbiotic Fungi and Plants Estimates Nitrogen and Carbon Flux Rates in Arctic Tundra. Ecology 87(4): 816-822.

Hobson KA, Alisauskas RT, Clark RG. 1993. Stable-Nitrogen Isotope Enrichment in Avian Tissues Due to Fasting and Nutritional Stress: Implications for Isotopic Analyses of Diet. The Condor 95(2): 388-394.

Hodgetts L, Eastaugh E, Moody J. 2009. The Aulavik Archaeology Project Report on the 2008 Field Season. Report on file, Parks Canada Western and Northern Service Centre, Winnipeg, Manitoba.

Hodgetts LM, Eastaugh E. 2010. The Aulavik Archaeology Project. Report on the 2009 Field Season. Report on file, Parks Canada Western and Northern Service Centre, Winnipeg, Manitoba.

Hodgetts LM. 2013. Gendered Inuinnait (Copper Inuit) Landscapes of Banks Island's Northern Interior, Arctic Canada, 17th-20th Centuries A.D. Journal of Field Archaeology 38(1): 54-67.

Hodgetts L, Eastaugh E, Haukaas C, Kelvin L. 2013. The Ikaahuk Archaeology Project: Report On the 2013 Field Season. Report on file, Parks Canada Western and Northern Service Centre, Winnipeg, Manitoba.

Hodgetts LM, Munizzi JS. 2015. The Ikaahuk Archaeology Project: 2014 Fieldwork in Aulavik National Park. Report on file, Parks Canada Western and Northern Service Centre, Winnipeg, Manitoba.

Hodgetts LM, Eastaugh E, Munizzi JS. 2015. The Ikaahuk Archaeology Project: Report on the 2014 Field Season. Report on file, Cultural Places Program, Prince of Wales Northern Heritage Centre, Yellowknife, Northwest Territories.

Hoeinghaus DJ, Zeug SC. 2008. Can Stable Isotope Ratios Provide for Community-wide Measures of Trophic Structure? Comment. Ecology 89(8): 2353-2357.

Hofmann RR. 2000. Functional and Comparative Digestive System Anatomy of Arctic Ungulates. Rangifer 20(2-3): 71-81.

Högberg P. 1997. Tansley Review 95: ^{15}N Natural Abundance in Soil-plant Systems. New Phytologist 137: 179-203.

Holá M, Ježek M, Kušta T, Košatová M. 2015. Trophic Discrimination Factors of Stable Carbon and Nitrogen Isotopes in Hair of Corn Fed Wild Boar. PLoS ONE 10(4): e0125042.

Humphries P, Winemiller KO. 2009. Historical Impacts on River Fauna, Shifting Baselines, and Challenges for Restoration. BioScience 59(8): 673-684.

Hut G. 1987. Consultants' Group Meeting on Stable Isotope Reference Samples for Geochemical and Hydrological Investigations, IAEA, Vienna, 16-18 September 1985. Vienna: Report to the Director General.

Hutchinson GE. 1957. Concluding Remarks. Cold Spring Harbor Symposia on Quantitative Biology 22: 415-427.

Hutchinson GE. 1978. An Introduction to Population Biology. New Haven: Yale University Press.

Iacumin P, Nikolaev V, Ramigni M. 2000. C and N Stable Isotope Measurements on Eurasian Fossil Mammals, 40 000 to 10 000 Years BP: Herbivore Physiologies and Palaeoenvironmental Reconstruction. Palaeogeography, Palaeoclimatology, Palaeoecology 163: 33-47.

Jackson AL, Inger R, Parnell AC, Bearhop S. 2011. Comparing Isotopic Niche Widths Among and Within Communities: SIBER – Stable Isotope Bayesian Ellipses in R. Journal of Animal Ecology 80: 595-602.

Jackson MC, Donohue I, Jackson AL, Britton JR, Harper DM, Grey J. 2012. Population-level Metrics of Trophic Structure Based on Stable Isotopes and Their Application to Invasion Ecology. PLoS ONE 7(2): e31757.

Jackson AL. 2017. Introduction to SIBER. Available from: https://cran.r-project.org/web/packages/SIBER/vignettes/Introduction-to-SIBER.html.

Jenkins SG, Partridge ST, Stephenson TR, Farley SD, Robbins CT. 2001. Nitrogen and Carbon Isotope Fractionation Between Mothers, Neonates, and Nursing Offspring. Oecologia 129: 336-341.

Jenness D. 1917. The Copper Eskimos. Geographical Review 4(2): 81-91.

Jenness D. 1923. Origin of the Copper Eskimos and Their Copper Culture. Geographical Review 13(4): 540-551.

Jensen JF. 1998. Dorset Dwellings in West Greenland. Acta Borealia 2: 59-80.

Joly K, Cole MJ, Jandt RR. 2008. Diets of Overwintering Caribou, Rangifer tarandus, Track Decadal Changes in Arctic Tundra Vegetation. Canadian Field Naturalist 121(4): 379-383.

Jones DL, Healey JR, Willett VB, Farrar JF, Hodge A. 2005. Dissolved Organic Nitrogen Uptake by Plants – an Important N Uptake Pathway? Soil Biology and Biochemistry 37: 413-427.

Jørkov MLS, Heinemeier J, Lynnerup N. 2007. Evaluating Bone Collagen Extraction Methods for Stable Isotope Analysis in Dietary Studies. Journal of Archaeological Science 34: 1824-1829.

Kappen L. 1993. Plant Activity Under Snow and Ice, with Particular Reference to Lichens. Arctic 46(4): 297-302.

Kaufman DS, Ager TA, Anderson NJ, Anderson PM, Andrews JT, Bartlein PJ, Brubaker LB, Coats LL, Cwynar LC, Duvall ML, Dyke AS, Edwards ME, Eisner WR, Gajewski K, Geirsdottir A, and fifteen others. 2004. Holocene Thermal Maximum in the Western Arctic (0-180°W). Quaternary Science Reviews 23: 529-560.

Keeling CD, Mook WG, Tans PP. 1979. Recent Trends in the $^{13}C/^{12}C$ Ratio of Atmospheric Carbon Dioxide. Nature 277: 121-123.

Kelly DJ, Robertson A, Murphy D, Fitzsimons T, Costello E, Gormley E, Corner AL, Marples NM. 2012. Trophic Enrichment Factors for Blood Serum in the European Badger (*Meles meles*). PLoS ONE 7(12): e53071.

Kelsall JP. 1968. The Migratory Barren-ground Caribou of Canada. Ottawa: Canadian Wildlife Service, Department of Northern Affairs and National Resources, Natural and Historic Resources Branch.

Kelvin LE. 2016. There Is More Than One Way to Do Something Right: Applying Community-Based Approaches to an Archaeology of Banks Island, NWT. [Dissertation]. [London (ON)]: University of Western Ontario.

Kerbes RH, Baranyuk VV, Hines JE. 1999. Estimated Size of the Western Canadian Arctic and Wrangel Island Lesser Snow Goose Populations, on Their Breeding and Wintering Grounds. Canadian Wildlife Service Occasional Papers 98: 25-38.

Kielland K. 1994. Amino Acid Absorption by Arctic Plants: Implications for Plant Nutrition and Nitrogen Cycling. Ecology 75: 2373-2383.

Kielland K. 1995. Landscape Patterns of Free Amino Acids in Arctic Tundra Soils. Biogeochemistry 31: 85-98.

Klein DR. 1987. Vegetation Recovery Patterns Following Overgrazing by Reindeer on St. Matthews Island. Journal of Range Management 40: 336-338.

Klein DR. 1992. Comparative Ecological and Behavioral Adaptation of *Ovibos moschatus* and *Rangifer tarandus*. Rangifer 12(2): 47-55.

Klein DR. 1999. The Roles of Climate and Insularity in Establishment and Persistence of *Rangifer tarandus* Populations in the High Arctic. Ecological Bulletins 47: 96-104.

Knott KK, Barboza PS, Bowyer RT, Blake JE. 2004. Nutritional Development of Feeding Strategies in Arctic Ruminants: Digestive Morphometry of Reindeer, *Rangifer tarandus,* and Muskoxen, *Ovibos moschatus*. Zoology 107: 315-333.

Knott KK, Barboza PS, Bowyer RT. 2005. Growth in Arctic Ungulates: Postnatal Development and Organ Maturation in *Rangifer tarandus* and *Ovibos moschatus*. Journal of Mammalogy 86(1): 121-130.

Knuth E. 1967. Archaeology of the Musk-Ox Way. Contributions du Centre d'Études Arctiques et Finno-Scandinaves Number 5. Paris: École Pratique Des Hautes Études – Sorbonne.

Koch PL. 2007. Isotopic Study of the Biology of Modern and Fossil Vertebrates. In: Michener R, Lajtha K, editors. Stable Isotopes in Ecology and Environmental Science. Malden: Blackwell. Pp. 99-154.

Koch PL, Fox LR. 2017. Browsing Impacts on the Stable Isotope Composition of Chaparral Plants. Ecosphere 8(2): e01686.

Kronfeld-Schor N, Dayan T. 2003. Partitioning of Time as an Ecological Resource. Annual Review of Ecology, Evolution, and Systematics 34: 153-181.

Krueger HW, Sullivan CH. 1984. Models for Carbon Isotope Fractionation Between Diet and Bone. In: Turnlund JR, Johnson PE, editors. ACS Symposium Series Number 258 Stable Isotopes in Nutrition. Pp. 205-220.

Larter NC, Nagy JA. 1997. Peary Caribou and Banks Island Forage: Assessing Seasonal Diet Similarities. Rangifer 17(1): 9-16.

Larter NC, Nagy JA. 2004. Seasonal Changes in the Composition of the Diets of Peary Caribou and Muskoxen on Banks Island. Polar Research 23(2): 131-140.

Latour PB. 1987. Observations on Demography, Reproductions, and Morphology of Muskoxen (*Ovibos moschatus*) on Banks Island, Northwest Territories. Canadian Journal of Zoology 65: 265-269.

Lawton JH, Brown VK. 1993. Redundancy in Ecosystems. In: Schulze ED, Mooney HA, editors. Biodiversity and Ecosystem Function. New York: Springer-Verlag.

Layman CA, Albrey Arrington D, Montaña CG, Post DM. 2007a. Can Stable Isotope Ratios Provide for Community-Wide Measures of Trophic Structure? Ecology 88(1): 42-48.

Layman CA, Quattrochi JP, Peyer CM, Allgeier JE. 2007b. Niche Width Collapse in a Resilient Top Predator Following Ecosystem Fragmentation. Ecology Letters 10: 937-944.

Layman CA, Araujo MS, Boucek R, Hammerschlag-Peyer CM, Harrison E, Jud ZR, Matich P, Rosenblatt AE, Vaudo JJ, Yeager LA, Post DM, Bearhop S. 2012. Applying Stable Isotopes to Examine Food-web Structure: An Overview of Analytical Tools. Biological Reviews 87: 545-562.

Lecavalier BS, Fisher DA, Milne GA, Vinther BM, Tarasov L, Huybrechts P, Lacelle D, Main B, Zheng J, Bourgeois J, Dyke AS. 2017. High Arctic Holocene Temperature Record from the Agassiz Ice Cap and Greenland Ice Sheet Evolution. Proceedings of the National Academy of Sciences 114(23): 5952-5957.

LeGeros RZ. 1991. Calcium Phosphates in Oral Biology and Medicine, Volume 15. Paris: Karger Press.

Lent PC. 1999. Muskoxen and Their Hunters: A History. Norman: University of Oklahoma Press.

Lévesque E, Svoboda J. 1999. Vegetation Re-establishment in Polar "Lichen-kill" Landscapes: A Case Study of the Little Ice Age Impact. Polar Research 18: 221-228.

Liengen T, Olsen RA. 1997. Nitrogen Fixation by Free-Living Cyanobacteria from Different Coastal Sites in a High Arctic Tundra, Spitsbergen. Arctic and Alpine Research 29(4): 470-477.

Linde A, Goldberg M. 1993. Dentinogenesis. Critical Reviews in Oral Biology and Medicine 4(5): 679-728.

Lipson D, Näsholm T. 2001. The Unexpected Versatility of Plants: Organic Nitrogen Use and Availability in Terrestrial Ecosystems. Oecologia 128: 305-316.

Locke CW, Locke WW, III. 1977 Little Ice Age Snow-cover Extent and Paleoglaciation Thresholds: North-central Baffin Island, N.W.T., Canada. Arctic and Alpine Research 9: 291-300.

Longin R. 1971. New Method of Collagen Extraction for Radiocarbon Dating. Nature 230: 241-242.

Lowenstam HA, Weiner S. 1989. On Biomineralization. New York: Oxford University Press.

Lyman RL. 2008. Estimating the Magnitude of Data Asymmetry in Palaeozoological Biogeography. International Journal of Osteoarchaeology 18: 85-94.

Mann DH, Groves P, Kunz ML, Reanier RE, Gaglioti BV. 2013. Ice-age Megafauna in Arctic Alaska: Extinction, Invasion, Survival. Quaternary Science Reviews 70: 91-108.

Marshall JD, Brooks JR, Lajtha K. 2007. Sources of Variation in the Stable Isotopic Composition of Plants. In: Michener R, Lajtha K, editors. Stable Isotopes in Ecology and Environmental Science, Second Edition. Malden: Blackwell. Pp. 22-60.

Martinez del Rio C, Wolf BO. 2005. Mass-balance Models for Animal Isotopic Ecology. In: Starck JM, Wang T, editors. Physiological and Ecological Adaptations to Feeding in Vertebrates. Enfield: Science Publishers. Pp. 141-174.

Matley JK, Simpfendorfer CA, Fisk AT, Heupel MR. 2017. Trophic Niche and Spatio-temporal Changes in the Feeding Ecology of Two Sympatric Species of Coral Trout (*Plectropomus leopardus* and *P. laevis*). Marine Ecology Progress Series 563: 197-210.

Matthews B, Mazumder A. 2004. A Critical Evaluation of Intrapopulation Variation of $\delta^{13}C$ and Isotopic Evidence of Individual Specialization. Oecologia 140: 361-371.

Maxwell MS. 1984. Pre-Dorset and Dorset Prehistory of Canada. In: Handbook of North American Indians, Volume 5: Arctic. Damas D, editor. Washington: Smithsonian Institution. Pp. 359-368.

Maxwell MS. 1985. Prehistory of the Eastern Arctic. New York: Academic Press.

McGhee R. 1976. Paleoeskimo Occupations of Central and High Arctic Canada. Memoirs of the Society for American Archaeology, No. 31, Eastern Arctic Prehistory: Paleoeskimo Problems: 15-39.

McGhee R. 1982. The Past Ten Years in Canadian Arctic Prehistory. Canadian Journal of Archaeology 6: 65-77.

McGhee R. 1983. Eastern Arctic Prehistory: The Reality of a Myth? Musk-Ox 33: 21-25.

McGhee R. 1984. Thule Prehistory of Canada. In: Damas D, editor. Handbook of North American Indians, Volume 5 Arctic. Washington, Smithsonian Institution Press. Pp. 369-376.

Michelsen A, Quarmby C, Sleep D, Jonasson S. 1998. Vascular Plant ^{15}N Natural Abundance in Heath and Forest Tundra Ecosystems is Closely Correlated with Presence and Type of Mycorrhizal Fungi in Roots. Oecologia 115: 406-418.

Miller GH. 1973. Variations in Lichen Growth from Direct Measurements: Preliminary Curves for *Alectoria miniscula* from Eastern Baffin Island, N. W. T., Canada. Arctic and Alpine Research 5(4): 333-339.

Miller FL. 1974. Biology of the Kaminuriak Population of Barren-ground Caribou. Park 2: Dentition as an Indicator of Age and Sex; Composition and Socialisation of the Population. Canadian Wildlife Service Report Series 31.

Møbjerg T. 1999. New Adaptive Strategies in the Saqqaq Culture of Greenland, c. 1600-1400 BC. World Archaeology 30: 452-465.

Müller-Beck H. 1977b. The Excavation at Umingmak, Banks Island 1970 & 1973. In: Müller-Beck H, editor. Excavations at Umingmak on Banks Island, N.W.T., 1970 and 1973: Preliminary Report. Urgeschichtliche Materialhefte 1. Pp. 1-6.

Münzel S. 1987. Umingmak: ein Muschusochsenjagdplatz auf Banks Island, N.W.T., Canada. Archäozoologische Auswertung des Areals ID. Urgeschichtliche Materialhefte 5(2): 1-188.

Naeem S. 1998. Species Redundancy and Ecosystem Reliability. Conservation Biology 12(1): 39-45.

Nagy M. 1999. Aulavik Oral History Project on Banks Island, NWT: Final Report. Prepared for Inuvialuit Social Development Program.

Navarro JCA, Varma V, Riipinen I, Seland Ø, Kirkevåg A, Struthers H, Iversen T, Hansson H-C, Ekman AML. 2016. Amplification of Arctic Warming by Past Air Pollution Reductions in Europe. Nature Geoscience 9: 277-282.

Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL. 2007. A Niche for Isotopic Ecology. Frontiers in Ecology and the Environment 5(8): 429-436.

Newsome SD, Yeakel JD, Wheatley PV, Tinker MT. 2012. Tools for Quantifying Isotopic Niche Space and Dietary Variation at the Individual and Population Level. Journal of Mammalogy 93(2): 329-341.

Oakes EJ, Harmsen R. 1992. Sex, Age, and Seasonal Differences in the Diets and Activity Budgets of Muskoxen (*Ovibos moschatus*). Canadian Journal of Zoology 70: 605-616.

Oelbermann K, Scheu S. 2002. Stable Isotope Enrichment (δ^{15}N and δ^{13}C) in a Generalist Predator (*Pardosa lugubris*, Araneae; Lycosidae): Effects of Prey Quality. Oecologia 130: 337-344.

Olofsson J, Oksanen L, Callaghan T, Hulme P, Oksanen T, Suominen O. 2009. Herbivores Inhibit Climate-driven Expansion on the Tundra. Global Change Biology 15: 2681-2693.

Overpeck J, Hughen K, Hardy D, Bradley R, Case R, Douglas M, Finney B, Gajewski K, Jacoby G, Jennings A, Lamoureux S, Lasca A, MacDonald G, Moore J, Retelle M, Smith S, Wolfe A, Zielinski G. 1997. Arctic Environmental Change of the Last Four Centuries. Science 278: 1251-1256.

Pajunen A, Virtanen R, Roininen H. 2008. The Effects of Reindeer Grazing on the Composition and Species Richness of Vegetation in Forest-tundra Ecotone. Polar Biology 31: 1233-1244.

Parker KL, White RG, Gillingham MP, Holleman DF. 1990. Comparison of Energy Metabolism in Relation to Daily Activity and Milk Consumption by Caribou and Muskox Neonates. Canadian Journal of Zoology 69: 106-114.

Parnell AC, Inger R, Bearhop S, Jackson AL. 2010. Source Partitioning Using Stable Isotopes: Coping with Too Much Variation. PLoS ONE 5(3): e9672.

Pianka ER. 1974. Niche Overlap and Diffuse Competition. Proceedings of the National Academy of Sciences 71(5): 2141-2145.

Peros MC, Gajewski K. 2009. Pollen-based Reconstructions of Late Holocene Climate from the Central and Western Canadian Arctic. Journal of Paleolimnology 41: 161-175.

Peros M, Gajewski K, Puall T, Ravindra R, Podritske B. 2010. Multi-proxy Record of Postglacial Environmental Change, South-central Melville Island, Northwest Territories, Canada. Quaternary Research 73: 247-258.

Podritske B, Gajewski K. 2007. Diatom Community Response to Multiple Scales of Holocene Climate Variability in a Small Lake on Victoria Island, NWT, Canada. Quaternary Science Reviews 26: 3179-3196.

Post E. 2013. Erosion of Community Diversity and Stability by Herbivore Removal Under Warming. Proceedings of the Royal Society B 280: 20122722.

Prévost D, Bordeleau LM, Antoun H. 1987. Symbiotic Effectiveness of Indigenous Arctic Rhizobia on a Temperate Forage Legume: Sainfoin (*Onobrychis viciifolia*). Plant and Soil 104: 63-69.

Prévost D, Jain DK, Bordeleau LM. 1990. Growth Inhibition of Rhizobia Isolated from Arctic Legumes (*Astragalus and Oxytropis* spp.) and Sainfoin (*Onobrychis viciifolia*) by Sainfoin Seed Diffusates. Phytoprotection 71: 113-119.

Qi H, Coplen TB, Geilmann H, Brand WA, Böhlke JK. 2004. Two New Organic Reference Materials for $\delta^{13}C$ and $\delta^{15}N$ Measurements and a New Value for the $\delta^{13}C$ of NBS 22 Oil. Rapid Communications in Mass Spectrometry 17: 2483-2487.

R Development Core Team. 2009. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. Available from: http://www.R-project.org.

Raghavan M, DeGiorgio M, Albrectsen A, Moltke I, Skoglund P, Korneliussen TS, Gronnow B, Appelt M, Gullov HC, Friesen TM, Fitzhugh W, Malmstrom H, Rasmussen S, Olsen J, Melchior L, and 41 others. The Genetic Prehistory of the New World Arctic. Science 345(6200): 1020-1031.

Read DJ. 1991. Mycorrhizas in Ecosystems. Experientia 47: 376-391.

Reimer PJ, Bard E, Bayliss A, Beck JW, Blackwell PG, Bronk Ramsey C, Buck CE, Cheng H, Edwards RL, Friedrich M, Grootes PM, Guilderson TP, Haflidason H, Hajdas I, Hatté C, and fifteen others. 2013. IntCal13 and Marine13 Radiocarbon Age Calibration Curves 0-50,000 Years Cal BP. Radiocarbon 55(4): 1869-1887.

Reynolds PE. 1998. Dynamics and Range Expansion of a Reestablished Muskox Population. The Journal of Wildlife Management 62(2): 734-744.

Ricklefs RE, Nealen P. 1998. Lineage-dependent Rates of Evolutionary Diversification: Analysis of Bivariate Ellipses. Functional Ecology 12: 871-885.

Robbins CT, Felicetti LA, Sponheimer M. 2005. The Effect of Dietary Protein Quality on Nitrogen Isotope Discrimination in Mammals and Birds. Oecologia 144(4): 534-540.

Robbins CT, Felicetti LA, Florin ST. 2010. The Impact of Protein Quality on Stable Nitrogen Isotope Ratio Discrimination and Assimilated Diet Estimation. Oecologia 162(3): 571-579.

Robinson D. 2001. δ^{15}N as an Integrator of the Nitrogen Cycle. TRENDS in Ecology & Evolution 16(3): 153-162.

Rosenfeld JS. 2002. Functional Redundancy in Ecology and Conservation. Oikos 98(1): 156-162.

Samuel MD, Takekawa JY, Samelius G, Goldberg DR. 1999. Avian Cholera Mortality in Lesser Snow Geese Nesting on Banks Island, Northwest Territories. Wildlife Society Bulletin 27(3): 780-787.

Savelle JM, Dyke AS. 2002. Variability in Paleoeskimo Occupation on South-western Victoria Island, Arctic Canada: Causes and Consequences. World Archaeology 33(3): 508-522.

Savelle JM, Dyke AS. 2009. Paleoeskimo Demography on Western Boothia Peninsula, Arctic Canada. Journal of Field Archaeology 34: 267-283.

Schimel JP, Chapin FS, III. 1996. Tundra Plant Uptake of Amino Acid and NH_4^+ Nitrogen in Situ: Plants Compete Well for Amino Acid N. Ecology 77(7): 2142-2147.

Schimel JP, Bennett J. 2004. Nitrogen Mineralization: Challenges of a Changing Paradigm. Ecology 85(3): 591-602.

Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG. 1990. Biological Feedbacks in Global Desertification. Science 247(4946): 1043-1048.

Schoener TW. 1968. The Anolis Lizards of Bimini: Resource Partitioning in a Complex Fauna. Ecology 49: 704-726.

Schoeninger MJ, Moore KM, Murray ML, Kingston JD. 1989. Detection of Bone Preservation in Archaeological and Fossil Samples. Applied Geochemistry 4: 281-292.

Shank CC, Barr W, Arnold CD. 1994. Muskox Hunting Sites on Northern Banks Island – Resolving the Contradictions. Unpublished manuscript on file at Prince of Wales Northern Heritage Centre, Yellowknife, Northwest Territories.

Skoog RO. 1968. Ecology of the Caribou (*Rangifer tarandus granti*) in Alaska. [Dissertation]. [Berkeley (CA)]: University of California Berkeley.Smith DL. 1996. Muskoxen/Sedge Meadow Interactions, North-Central Banks Island, Northwest Territories, Canada. [Dissertation]. [Saskatoon (SK)]: University of Saskatchewan.

Smith TB, Skúlason S. 1996. Evolutionary Significance of Resource Polymorphisms in Fishes, Amphibians, and Birds. Annual Review of Ecology and Systematics 27: 111-133.

Soberón J. 2007. Grinnellian and Eltonian Niches and Geographic Distributions of Species. Ecology Letters 10: 1115-1123.

Solheim B, Endal A, Vigstad H. 1994. Nitrogen Fixation in Arctic Vegetation and Soils from Svalbard, Norway. Polar Biology 16: 35-40.

Stefansson V. 1921. The Friendly Arctic: The Story of Five Years in Polar Regions. New York: The MacMillan Company.

Stevens RE, Hedges REM. 2004. Carbon and Nitrogen Stable Isotope Analysis of Northwest European Horse Bone and Tooth Collagen, 40,000 BP-Present: Palaeoclimatic Interpretations. Quaternary Science Reviews 23: 977-991.

Stevens RE, Jacobi R, Street M, Germonpré M, Conard NJ, Münzel SC, Hedges REM. 2008. Nitrogen Isotope Analyses of Reindeer (Rangifer tarandus), 45,000 BP to 9,000 BP: Paleoenvironmental Reconstructions. Palaeogeography, Palaeoclimatology, Palaeoecology 262: 32-45.

Stuiver M, Reimer PJ, Reimer RW. 2017. CALIB 7.1 (WWW Program). Available from: http://calib.org.

Stutz RC. 1977. Biological Nitrogen Fixation in High Arctic Soils, Truelove Lowland. In: Bliss LC, editor. Truelove Lowland, Devon Island, Canada: A High Arctic Ecosystem. Edmonton: University of Alberta Press. Pp. 301-314.

Svanbäck R, Bolnick DI. 2007. Intraspecific Competition Drives Increased Resource Use Diversity Within a Natural Population. Proceedings of the Royal Society B 274: 839-844.

Syväranta J, Lensu A, Marjomäki TJ, Oksanen S, Jones RI. 2013. An Empirical Evaluation of the Utility of Convex Hull and Standard Ellipse Areas for Assessing Population Niche Widths from Stable Isotope Data. PLoS ONE 8(2): e56094.

Szpak P, Millaire J-F, White CD, Longstaffe FJ. 2014. Small Scale Camelid Husbandry in the North Coast of Peru (Virú Valley): Insight from Stable Isotope Analysis. Journal of Anthropological Archaeology 36: 110-129.

Tans PP, DeJong AFM, Mook WG. 1979. Natural Atmospheric ^{14}C Variation and the Suess Effect. Nature 280: 826-828.

Taylor WE. 1967. Summary of Archaeological Field Work on Banks and Victoria Islands, Arctic Canada, 1965. Arctic Anthropology 4(1): 221-243.

Tener JS. 1965. Muskoxen in Canada: A Biological and Taxonomic Review. Ottawa: Canadian Wildlife Service, Department of Northern Affairs and National Resources, Natural and Historic Resources Branch.

Thing H, Klein DR, Jingfors K, Holt S. 1987. Ecology of Muskoxen in Jameson Land, Northeast Greenland. Holarctic Ecology 10(2): 95-103.

Tieszen LL, Boutton TW, Tesdahl KG, Slade NA. 1983. Fractionation and Turnover of Stable Carbon Isotopes in Animal Tissues: Implications for $\delta^{13}C$ Analysis of Diet. Oecologia 57: 32-37.

Tieszen LL, Fagre T. 1993. Effect of Diet Quality and Composition on the Isotopic of Respiratory CO_2, Bone Collagen, Bioapatite, and Soft Tissues. In: Lambert JB, Grupe G, editors. Prehistoric Human Bone: Archaeology at the Molecular Level. Berlin: Springer-Verlag. Pp. 121-156.

Toews S. 1998. "The Place Where People Travel". The Archaeology of Aulavik National Park, Banks Island. Report on File, Cultural Resource Management Canadian Heritage, Western Canada Service Centre, Winnipeg, Manitoba.

Tozer WC, Hackell D, Miers DB, Silvester WB. 2005. Extreme Isotopic Depletion of Nitrogen in New Zealand Lithophytes and Epiphytes; the Result of Diffusive Uptake of Atmospheric Ammonia? Oecologia 144: 628-635.

Trouet V, Esper J, Graham NE, Baker A, Scourse JD, Frank DC. 2009. Persistent Positive North Atlantic Oscillation Mode Dominated the Medieval Climate Anomaly. Science 324: 78-80.

Tyler NJC. 2010. Climate, Snow, Ice, Crashes, and Declines in Populations of Reindeer and Caribou (*Rangifer tarandus L.*). Ecological Monographs 80(2): 197-219.

Van Cleve K, Alexander V. 1981. Nitrogen Cycling in Tundra and Boreal Ecosystems. In: Clark FE, Rosswall T, editors. Terrestrial Nitrogen Cycles. Ecological Bulletins 33: Stockholm: Swedish Natural Science Research Council. Pp. 375-404.

van Klinken GJ. 1999. Bone Collagen Quality Indicators for Palaeodietary and Radiocarbon Measurements. Journal of Archaeological Science 26: 687-695.

Vitousek PM, Cassman K, Cleveland C, Crews T, Field CB, Grimm NB, Howarth RW, Marino R, Martinelli L, Rastetter EB, Sprent JI. 2002. Towards an Ecological Understanding of Biological Nitrogen Fixation. Biogeochemistry 57/58: 1-45.

Welker JM, Fahnestock JT, Povirk KL, Bilbrough CJ, Piper RE. 2004. Alpine Grassland CO_2 Exchange and Nitrogen Cycling: Grazing History Effects, Medicine Bow Range, Wyoming, U.S.A. Arctic, Antarctic, and Alpine Research 36(1): 11-20.

White RG, Rowell JE, Hauer WE. 1997. The Role of Nutrition, Body Condition and Lactation on Calving Success in Muskoxen. Journal of the Zoological Society of London 243: 13-20.

Wilkinson PF, Shank CC. 1975. Archaeological Observations in North Central Banks Island. Arctic Anthropology 12(1): 104-112.

Wilkinson PF, Shank CC, Penner DF. 1976. Muskox-Caribou Summer Range Relations on Banks Island, N.W.T. Journal of Wildlife Management 40(1): 151-162.

Will RT. 1985. Nineteenth Century Copper Inuit Subsistence Practices on Banks Island, N.W.T. [Dissertation]. [Edmonton (AB)]: University of Alberta.

Wilmeth R. 1978. Canadian Archaeological Radiocarbon Dates (Revised Edition). Mercury Series, Archaeological Survey of Canada Paper 77. Quebec: Canadian Museum of Civilization.

Zahran HH. 1999. *Rhizobium*-legume Symbiosis and Nitrogen Fixation Under Severe Conditions and in an Arid Climate. Microbiology and Molecular Biology Reviews 63(4): 968-989.

Zazzo A, Balasse M, Patterson WP. 2006. The Reconstruction of Mammal Individual History: Refining High-resolution Isotope Record in Bovine Tooth Dentine. Journal of Archaeological Science 33: 1177-1187.

Chapter 4

4 Assessing the Potential of Enamel $\delta^{18}O$ for the Reconstruction of Seasonal Movements in Caribou (*Rangifer tarandus* spp.) and Muskoxen (*Ovibos moschatus*) on Banks Island, NWT, Canada. A Test Using GIS, FTIR and LA-GC-IRMS

The $\delta^{18}O$ of incrementally-forming tissues like tooth enamel are commonly used as paleoenvironmental proxies. Under certain conditions, enamel $\delta^{18}O$ also provides information about geographic movements during tooth formation. Caribou (*Rangifer tarandus* spp.) and muskoxen (*Ovibos moschatus*) have limited water intake requirements, and may obtain most or all their required water from forage. If this is the case, the $\delta^{18}O$ of incrementally growing tooth enamel in both species should reflect geographic variation in forage $\delta^{18}O$ during the brief Arctic summer. Consequently, tooth enamel $\delta^{18}O$ will be useful for reconstructing ancient faunal movements, and will potentially enhance our understanding of the relationship between the seasonal movements of caribou and muskoxen and their interactions with ancient hunters on Banks Island. Using laser ablation-GC-IRMS, we test the hypothesis that enamel $\delta^{18}O$ records seasonal movements using the $\delta^{18}O$ of modern surface water samples collected during summer and tooth enamel from modern and archaeological caribou and muskoxen from Banks Island, NWT, Canada.

Our results suggest that there is a latitudinal gradient of ~ 5‰ in the $\delta^{18}O$ of meteoric surface waters on Banks Island during summer (June-August). Our hypothesis that the $\delta^{18}O$ of sequentially sampled enamel from caribou and muskox teeth reflects seasonal movements, however, is not supported. Instead, intra-tooth variation in enamel $\delta^{18}O$ in both species appears to correspond to seasonal variation in precipitation $\delta^{18}O$. This suggests that snow or ice is regularly consumed during the winter by caribou and muskoxen. Despite its utility in reconstructing mobility in other contexts, this approach is therefore not useful for reconstructing seasonal movements in caribou and muskoxen on Banks Island. Sequences of $\delta^{13}C$ in tooth enamel analyzed via laser ablation also agree with sequential crown dentin collagen $\delta^{13}C$ results from Chapters 2 and 3, which suggest that caribou and muskoxen

both alternate between forage with lower $\delta^{13}C$ during the summer and forage with higher $\delta^{13}C$ during winter.

4.1 Introduction

Caribou (*Rangifer tarandus* spp.) and muskoxen (*Ovibos moschatus*) are the only large-bodied ungulates to have inhabited the High Arctic of Canada and Greenland during the Holocene. Today, large portions of the global Peary caribou (*Rangifer tarandus Pearyi*)[18] and muskox populations inhabit Banks Island (COSEWIC 2004), which is located in the Northwest Territories of Canada (Figure 4.1, inset). Traditional ecological knowledge (Nagy 1999; Kelvin 2016, personal communication) and observational data (Usher 1965; Kelsall 1968; Nieminen 1980; Lent 1999; Hummel and Ray 2008) suggest that both species spend springs and summers in the northern part of the island, and move south during the winter. Further, oral accounts suggest that landscape use by caribou and muskoxen on Banks Island changes as the muskox population fluctuates in size (Nagy 1999; Kelvin 2016). Researchers have also suggested that while muskoxen do not leave the island, Peary caribou may travel across ice to the mainland when forage conditions are poor (Manning and MacPherson 1958; Miller 1990; Miller et al. 2005). Consequently, the relationship between range conditions, muskox demography, and caribou and muskox landscape use may have affected the availability of both species to ancient hunters across archaeological periods on Banks Island (Table 4.1).

[18] To account for possible admixture of caribou subspecies on Banks Island, we use the generalized taxonomic identifiers "*Rangifer tarandus* spp." and "caribou" in this paper, unless referring to studies specific to Peary caribou.

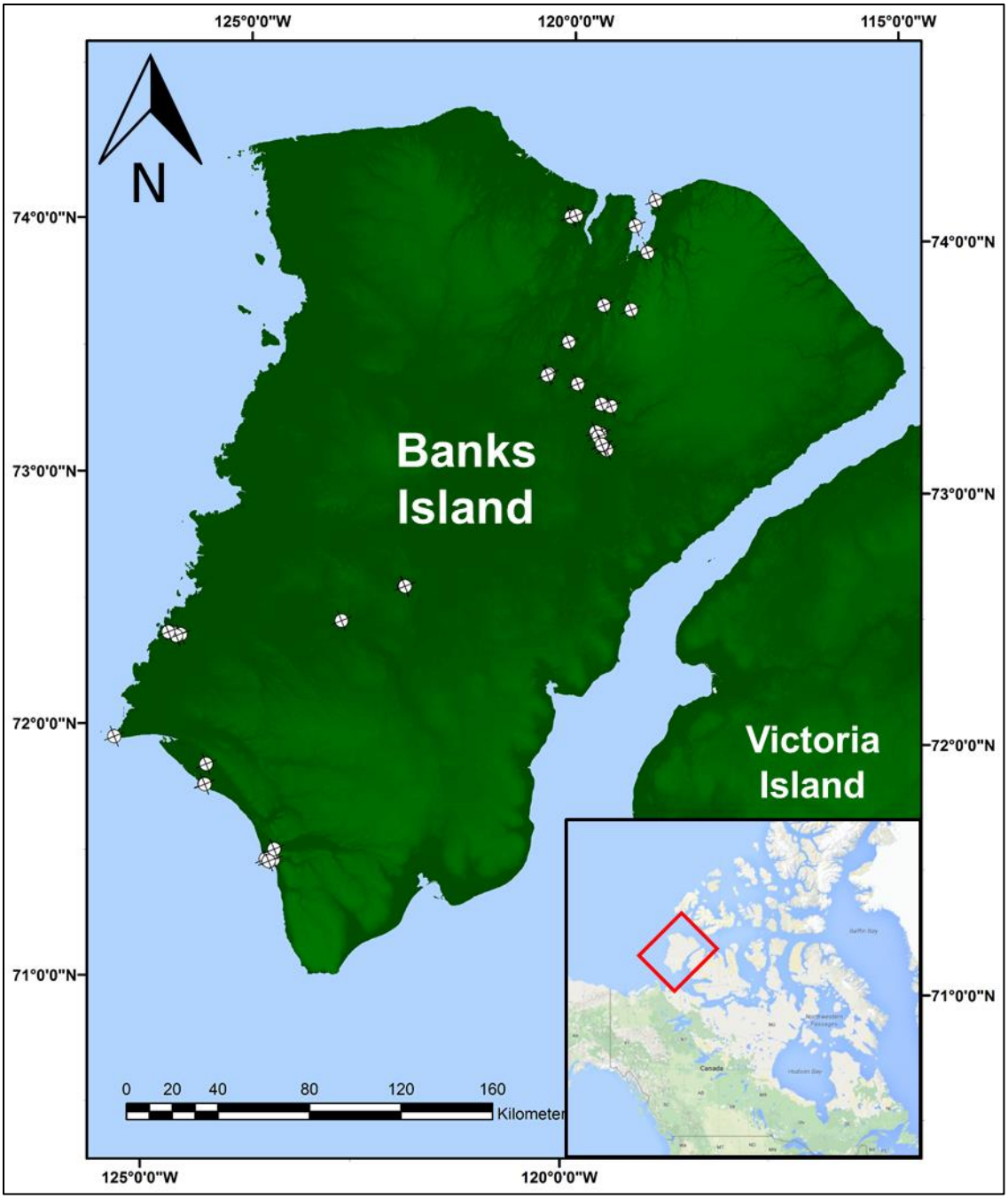


Figure 4.1. Location of Banks Island within North America (inset), and the location of meteoric surface water sampling sites.

Table 4.1. The division of archaeological periods on Banks Island. Note the large apparent occupational hiatuses preceding and following the Lagoon period. For further discussion, see Chapter 3.

Cultural Period	Approximate Duration (cal. ^{14}C BP)
Pre-Dorset	4000 – 3400
Lagoon	2700 – 2100
Early Thule	950 – 700
Classic Thule	700 – 500
Inuit	500 – 100

In this chapter, we test the hypothesis that oxygen isotope ($\delta^{18}O$) compositions of sequentially-sampled tooth enamel, obtained using laser ablation-gas chromatography-isotope ratio mass spectrometry (LA-GC-IRMS) can be used to investigate the seasonal movements of caribou and muskoxen on and off Banks Island over the last 4000 years. Additionally, we hypothesize that the stable carbon isotope ($\delta^{13}C$) composition of the structural carbonate component of tooth enamel, which is obtained simultaneously during LA-GC-IRMS analysis, can provide information about seasonal dietary variation during the time of enamel formation.

4.1.1 Rationale

The inorganic phase of mammalian bone and tooth enamel is composed of a calcium phosphate biomineral similar in structure to hydroxylapatite [$Ca_{10}(PO_4)_6(OH)_2$] (Young 1975; LeGeros 1991; Elliott 2002; Hughes and Rakovan 2002). The reconstruction of human or faunal movements using bioapatite (i.e. biological apatite) $\delta^{18}O$ is predicated on the relationship between the $\delta^{18}O$ of the oxygen-bearing moieties in bioapatite, body water, and sources of ingested water (Longinelli 1984; Luz et al. 1984, 1990).

Nearly all drinking water sources (e.g. surface, phreatic, and plant water) ultimately derive from meteoric precipitation, the $\delta^{18}O$ of which varies spatially (Epstein and Mayeda 1953; Craig and Gordon 1965; Yurtsever and Gat 1981; Rozanski et al. 2001; Bowen and Wilkinson 2002; Bowen and Revenaugh 2003) and seasonally (Dansgaard 1964; Gat 1981a, b; Yurtsever and Gat 1981; Horita and Wesoloski 1994; Gat et al. 2001; Darling et al. 2005). In temperate regions, seasonal variation in meteoric precipitation will therefore dominate the $\delta^{18}O$ of incrementally growing tissues in obligate drinkers (i.e. those animals who obtain most of their water from meteorically-derived water sources) (Kohn 1996; Kohn et al. 1998; Kohn and Cerling 2002; Kohn 2004).

Many herbivores living in arid regions, however, nearly or entirely satisfy their water requirements with vegetation alone (Ayliffe and Chivas 1990; Huertas et al. 1995; Sponheimer and Lee-Thorp 1999). Tundra environments, particularly during winter, are comparable in some ecological respects to arid and semi-arid ecosystems (Bliss et al. 1973;

Caughley and Gunn 1993; Gray 1997a; Behnke 2000; Miller and Gunn 2003). Accordingly, several researchers (Gray 1973; Bocherens et al. 1996; Britton et al. 2009) have suggested that caribou and muskoxen probably obtain most of their water from forage, with only occasional inputs from surface waters during the brief summer. In the Arctic, vascular plants are only metabolically active for two to three months (Allessio and Tieszen 1975; Gray 1997b; Larter and Nagy 2001) and during this period, most water is available to plants in the form of shallow soil meltwater derived from winter precipitation, which is further enriched in ^{18}O through sublimation and evaporation (Halevy 1970; Arnason 1981; Cooper et al. 1993; Gibson 2002; Gibson and Edwards 2002; Gibson et al. 2010; Lechler and Niemi 2012).

Typically, no isotopic exchange occurs between meltwater and soil during percolation (Gat 1981c) or during uptake of soil water by plant roots (White et al. 1985; Ehleringer et al. 2000; Yakir and Sternberg 2000). Hence, the $\delta^{18}O$ of water in the roots, stems, and other non-photosynthesizing plant tissues (xylem water) should correspond closely to that of soil water. Leaf water, however, is enriched in ^{18}O relative to xylem water because water isotopologues containing ^{16}O have a faster rate of diffusion and higher vapor pressure and are therefore preferentially transpired from leaf stomata (Gonfiatini et al. 1965; Dongmann et al. 1974; Epstein et al. 1977; Yakir et al. 1990; Flanagan 1993; Yakir and Sternberg 2000; Cuntz et al. 2007; Sullivan and Welker 2007). During the summer, and especially at coastal sites, fog (which is either enriched in, or depleted of ^{18}O depending on the geographic origin of the parent cloud system; see Ingraham and Matthews 1988, 1990; Dawson 1998) may also constitute a source of water for vegetation (Sullivan and Welker 2007; Eller et al. 2013). Still, because soil water is the dominant water source during the growing season, its $\delta^{18}O$ should ultimately control the baseline $\delta^{18}O$ of plant material (Alstad et al. 1999; Yakir and Sternberg 2000; Welker et al. 2005). If there is significant geographic variation in the $\delta^{18}O$ of plant source water during the growing season, then the $\delta^{18}O$ of dormant or frozen forage tissues may partially reflect this variation (plus some degree of enrichment in ^{18}O due to transpiration) throughout the remainder of the year. As a result, the $\delta^{18}O$ of incrementally-growing tissues like tooth enamel in caribou and muskoxen may record geographic variation in ingested plant $\delta^{18}O$.

We hypothesize that if: (1) caribou and muskoxen derive most of their body water from vegetation; (2) there is significant geographic variation in summer meltwater $\delta^{18}O$ on Banks Island; and (3) frozen vegetation reflects or is influenced by its growing season $\delta^{18}O$ throughout the rest of the year, the $\delta^{18}O$ of incrementally growing tissues like tooth enamel can be used to investigate migration or seasonal movements.

4.1.2 Tooth Enamel Formation

Although we know of no published studies of tooth development in caribou or muskoxen, several researchers have documented the tooth eruption process in both species (Banfield 1954; Tener 1965; Miller 1974; Henrichsen and Grue 1980). These data are plotted as figures in this chapter (Figures 4.2 and 4.3). The temporal relationship among tooth growth, enamel mineralization, and eruption, however, is complex and varies significantly across species (Balasse 2002; Hoppe et al. 2004; Kohn 2004). In most mammals, gross tooth development proceeds from the apex of the tooth crown towards the roots (Figure 4.4a; Hillson 2000). Enamel formation begins with the secretion of "mineral-poor, protein-rich hydrated matrix" (Passey and Cerling 2002:3225) by ameloblasts, proceeding outwards from the dentinoenamel junction (DEJ) (Figure 4.4b; Arsenault and Robinson 1989). The innermost enamel layer is rapidly and almost entirely mineralized during this first stage (Suga et al. 1979; Suga 1983). The completion of the matrix deposition stage is followed by its rapid but discontinuous mineralization, which starts from the outer enamel surface and moves back towards the DEJ. During this first phase of mineralization, most of the mineral content composing the tooth enamel is deposited (Suga et al. 1970, 1983). Additional mineral content is then deposited in smaller amounts sweeping from the DEJ back to the tooth surface (Suga 1982).

Significantly, tooth enamel does not remodel after mineralization is complete (Longinelli 1984; Luz et al. 1984; Lowenstam and Weiner 1989; Hillson 2000), which means that its isotopic compositions will remain intact throughout life and, barring chemical alteration in the depositional environment, after death. Isotopic signal attenuation (i.e. the averaging or dampening of an isotopic signal) in tooth enamel is directly proportional to the duration of the mineralization process. Isotopic (Fricke et al. 1998; Kohn et al. 1998; Bocherens et al. 2001; Balasse et al. 2002, 2003) and fluorochrome labeling (Kierdorf et al. 2013) studies

suggest that in caprines like muskoxen, enamel mineralization is completed in a month or less. Consequently, there should be minimal inherent attenuation of environmental isotopic signals in muskox tooth enamel. Conversely, Fricke et al. (1998) suggest that the enamel mineralization process in cervids takes closer to six months, although their analysis is limited to elk (*Cervus canadensis*), and enamel mineralization in diminutive Peary caribou may require less time.

Assuming that enamel is completely mineralized shortly following the apposition of the enamel matrix, and accounting for occlusal wear in the tooth crown, the seasonal isotopic patterns integrated by tooth enamel in caribou and muskoxen should correspond roughly to the eruption schedules reproduced in Figures 4.1a and b. In caribou, first molars (M1s) should integrate isotopic signals between birth and the end of the first winter, second molars (M2s) should integrate isotopic signals between the first winter and the end of the second summer, and fourth permanent premolars (P4s) and third molars (M3s) should integrate isotopic signals between the second summer and third summer. Likewise, the tooth enamel of muskox M1s should integrate isotopic signals between birth and the second summer of life.

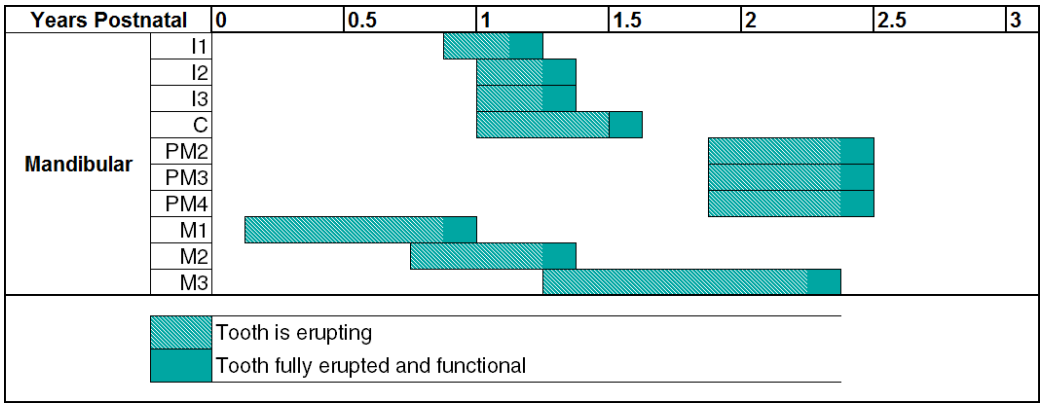


Figure 4.2. Eruption sequence of permanent dentition in barren ground caribou, reproduced from Chapter 2. “I” = incisor, “C” = canine, “PM” = premolar, and “M” = molar. Data are from Banfield (1954) and Miller (1974).

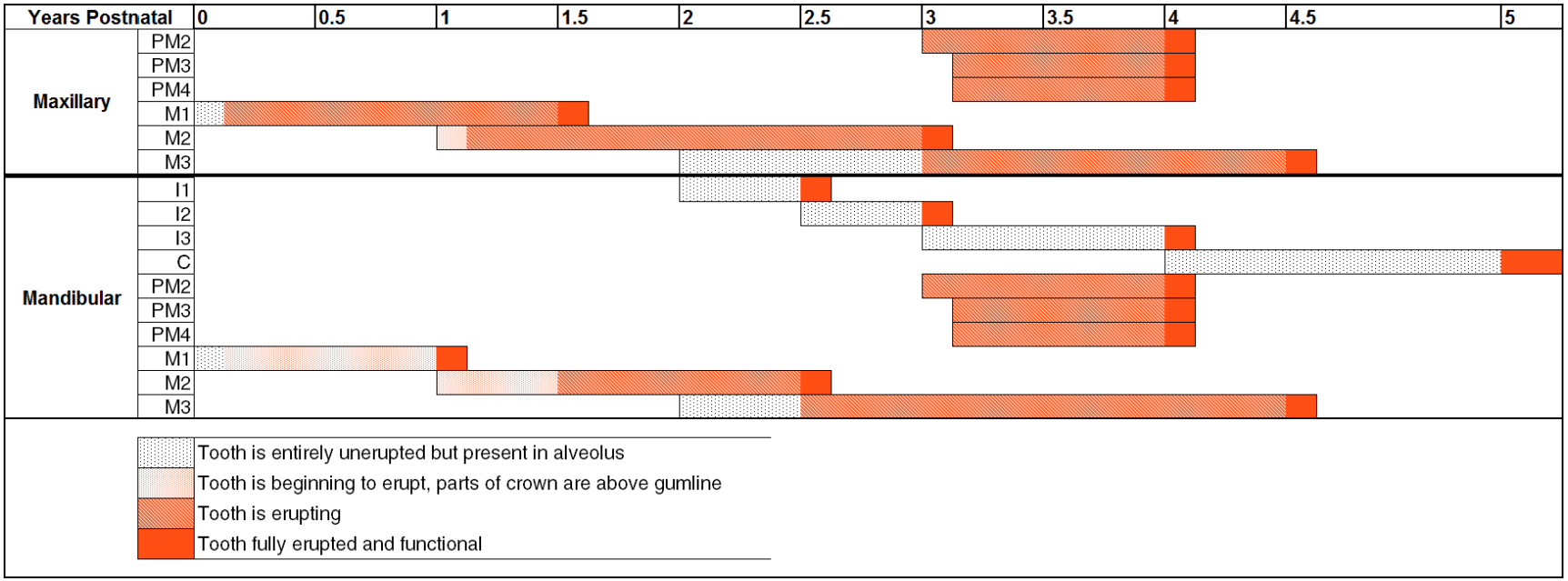


Figure 4.3. Eruption sequence of permanent dentition in muskoxen, reproduced from Chapter 2. "I" = incisor, "C" = canine, "PM" = premolar, and "M" = molar. Data are from Tener (1965) and Henrichsen and Grue (1980).

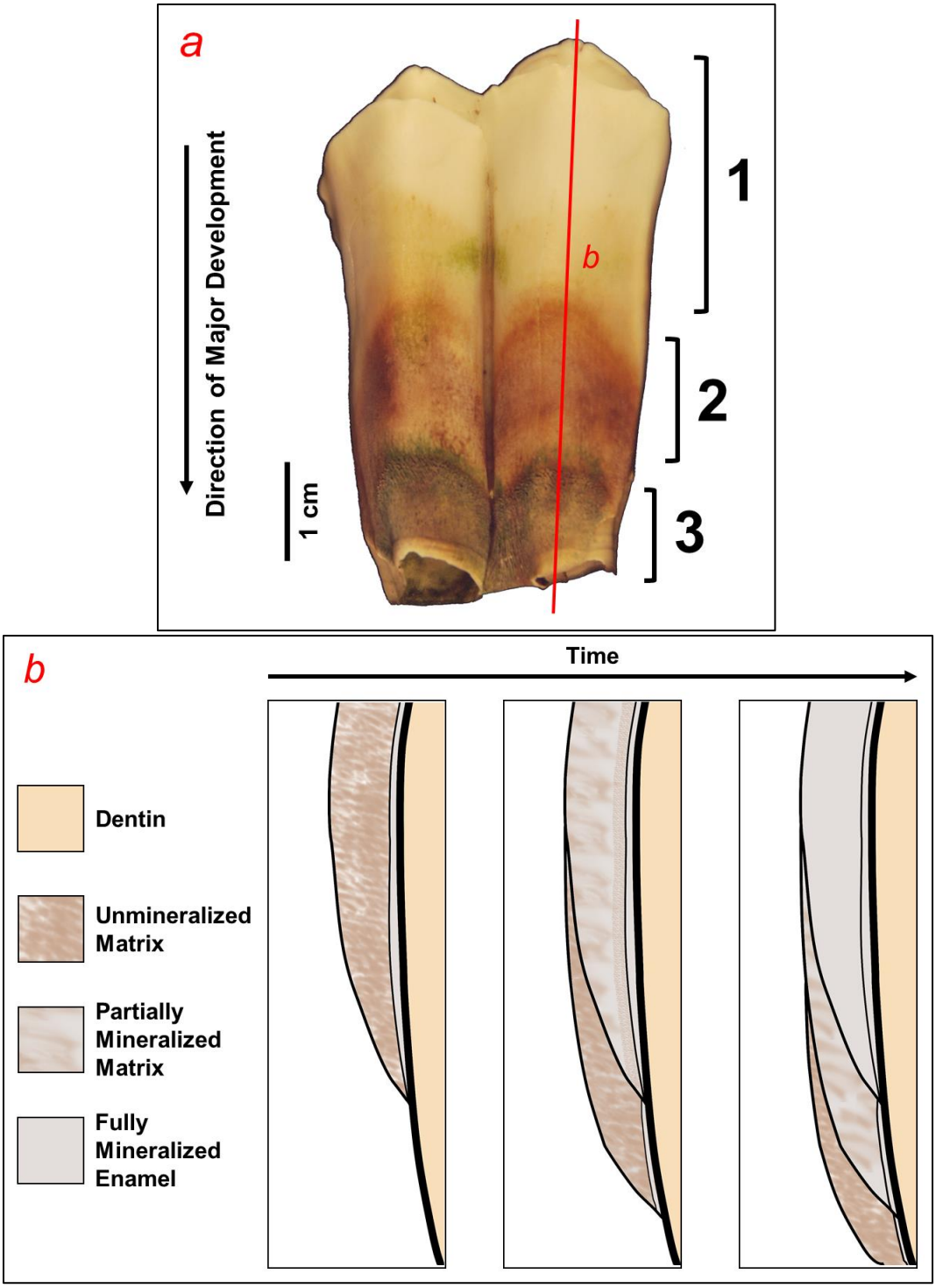


Figure 4.4. (*a*) buccal view of an unworn muskox M2 crown showing enamel in different stages of the mineralization process in brackets: (1) fully mineralized enamel; (2) partially mineralized enamel; and (3) area of unmineralized, partially-deposited enamel matrix. **(*b*)** simplified model of enamel development in a transverse tooth crown section showing the successive deposition and mineralization of enamel layers.

4.1.3 Stable Carbon and Oxygen Isotope Signals in Tooth Enamel

Of the oxygen-bearing moieties in the bioapatite phase in enamel, phosphate (PO_4) accounts for ~ 90% by weight, while structural carbonate (CO_3) substitutions account for 4-6% by weight, and hydroxyl groups (OH^-) account for ~ 3% by weight (LeGeros 1991; Penel et al. 1998; Elliott 2002). The relationships among the $\delta^{18}O$ of drinking water, body water, bioapatite phosphate, and bioapatite structural carbonate are represented graphically in Figure 4.5. In mammals, there is a ~ +17.5‰ fractionation of ^{18}O between body water and bioapatite phosphate (Longinelli and Nuti 1973; Kolodny et al. 1983; Bryant et al. 1996; Lécuyer et al. 1996). Likewise, catalysis of blood CO_2 by the enzyme carbonic anhydrase results in a ~ +26‰ fractionation in ^{18}O between body water and structural carbonate in large mammals (Silverman 1982; Bryant et al. 1996).

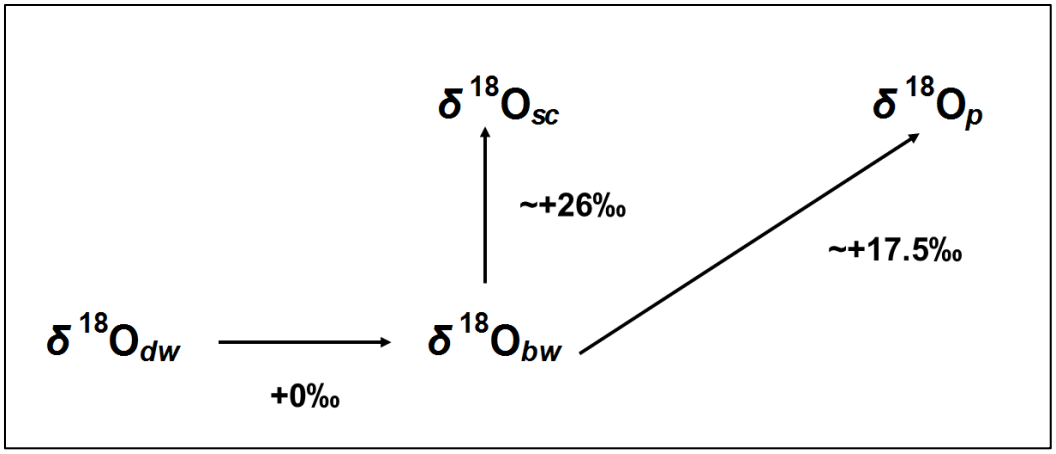


Figure 4.5. Diagram of the fractionation of ^{18}O between drinking water ($\delta^{18}O_{dw}$), body water ($\delta^{18}O_{bw}$), and tooth enamel structural carbonate ($\delta^{18}O_{sc}$) and phosphate ($\delta^{18}O_{p}$). The $\delta^{18}O$ of carbonate and phosphate in bioapatite is determined by the $\delta^{18}O$ of body water ($\delta^{18}O_{bw}$), which is in turn determined by the $\delta^{18}O$ of ingested water (Bryant et al. 1996). There is typically no fractionation of ^{18}O during the ingestion of water (Luz et al. 1984; White et al. 1985; Ayliffe and Chivas 1990; Bryant and Froelich 1995). Liberation of CO_2 from apatite with phosphoric acid also causes a minor fractionation of ^{18}O of +0.1 to +0.4‰ (the "acid fractionation factor") (Bryant et al. 1996) although this is accounted for during the production of isotopic data.

The carbon in structural carbonate derives from CO_2 dissolved in blood bicarbonate (HCO_3^-) through a temperature-dependent +8-12‰ fractionation (at normal mammalian body temperature, ~ 37°C) and a +1-2‰ fractionation between HCO_3^- and structural carbonate (Bryant et al. 1996; Cerling and Harris 1999; Hedges and van Klinken 2000; Passey et al. 2005). Since dietary inputs are the main source of CO_2 incorporated into the blood bicarbonate pool, the $\delta^{13}C$ of structural carbonate should reflect the average $\delta^{13}C$ of all dietary contributions during the time of formation, plus 9-14‰. Controlled experiments (Hedges and Van Klinken 2000; Balasse 2002; Hedges 2003; Passey et al. 2005) suggest that the enrichment in ^{13}C between structural carbonate and diet ($\Delta^{13}C_{sc\text{-}diet}$) in large ruminant herbivores is consistently near the higher end (~ +14‰) of this range. This additional enrichment in ^{13}C occurs because the fermentation of forage by gut microbes in ruminants produces ^{13}C-depleted methane (Metges et al. 1990), which is expelled from the body, and leaves behind ^{13}C-enriched CO_2 which then exchanges with blood bicarbonate.

4.2 Materials

4.2.1 Meteoric Surface Water Samples

Twenty water samples were collected from fresh water bodies (ponds and lakes) and water courses (rivers and meltwater streams) during helicopter visits across Banks Island in July 2014 (Figure 4.1). Water samples were collected in 8 mL Nalgene® HDPE bottles and their lids were wrapped with Parafilm® upon sealing, kept cool in transit, and kept refrigerated upon their arrival at the University of Western Ontario. The 2014 water samples were supplemented by eleven samples collected in June and July of 2008 and eight samples collected in July and August of 2010 as part of a pilot project (Hodgetts and Longstaffe, unpublished data). Collection site information for all water samples is listed in Table 4.2.

Table 4.2. Oxygen and hydrogen isotope compositions of meteoric surface water samples collected from Banks Island in 2008, 2010, and 2014.

Sample ID	Collection Date	Type	Site Name	Northing (NAD83, DDD)	Westing (NAD83, DDD)	Elev (m)	$\delta^{18}O$ (‰, VSMOW)	$\delta^{2}H$ (‰, VSMOW)
08WS-1	June 27, 2008	Stream	Painted Sands Creek	73.2108	119.48338	35	–21.7	–173
08WS-2	July 9, 2008	Pond		73.2286	119.54795	37	–10.9	–111
08WS-3	July 16, 2008	River	Thomsen River	73.23017	119.53855	32	–19.3	–156
08WS-4	July 18, 2008	Lake	Nangmagvik Lake	74.13798	119.99563	16	–21.1	–166
08WS-5	July 18, 2008	Lake	Twin Lakes	73.78485	119.53173	59	–19.6	–156
08WS-6	July 19, 2008	Stream	Dissection Creek	73.27522	119.57112	37	–18.4	–158
08WS-7	July 19, 2008	Pond		73.28178	119.63098	59	–15.3	–132
08WS-8	July 1, 2008	Pond		72.3927	125.17542	30	–14.4	–121
08WS-9	July 1, 2008	Lake		72.39307	125.09978	50	–14.6	–121
08WS-10	July 1, 2008	Stream		72.3854	125.15588	30	–15.0	–130
08WS-11	July 1, 2008	Stream		72.39753	125.26372	10	–19.4	–154
10WS-1	July 22, 2010	Lake		74.10065	119.0858	25	–19.9	–158
10WS-2	July 22, 2010	Lake	Nangmagvik Lake	74.13507	120.01413	14	–21.1	–165
10WS-3	July 28, 2010	Stream		73.99437	118.90913	91	–18.0	–142
10WS-4	August 4, 2010	River	Desert River	74.14012	119.93952	19	–17.5	–141
10WS-5	August 11, 2010	Stream		73.4718	119.89092	15	–19.4	–153
10WS-6	July 12, 2010	Lake	Joe Lake	73.63795	120.0245	15	–20.3	–161
10WS-7	July 13, 2010	Stream		73.76717	119.1423	295	–15.4	–123
10WS-8	August 12, 2010	Stream	Dissection Creek	73.26337	119.59688	35	–21.4	–171

14WS-1	July 1, 2014	Lake		71.52546	123.66863	80	–12.6	–102
14WS-2	July 1, 2014	Pond		71.52678	123.76323	80	–9.7	–90
14WS-3	July 3, 2014	Lake	Shoran Lake	73.51107	120.29798	31	–16.5	–149
14WS-4	July 3, 2014	Pond		73.50518	120.31715	73	–19.7	–157
14WS-5	July 3, 2014	River	Shoran River	73.50534	120.31846	69	–18.9	–156
14WS-6	July 3, 2014	Lake		73.50518	120.31715	73	–19.2	–151
14WS-7	July 3, 2014	Lake	Twin Lakes	73.38406	119.42425		–21.7	–164
14WS-8	July 3, 2014	Lake	Char Lake	73.39268	119.56048	30	–21.0	–165
14WS-9	July 3, 2014	River	Thomsen River	73.23099	119.53828	34	–21.1	–168
14WS-10	July 4, 2014	Lake		73.23111	119.54727	46	–16.5	–144
14WS-11	July 4, 2014	Stream		74.20025	118.78678	14	–22.3	–171
14WS-12	July 4, 2014	River	Bernard River	72.64622	122.17793		–18.2	–144
14WS-13	July 4, 2014	Lake		72.64634	122.16920		–18.4	–142
14WS-14	July 4, 2014	River	Big River	72.49654	122.99009	59	–18.4	–136
14WS-15	July 5, 2014	River	Sachs River	71.88650	124.61675	11	–21.1	–156
14WS-16	July 5, 2014	Pond		71.96143	125.82905	-6	–8.4	–69
14WS-17	July 5, 2014	River	Masik River	71.56788	123.66692		–18.3	–128
14WS-18	July 5, 2014	Pond		71.51907	123.72367	4	–12.8	–103
14WS-19	July 30, 2014	Lake		71.80630	124.61629	-17	–10.6	–93
14WS-20	July 30, 2014	Lake	Emegak Lake	71.80521	124.61201	22	–12.7	–110

4.2.2 Tooth Enamel

For caribou, we sampled as many teeth from single tooth rows as possible to increase the likelihood of tracking multiple movements or migrations over the first several years of life. For muskoxen, we sampled only M1s under the assumption that interannual variability in seasonal movements is limited and enamel mineralizes rapidly. Modern caribou tooth samples originate from caribou harvested in 2015 and 2016, and modern muskox teeth come from two recently-deceased muskoxen found near archaeological sites visited in 2014. We also collected ancient caribou and muskox teeth from radiocarbon-dated archaeological sites on Banks Island in 2014.

Our caribou tooth dataset is limited to teeth from two modern caribou, two Inuit period caribou, and three Classic Thule period caribou (Table 4.3). The muskox tooth dataset is limited to M1s from: two recently-deceased muskoxen, one Inuit period muskox, one Classic Thule period muskox, one Early Thule period muskoxen; two Lagoon period muskoxen, and two Pre-Dorset period muskoxen (Table 4.3). Because of the small sample sizes, we cannot adequately assess intra-herd variability in isotopic compositions across cultural periods (Hoppe 2006; Britton et al. 2009; Pearson and Grove 2013).

Table 4.3. Caribou and muskox tooth sample information.

Sample ID	Borden	Site Name	Taxon	Tooth
Pre-Dorset				
BIBS14-407	PjRa-1	Shoran Lake	Muskox	M1
BIBS14-409	PjRa-2	Umingmak	Muskox	M1
Lagoon				
BIBS14-162	QaPv-5		Muskox	M1
BIBS16-209	QaPv-5		Muskox	M1
Early Thule				
BIBS16-30	OhRh-1	Nelson River	Muskox	M1
Classic Thule				
BIBS14-298	OlRr-1	Cape Kellett	Caribou	M1 M2 M3
BIBS14-494	OkRn-1	Agvik	Caribou	M1
BIBS14-502	OkRn-1	Agvik	Caribou	M1
BIBS14-474	QbPu-1	Back Point	Muskox	M1
Inuit				
BIBS14-214	PdRi-1	Sunnguqpaaluk	Caribou	M1 M2 M3 P4
BIBS14-360	PlPx-1	Head Hill	Caribou	M1
BIBS14-456	PlPx-1	Head Hill	Muskox	M1
Modern				
BIBS15-67			Caribou	M2
BIBS16-19			Caribou	dp4 M1 M2
BIBS14-169			Muskox	M1
BIBS14-445			Muskox	M1

4.3 Methods

Tooth thick sections were produced at the Zooarchaeology Laboratory at the University of Western Ontario, London, Ontario, Canada. All micromilling, spectroscopic and isotopic analyses were performed at the Laboratory for Stable Isotope Science (LSIS) at the University of Western Ontario, London, Ontario, Canada.

4.3.1 Sample Preparation

No pH balancing (Mills and Urey 1940), filtration, or other treatments were applied to water samples prior to isotopic analysis. See Section 4.3.5 (below) for methods used in oxygen and hydrogen isotope GC-IRMS analysis of the water samples.

Selected teeth were cleaned of soil, debris, and cementum with a soft-bristle toothbrush and dental scaler and rinsed with ultrapure water (Figure 4.6a). After drying under constant airflow in a fume hood, whole teeth were embedded under vacuum in clear epoxy resin (Struers EpoFix®) (Figure 4.6b) and each epoxy "block" was allowed to cure at room temperature for at least seven days. After curing, we used a Buehler® IsoMet™ low-speed saw to produce two 250 μm-thick buccolingual thick sections (henceforth the "A-section" and "B-section") through the highest point of the least worn tooth loph (Figure 4.6c).

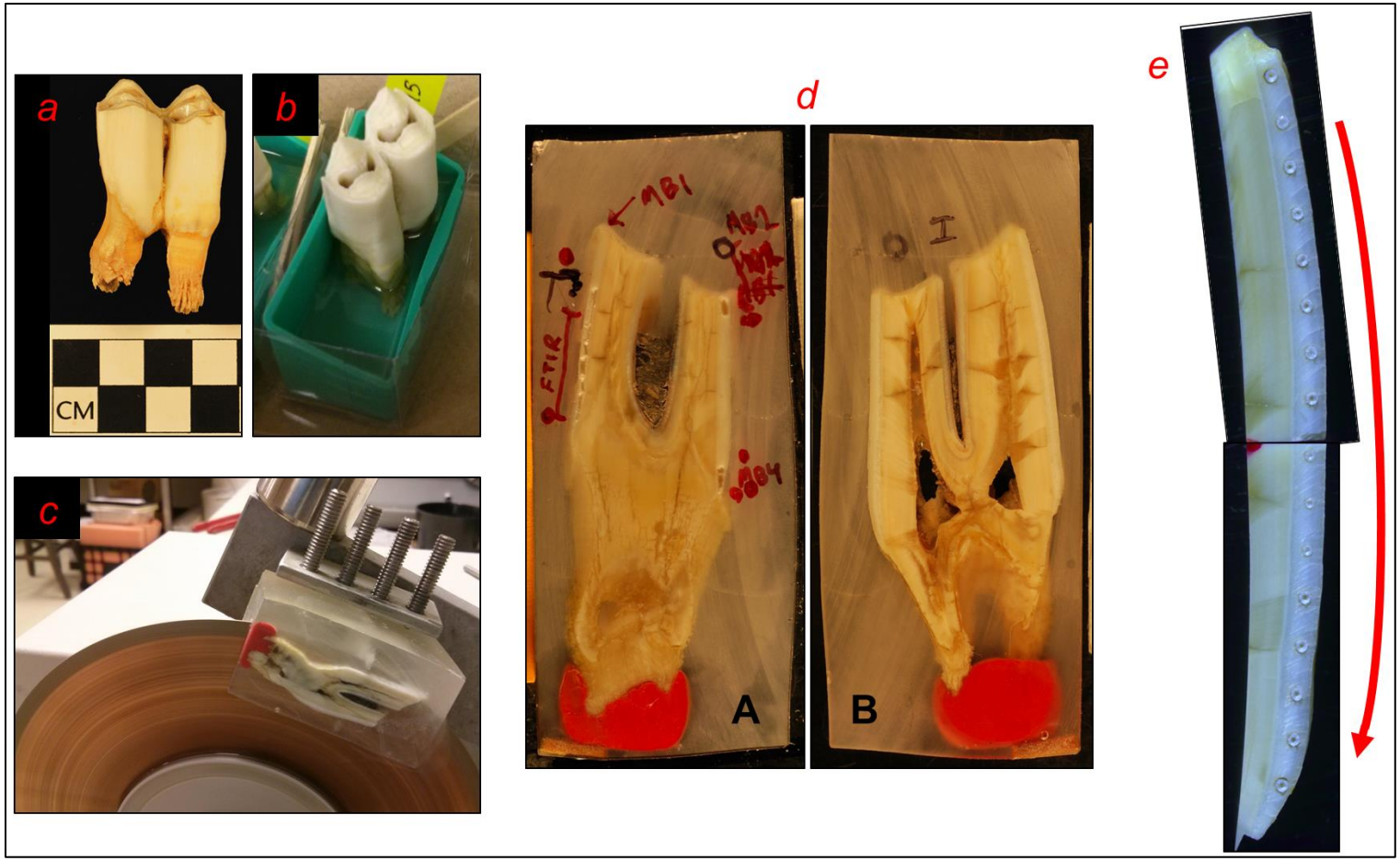


Figure 4.6. Workflow for tooth enamel sample preparation: **(*a*)** liberated and cleaned tooth (note the substantial occlusal wear on the tooth crown compared to the tooth crown in Figure 4.4a); **(*b*)** tooth being embedded in epoxy resin; **(*c*)** production of thick sections using low-speed sectioning machine (red material is modeling clay used to position tooth during embedding); **(*d*)** corresponding "A" and "B" sections (note the sampled areas for FTIR and structural carbonate on A-section); **(*e*)** ablation pits on an enamel segment from a B-section (red arrow denotes the sequence of ablation and order of IDs in relevant tables).

4.3.2 Fourier Transform Infrared Spectroscopy (FTIR)

Fourier transform infrared spectroscopy (FTIR) is commonly used to rapidly assess archaeological bone, dentin, and enamel samples for chemical alteration or the presence of exogenous organic and inorganic substances. We used a Merchantek/New-Wave™ micromill to remove several milligrams of enamel near the middle of each A-section. Due to scheduling constraints and the considerable amount of time required to produce the requisite amount of enamel for FTIR, we micromilled from M1s exclusively. As it was milled, enamel powder was collected using a purpose-built vacuum-collection system developed by Sakai and Kodan (2011). After collection, 2 mg of enamel powder was mixed with 200 mg of fresh IR spectroscopic-grade KBr powder, allowed to dry in an oven at 90°C overnight, and then pressed into a 12-mm pellet with a hydraulic press at 11 tons for 10 minutes. FTIR absorbance spectra were obtained using a Bruker™ Vector 22® IR spectrometer. Each pellet was scanned 16 times from wavenumbers between 400 and 4000 cm^{-1}, with a spectral resolution of 4 cm^{-1}. No deconvolution/decomposition (Kauppinen et al. 1981; Metcalfe et al. 2009; Roche et al. 2010) was applied to FTIR spectra after integration.

We calculated five common indices of preservation/alteration in bioapatites: (1) crystallinity index (CI); (2) carbonate-to-phosphate (CO_3/PO_4) index; (3) carbonyl-to-carbonate (CO/CO_3) ratio; (4) B-site carbonate on phosphate (BPI); and (5) weight percent carbonate (wt% CO_3). The formulas for each index are listed in Table 4.4. The crystallinity index assesses whether postmortem recrystallization of bioapatite is likely to have occurred (Weiner and Bar-Yosef 1990; Hedges and Millard 1995; Hedges et al. 1995; Person et al. 1996; Wright and Schwarcz 1996; Surovell and Stiner 2001) though tooth enamel should be less susceptible to this process than bone (LeGeros 1981; LeGeros and LeGeros 1984; Kohn and Cerling 2002). The B-site carbonate-to-phosphate (C/P) index should indicate whether carbonate has been gained or lost in the depositional environment (Wright and Schwarcz 1996; Smith et al. 2007). More recently, Pucèat et al. (2004) proposed a CO_3/PO_4 index that also incorporates B-type carbonate substitutions at ~ 1415 and ~ 1450 cm^{-1} alongside phosphate and carbonate peaks at ~ 1033 and ~ 1425 cm^{-1}, respectively, used in the B-site carbonate-to-phosphate index. The CO_3/PO_4 index should therefore provide a

more accurate assessment of the overall carbonate-to-phosphate ratio in the sample than the B-site C/P ratio. Carbonyl-to-carbonate ratio has been used to evaluate changes in the organic content of bioapatite associated with high temperatures (Thompson et al. 2009; Scorrano et al. 2016). BPI provides an estimate of B-site carbonate content, and can subsequently be used to calculate wt% CO_3 (LeGeros 1991). Additionally, we examined each absorbance spectrum for anomalous peaks located at ~ 710, ~ 1096, ~ 1655, and ~ 3564 cm^{-1} wavenumbers which are known to be associated with chemical alteration or the presence of exogenous substances (Table 4.5).

Table 4.4. FTIR indices used to evaluate enamel preservation in this study. Formula values are wavenumbers (in cm^{-1}).

Index	Abbreviation	Formula	References
Crystallinity Index	CI	$\frac{*(605 + 565)}{V(590)}$	Shemesh 1990; Rey et al. 1990; Weiner and Bar-Yosef 1990
Carbonate-to-phosphate index	CO_3/PO_4	$\frac{(1450) + (1415)}{(605) + (565)}$	Pucéat et al. 2004; Roche et al. 2010
Carbonyl-to-carbonate ratio	CO/CO_3	$\frac{(1450) + (1425)}{(1425)}$	Thompson et al. 2009
β-site carbonate on phosphate	BPI	$\frac{(1415)}{(605)}$	LeGeros 1991; Roche et al. (2010)
Calculated weight percent carbonate	wt% CO_3	(10*BPI) + 0.7	LeGeros 1991; Roche et al. (2010)

*"V" refers to valley at wavenumber

Table 4.5. Wavenumbers at which the presence of absorbance peaks is commonly associated with chemical alteration or exogenous substances.

Peak Wavenumber (cm^{-1})	Indication	Source(s)
710	Presence of exogenous calcite	Lee-Thorp and van der Merwe 1991
1096	Exogenous fluorapatite substitutions for structural carbonate	Shemesh 1990; Wright and Schwarcz 1996
~ 1655	Exogenous organic material	Boyar et al. (2004); Metcalfe et al. (2009)
3565	Recrystallization of apatite	Rey et al. (1995); Pasteris et al. (2004); Metcalfe et al. (2009)

4.3.3 Micromilled Tooth Enamel for Structural Carbonate Isotopic Analysis

After obtaining enamel samples for FTIR, we milled ~ 1 mg of enamel from several spots on each A-section (Figure 4.6d). These milled enamel samples were analyzed for their structural carbonate carbon and oxygen isotope compositions ($\delta^{13}C_{sc}$ and $\delta^{18}O_{sc}$, respectively) via the conventional H_3PO_4 method (Land et al. 1980; McArthur et al. 1980) for comparison with enamel $\delta^{13}C$ and $\delta^{18}O$ obtained via laser ablation ($\delta^{13}C_{LA}$ and $\delta^{18}O_{LA}$, respectively) at corresponding locations on the B-sections (Figure 4.6e). The milled enamel samples were too small (<1.5 mg) to treat for removal of organic material or potential adsorbed carbonates (Lee-Thorp and van der Merwe 1987, 1991; Lee-Thorp et al. 1989, Wright and Schwarcz 1996; Koch et al. 1997; Iacumin and Longinelli 2002). Recent work (Garvie-Lok et al. 2004; Grimes and Pellegrini 2013; Snoeck and Pellegrini 2015; Pellegrini and Snoeck 2016), however, indicates that depending on the reactants used, traditional treatment processes intended to remove organic matter and secondary carbonates from primary bioapatite can adversely affect the original isotopic composition of enamel by degrading the structural carbonate or introducing exogenous carbonates to the sample.

4.3.4 Tooth Enamel Thick Sections for LA-GC-IRMS

Passey and Cerling (2006:241) found that whole teeth are unsuitable for LA-GC-IRMS because the amount of CO_2 naturally outgassed by large samples is often "as much or more…than is generated during a typical laser-ablation event…even after overnight purging" with helium. We therefore used a second, smaller sectioning machine to remove the entire length of crown enamel from one side of each B-section (Figure 4.6e). After rinsing with ultrapure water, these enamel sections were stored in a vacuum oven at ~ 90°C/~ 25 mTorr until being placed in the laser ablation chamber. Cerling and Sharp (1996) report that enamel samples treated with NaClO to remove organics produced erratic isotopic data during laser ablation, despite thorough previous rinsing with distilled water and ethanol. Consequently, we also chose to forego any treatment of the enamel section surfaces used for laser ablation.

Aside from limiting contamination from outgassing, there are several advantages to ablating an enamel section or slice as opposed to an intact tooth or large piece of intact enamel. First, no refocusing of the laser is required when moving across the surface of a uniformly-thick section. Sharp and Cerling (1996) and Cerling and Sharp (1996) demonstrate that focal distance (i.e. the distance between the laser aperture and the sample surface) affects the $\delta^{13}C$ and $\delta^{18}O$ values produced by laser ablation, and it is difficult to maintain a uniform focal distance "on the fly" using an intact tooth with variable surface geometry. Second, for fauna with relatively thin tooth enamel, as is the case here, ablation of the outer enamel surface may cause the laser to penetrate into underlying dentin. Because of its thickness (~ 250 μm), overpenetration of the mesiodistal enamel surface on a buccolingual thick section is improbable, and because the thick section sits flat on the floor of the non-reactive nickel sample chamber, there is no effect on produced sample gas should overpenetration occur.

4.3.5 Isotopic Analysis

All isotopic compositions are reported in per mil (‰) using delta notation (δ) (Equation 4.1):

$$\delta = \left[\frac{R_{Sample}}{R_{Standard}} - 1\right]$$

[Equation 4.1]

where R is the ratio of heavy to light isotopes in the analyte.

The $\delta^{18}O$ and $\delta^{2}H$ of surface water samples collected in 2008 and 2010 were obtained simultaneously in two analytical sessions using a Picarro™ L1102-i cavity ring-down spectrometer. Cavity ring-down spectroscopy (CRDS) capitalizes on the ability of molecules to absorb light, measuring the *rate* of absorption over time (Berden et al. 2000). In practice, the Picarro introduces tuned pulses of infrared laser light from a source into a cavity in which three high-reflectivity mirrors sit. In an empty cavity, the light will continue traveling between the mirrors for several microseconds until all of the energy is transmitted through the mirrors, which are only 99.999% reflective. The absorptive decay of the light

intensity over time ("ring-down") is measured by a photodetector. When a gas (in this case, a vaporized water sample) is introduced into the cavity, the absorption increases and the ring-down time decreases further. By calculating the relationship between ring-down time and the laser frequency, a CRDS spectrum is obtained for the sample (O'Keefe and Deacon 1988; Wheeler et al. 1998). Given the CRDS spectrum and the ring-down time, the quantitative concentrations of oxygen and stable hydrogen isotopes in the sample are determined.

The $\delta^{18}O$ and $\delta^{2}H$ of water samples collected in 2014 were obtained in separate analytical sessions using a Thermo Scientific™ GasBench II® device interfaced with a Thermo Scientific™ DELTA^{plus} XL® isotope ratio mass spectrometer (IRMS) operating in continuous-flow (CF) mode.

Oxygen isotope compositions of water samples were obtained by equilibration with high purity CO_2 (Epstein and Mayeda 1953). Briefly, 1 mL of each water sample is pipetted into individual glass Labco™ Exetainer® vials with gas-tight rubber septa, and the vials are placed in a heating block at 30°C. A robotic autosampler then pumps away atmosphere in the headspace of each Exetainer® vial and fills it with a mixture of 0.3% CO_2 and high purity helium. The samples equilibrate for ~ 20 hours, and the equilibrated CO_2 in each vial headspace is pumped through a Nafion® water trap to a Chrompack PoraPlot Q® fused silica GC column inside the GasBench II® to separate residual N_2 and CO_2. The gas from each water sample is then passed through a second Nafion® water trap and then to the IRMS via open split without dilution for isotopic measurement.

Hydrogen isotope compositions of water samples were obtained using the H_2-equilibration method (Horita 1988; Coplen et al. 1991). The benefits of this method over zinc (Friedman 1953; Kendall and Coplen 1985) or uranium (Bigeleisen et al. 1952; Godfrey 1962) reaction methods are that it is safer, faster, and can be largely carried out with a robotic autosampler. In this procedure, 1 mL of each water sample is pipetted into individual glass Exetainer® vials and a small stick of styrene-divinylbenzene (SDB) copolymer doped with 3 wt% platinum is added. The sealed Exetainer® vials are then placed in a heating block at 30°C and the autosampler is used to pump a mixture of 2% H_2 and high purity helium into

each Exetainer® vial, which is then allowed to equilibrate for ~ 2 hours. The SDB-platinum stick reacts with both the H_2 gas and hydrogen in the water sample, promoting equilibration between the two (Kirshenbaum 1951; Horita 1988). The equilibrated gas from each water sample is then passed to the Gasbench II® for the separation of gas species and on to the IRMS for isotopic measurement in the same manner as above.

The oxygen and hydrogen isotope compositions of water samples analyzed via both CRDS and GC-IRMS were calibrated to Vienna Standard Mean Ocean Water (VSMOW) ($\delta^{18}O$ and $\delta^{2}H = 0‰$) using two internal standards: "LSD" (average $\delta^{18}O$ and $\delta^{2}H$ –22.57‰ and –161.8‰, respectively) and "Heaven" (average $\delta^{18}O$ and $\delta^{2}H$ –0.27‰ and +88.7‰, respectively). Two other internal standards, "MID" (average $\delta^{18}O$ and $\delta^{2}H$ –13.08‰ and –108.1‰, respectively) and "EDT" (average $\delta^{18}O$ and $\delta^{2}H$ –7.27‰ and –56.0‰, respectively) were used to evaluate the accuracy of the calibration curve for each analytical session.

Micromilled enamel samples were analyzed for their structural carbonate $\delta^{13}C$ and $\delta^{18}O$ using an VG Micromass™ Optima® Dual Inlet (DI) IRMS equipped with a VG Micromass™ Multiprep® carbonate preparation module and Gilson™ autosampler. All samples and standards were reacted with orthophosphoric acid (H_3PO_4) for 25 minutes at 90°C to produce CO_2 gas that was then passed to the IRMS for measurement after cryogenic purification.

The stable carbon isotope compositions measured via DI-IRMS were calibrated to Vienna Pee Dee Belemnite (VPDB) ($\delta^{13}C = 0‰$) using NBS-19 (calcite; accepted $\delta^{13}C$ +1.95‰) and an international lithium carbonate standard (LSVEC, NIST RM 8545; accepted $\delta^{13}C$ –46.60‰) (Coplen et al. 2006). Oxygen isotope compositions were calibrated to VSMOW using NBS-19 (calcite; accepted $\delta^{18}O$ +28.65‰) and NBS-18 (carbonatite; accepted $\delta^{18}O$ +7.20‰). Suprapur (marble; accepted $\delta^{13}C$ –35.28‰), NBS-18 (carbonatite; accepted $\delta^{13}C$ –5.00), and an internal calcite standard (WS-1; average $\delta^{13}C$ +0.76‰) were used to evaluate the accuracy of carbon isotope measurements. Suprapur (accepted $\delta^{18}O$ +13.30) and WS-1 (average $\delta^{18}O$ +26.23‰) were used to evaluate the accuracy of oxygen isotope measurements.

The LA-GC-IRMS system used in this study is described in detail by Larson and Longstaffe (2007) and is adapted from Sharp and Cerling (1996) and Cerling and Sharp (1996). The system works as follows: one or two enamel sections, plus an internal enamel standard (see below) and a small piece of the WS-1 internal calcite standard, are placed inside a small vacuum-sealable metal chamber (interior diameter = 2.5 cm) fitted with a KCl window and equipped with inflow and outflow tubing for ultra-high purity helium carrier gas. The chamber is then sealed, wrapped in heating tape set to 70°C, and flushed with helium for a minimum of three hours to promote outgassing of labile CO_2 from the sample and removal of water vapor from the sample or sample chamber. The background scan function in the ISODAT™ software that controls the LA-GC-IRMS system can also be used to monitor the mass 44 background, which provides some measure of outgassing progress.

Samples are ablated using a 25-watt New-Wave™ MIR 10® CO_2 gas source IR laser operating at a wavelength of 10.66 μm. The laser pulse (or pulses) pass through the KCl window, which absorbs only ~ 10% of the laser energy, producing a ~ 180 μm pit in the sample surface. Volatilized sample gas produced by the ablation event is passed along with the helium carrier gas to a liquid nitrogen (LN_2) trap, where it is cryofocused for several minutes. The focused pulse of sample gas is then passed through a Nafion® water trap to a Chrompack PoraPlot Q® fused silica GC column inside a Gasbench II® device where CO_2 is separated from the helium as well as other gases such as SO_2 produced by the ablation event (Sharp and Cerling 1996). The CO_2 sample gas is passed through a second Nafion® water trap and then sent through an open split without dilution to a Thermo Scientific™ DELTA^{plus} XL® IRMS operating in dual-inlet (DI) mode for analysis. Cycle time is less than 10 minutes, and primary consumables are limited to LN_2, and carrier and reference gas, enabling the relatively rapid and inexpensive (per data point) acquisition of large datasets.

In each analytical session, we only proceeded with the ablation of standards and samples when the mass 44 background stabilized at 0 mV, and the mass 44 amplitudes of several analytical blanks were less than 50 mV. We then obtained a sequence of enamel $\delta^{13}C$ and $\delta^{18}O$ at ~ 1 mm intervals along the major axis of each enamel slice from the B-section,

moving towards the root-enamel junction (REJ) (Figure 4.6e). At each sampling spot, we fired the laser four times with two second spacings, at 15.5% laser power, a pulse width of 60 milliseconds, a spot size of 180 μm, and a focal length of ~ 19 cm, producing an average mass 44 peak intensity of 1520 mV. This peak intensity was just above the minimum amplitude necessary for accurate $\delta^{13}C_{LA}$ and $\delta^{18}O_{LA}$ measurements (Larson and Longstaffe 2007).

Because all three oxygen-bearing moieties in tooth enamel (phosphate, structural carbonate, hydroxyl groups) are volatilized by the IR laser, the $\delta^{18}O$ measured from a single spot represents a "bulk" enamel $\delta^{18}O$ profile dominated by phosphate (Cerling and Sharp 1996; Sharp and Cerling 1996; Kohn and Cerling 2002; Larson and Longstaffe 2007). On the contrary, neither phosphate nor hydroxyl groups contain carbon atoms, and carbon-bearing organic material constitutes only 1-2% of enamel (Lowenstam and Weiner 1989; Hillson 2000; Kohn and Cerling 2002). Consequently, enamel $\delta^{13}C$ (but not bone $\delta^{13}C$, see Brady et al. 2008) measured via LA-GC-IRMS is typically as accurate as that obtained from structural carbonate using the conventional H_3PO_4 method of analysis (Passey and Cerling 2006).

4.3.6 Internal Enamel Standard

In this study, the carbon and oxygen isotope compositions of microbulk enamel measured via LA-GC-IRMS were calibrated to VPDB and VSMOW, respectively, with the assistance of an internal enamel standard (164 P4, accepted $\delta^{13}C_{LA}$ and $\delta^{18}O_{LA}$ –13.6‰ and +6.3‰, respectively). Typically, standards used in isotopic analysis are of similar – but not always exact – physical and chemical composition to the samples. In standard gas-source IRMS analyses, this is not a major issue because samples and standards are similar enough in their physical and chemical compositions that combustion or chemical reaction produces gas from analytes in essentially the same manner. The incorporation of an optical component (the laser) into the analytical system, however, introduces additional complexity. Absorptive and reflective interactions between the laser beam and the sample surface depend on the structural composition of the sample, and the degree of absorption of the laser directly affects the isotopic compositions derived from the ablation event(s) (Cerling and Sharp 1996; Larson and Longstaffe 2007). Thus, the use of inorganic

carbonate standards alone to calibrate the isotopic compositions of tooth enamel, a prismatic tissue composed of both inorganic and organic phases, may not be appropriate because their physical compositions (i.e. structural matrices) are considerably different and the laser ablates them with variable efficiency. Although international reference materials exist (NIST SRM 1400; IAEA-A-12) or are in development (USGS MAPS-4 and MAPS-5) for bone, we know of no widely-used, matrix-matched standard for tooth enamel.

We first attempted to develop an internal enamel standard from the enamel of a modern muskox third molar (M3) for which we obtained infrared absorbance spectra, and phosphate and structural carbonate carbon and oxygen isotope compositions. Using a Dremel® rotary tool fitted with a diamond wheel point bit, we milled enamel from the outer surface of the tooth. The enamel powder was crushed to <63 μm, and we then used a hydraulic press to compress the powder at 13 tons of pressure for 20 minutes to produce a 12-mm pellet. The pellet was permitted to outgas in a vacuum oven at ~ 90°C/30 mTorr for one week, then transported in a desiccator filled with fresh desiccant directly to the laser sample chamber and allowed to outgas under the flow of helium for 36 hours.

This approach circumvents issues associated with using intact enamel as a standard, in particular, isotopic heterogeneity due to changing conditions during enamel formation. The enamel pellet, however, is not matrix-matched since it is composed of compressed powdered enamel rather than intact prismatic enamel. Additionally, while we were able to outgas the enamel pellet enough to produce analytical blanks with mass 44 amplitudes <50 mV, analytical tests demonstrated that the presence of the enamel pellet inside the chamber resulted in a gradual but significant (3.1‰) depletion of ^{13}C in gas evolved from the block of WS-1 calcite standard. Additionally, although we obtained consistent $\delta^{13}C$ data for the pellet (–11.1 ±0.3‰), intra-session variability in $\delta^{18}O$ exceeded ±2‰. We suspect that the decrease in measured $\delta^{13}C$ of WS-1 block arose from cross-contamination with spall from the ablated enamel pellet. Regardless of the cause, we chose not to use the pellet as a standard for our analyses.

A spare enamel section from a modern muskox 4th premolar (BIBS14-169 P4) that we used to optimize the laser settings for the ablation of tooth enamel proved to have relatively

homogenous carbon and oxygen isotope compositions along its major axis. This consistency is likely due to the small size and rapid development of permanent premolars in muskoxen (Figure 4.3). We measured enamel $\delta^{13}C_{sc}$ and $\delta^{18}O_{sc}$ for this tooth using the conventional H_3PO_4 method. We also measured its enamel phosphate $\delta^{18}O$ ($\delta^{18}O_p$) following procedures and using instrumentation described in Matthews et al. (2016). These isotopic data allowed us to determine an accepted value of $\delta^{13}C_{LA}$ (–13.6‰), and by making a simple calculation based on the relative contributions of structural carbonate and phosphate oxygen to mammalian enamel, we also obtained an accepted value of $\delta^{18}O_{LA}$ (+6.3‰), for the 169 P4 enamel standard. We then produced additional enamel sections from this tooth and used them alongside a block of WS-1 as calibration checks during each analytical session.

We developed a calibration curve for laser isotopic data with the same standards used in the DI-IRMS analysis of structural carbonate. NBS-19 (calcite; accepted $\delta^{13}C$ +1.95‰) and Suprapur (marble; accepted $\delta^{13}C$ –35.28‰) were used to calibrate measured $\delta^{13}C$ to VPDB, and NBS-18 (carbonatite; accepted $\delta^{18}O$ +7.20‰) and NBS-19 (accepted $\delta^{18}O$ +28.65‰) were used to calibrate measured $\delta^{18}O$ to VSMOW/SLAP. The internal WS-1 calcite standard was then used as a check on both the carbon and oxygen calibration curves. To adapt this calibration system to bioapatite samples, we used the offsets between accepted $\delta^{13}C$ and $\delta^{18}O$ for the 169 P4 enamel standard and $\delta^{13}C$ and $\delta^{18}O$ measured in each analytical session to correct for matrix effects.

4.3.7 Spatial Analysis of Water Sample $\delta^{18}O$

We created a map of spatial variation (i.e. an "isoscape") of meteoric surface water $\delta^{18}O$ ($\delta^{18}O_{mw}$) in ArcGIS® ArcMap™ (version 10.4.1) using empirical Bayesian Kriging (EBK) (Pilz and Spöck 2008; Krivoruchko 2012). We chose this interpolation method because we were only able to sample surface waters along a relatively narrow north-south transect, with low sample coverage in the middle of the island, and other approaches to spatial prediction struggle when sample coverage is irregular (Christensen 1991; Dutton et al. 2005). EBK also expedites the modeling process by using a restricted maximum likelihood function to automatically calculate optimal model parameters through iterative simulation (ESRI 2016). Semivariogram cross-validation in ArcGIS® also demonstrated that

predictive parameters (Johnston et al. 2003) were significantly closer to their target values using EBK than other Kriging types (e.g. simple, ordinary, universal) or deterministic approaches to interpolation (e.g. Triangulated Irregular Network, Inverse Distance Weighting).

4.4 Results

4.4.1 Surface Water $\delta^{18}O$ and $\delta^{2}H$ Results and $\delta^{18}O$ Isoscape

Across three CRDS analyses of the LSD internal water standard (accepted VSMOW/SLAP calibrated $\delta^{18}O$ and $\delta^{2}H$ = –22.57‰ and –161.80‰, respectively), which is one anchor of the calibration curve, reproducibility was ±0.03‰ for $\delta^{18}O$ and ±0.54‰ for $\delta^{2}H$. Across six CRDS analyses of the Heaven internal water standard (accepted VSMOW/SLAP calibrated $\delta^{18}O$ and $\delta^{2}H$ –0.27‰ and +88.7‰, respectively), the other anchor of the calibration curve, reproducibility was ±0.07‰ for $\delta^{18}O$ and ±0.59‰ for $\delta^{2}H$. Across three CRDS analyses of the MID internal water standard (accepted VSMOW/SLAP calibrated $\delta^{18}O$ and $\delta^{2}H$ = –13.08‰ and –108.10‰, respectively), $\delta^{18}O$ was –13.09±0.02‰ and $\delta^{2}H$ was –107.09±0.22‰. Across eleven CRDS analyses of the EDT internal water standard (accepted VSMOW/SLAP calibrated $\delta^{18}O$ and $\delta^{2}H$ = –7.27‰ and –56.0‰, respectively), $\delta^{18}O$ was –7.32±0.05 and $\delta^{2}H$ was –54.44±0.54. The standard deviation of water samples analyzed via CRDS as instrumental duplicates (n = 3) was $\delta^{18}O$ = ±0.1‰ and $\delta^{2}H$ = ±0.2‰ indicating high reproducibility.

Across three GasBench II®-IRMS analyses of the LSD internal water standard, $\delta^{18}O$ was ±0.03‰ and $\delta^{2}H$ was ±0.54‰. Across three analyses of the Heaven internal water standard, $\delta^{18}O$ was ±0.07‰ and $\delta^{2}H$ was ±0.59‰. Across three analyses of the MID internal water standard, $\delta^{18}O$ was –13.09±0.10‰ and $\delta^{2}H$ was –103.65±0.43‰. Across 11 analyses of the EDT internal water standard, $\delta^{18}O$ was –7.40±0.08‰ and $\delta^{2}H$ was –55.60±0.46‰. The standard deviation of duplicate water sample analyses (n = 2) was $\delta^{18}O$ = ±0.0‰ and $\delta^{2}H$ = ±1.1‰ again indicating high reproducibility in the oxygen isotope data.

Although for this study we focus mainly on the oxygen isotope data, oxygen and hydrogen isotope compositions of all water samples are presented in Table 4.2. In Figure 4.7, the $\delta^{18}O$ and $\delta^{2}H$ of water samples are plotted by type (lake, pond, river, stream). In Figure

4.8, all surface water samples from Banks Island are plotted against precipitation δ^2H and δ^{18}O at the same coordinates, as calculated using the Online Isotopes in Precipitation Calculator (OIPC) (Bowen et al. 2005; IAEA/WMO 2017; Bowen 2017), and the Global Meteoric Water Line (GMWL).

The mean δ^{18}O of all "summer" meteoric surface water samples is –17.5‰ (min = –22.3‰, max = –8.4‰. The mean δ^2H of all "summer" meteoric surface water samples is –141‰ (min = –174‰, max = –69‰). Figure 4.7 demonstrates some difference in oxygen and hydrogen isotope compositions in different water sample types, which may be related to their evaporative potential. Water samples from ponds have the highest δ^{18}O and δ^2H, and plot farther from the GMWL, indicative of their greater surface area relative to water volume, which can accentuate the isotopic effects of evaporation. Conversely, the δ^{18}O and δ^2H of rivers and streams are lower and cluster closer to the GMWL, as would be expected from well-mixed reservoirs receiving meltwater or rainwater drained from large watersheds in a setting where water residence times are short and evaporative effects on isotopic compositions much more attenuated. Figure 4.8 further indicates that the δ^{18}O and δ^2H of 'summer' meteoric surface water samples collected on Banks Island define a local meteoric water line (technically, a local evaporation line (LEL)) that falls to the right of the Global Meteoric Water Line (GMWL), typical of surface waters in northern Canada (Bursey et al. 1990; Gibson et al. 1993, 2002; Gibson 2001, 2002; Yi et al. 2012). Gibson et al. (1993, 2005) also demonstrate that the intersection of local evaporation lines and the GMWL tends to approximate the mean δ^{18}O and δ^2H of precipitation in the entire catchment area. In this case, the intersection of the Banks Island LEL and GMWL is δ^{18}O = –27.6‰ and δ^2H = –211‰, which is consistent with existing estimates for mean precipitation δ^{18}O and δ^2H in this area (Rozanski et al. 1993; Bowen and Wilkinson 2002; Bowen and Revenaugh 2003; Bowen et al. 2005; Bowen 2008).

The interpolated oxygen isoscape presented in Figure 4.9 suggests that there is a north-south gradient of approximately 5‰ in the δ^{18}O of meteoric surface water on Banks Island during the growing season. This north-south isotopic gradient is in line with climatic (Usher 1965; Maxwell 1980; Edlund 1986; Gray 1997a) and bioclimatic (Walker 2000; Gould et al. 2003) data demonstrating a steep northward decline in temperature and

moisture on Banks Island. Due to the absence of any water samples, however, the accuracy of the predicted $\delta^{18}O$ rapidly decreases to the northwest and southeast of the sampling transect (see map of standard error; Figure 4.9, inset).

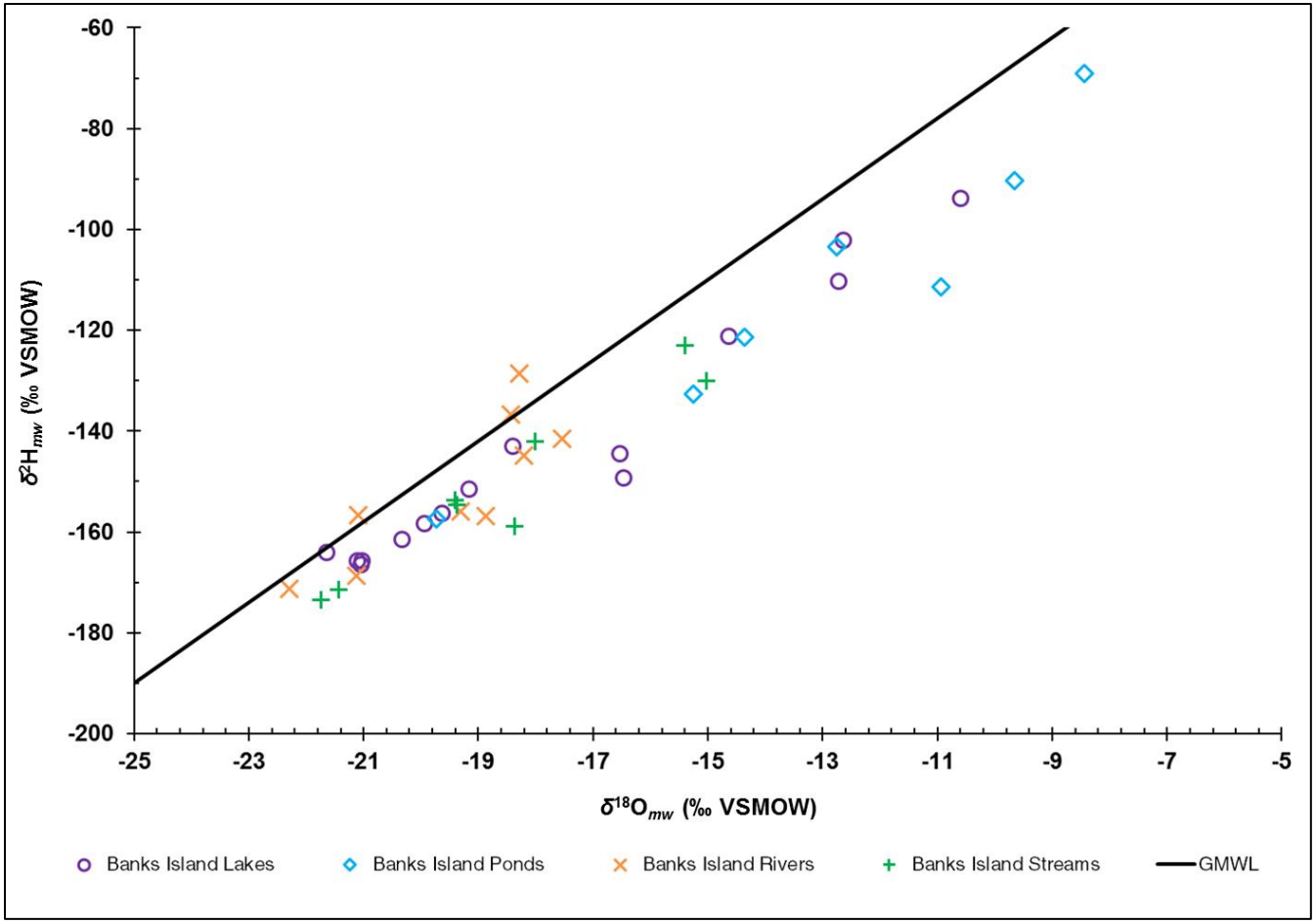


Figure 4.7. Values of $\delta^{18}O$ and $\delta^{2}H$ for meteoric surface water samples collected on Banks Island in the summers of 2008, 2010, and 2014, split by type and compared to the Global Meteoric Water Line ("GMWL", solid black line).

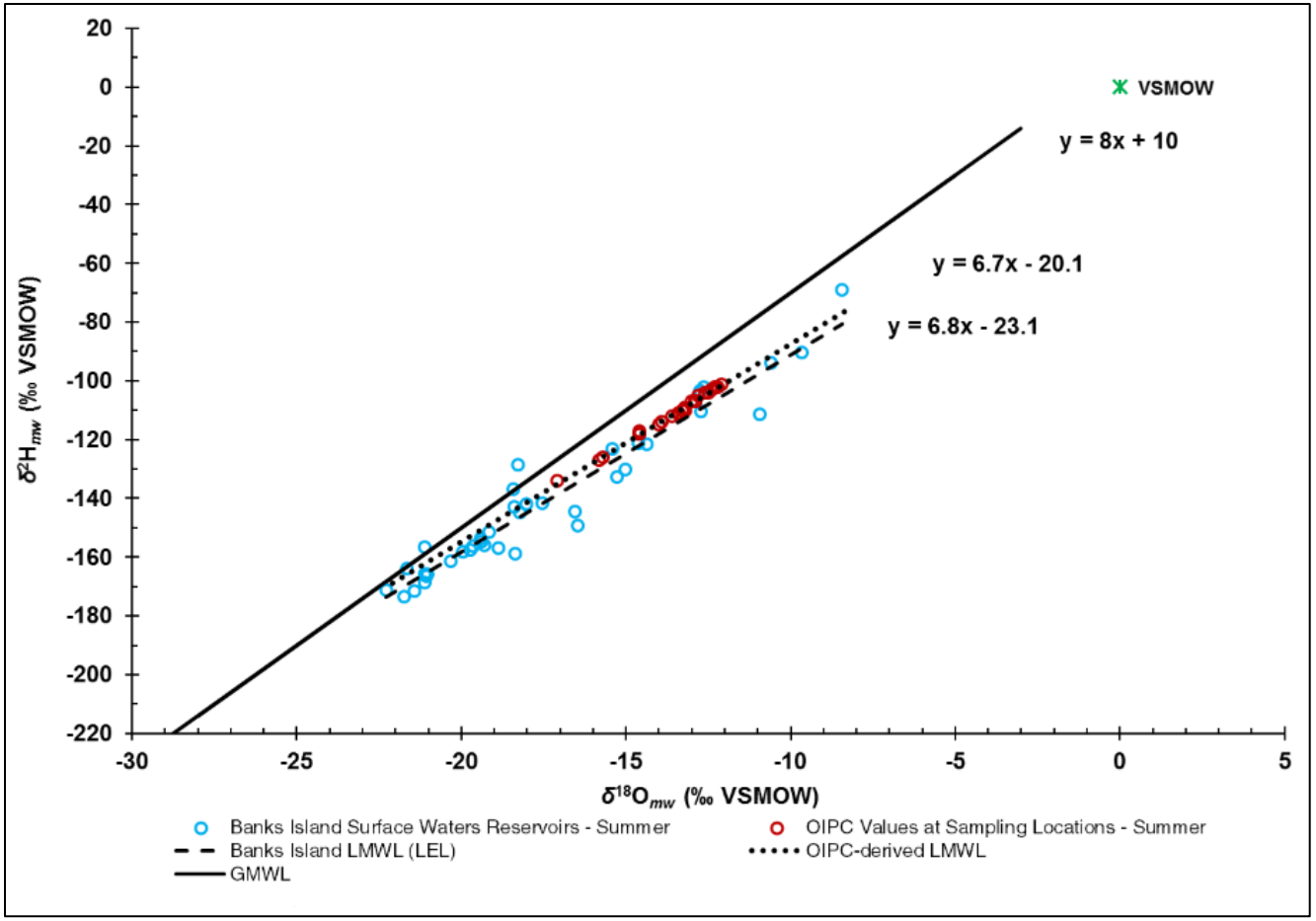


Figure 4.8. Values of $\delta^{18}O$ and $\delta^{2}H$ for grouped meteoric surface water samples collected on Banks Island in the summers of 2008, 2010, and 2014, in comparison to precipitation $\delta^{18}O$ and $\delta^{2}H$ from the same coordinates and collection months, estimated using the Online Isotopes in Precipitation Calculator (OIPC) (IAEA/WMO 2017; Bowen 2017). The dashed line represents the Local Meteoric Water Line (LMWL) (actually a Local Evaporation Line [LEL]) created by water samples. The dotted line represents the Local Meteoric Water Line (LMWL) created by OIPC-estimated precipitation data. The solid line is the Global Meteoric Water Line.

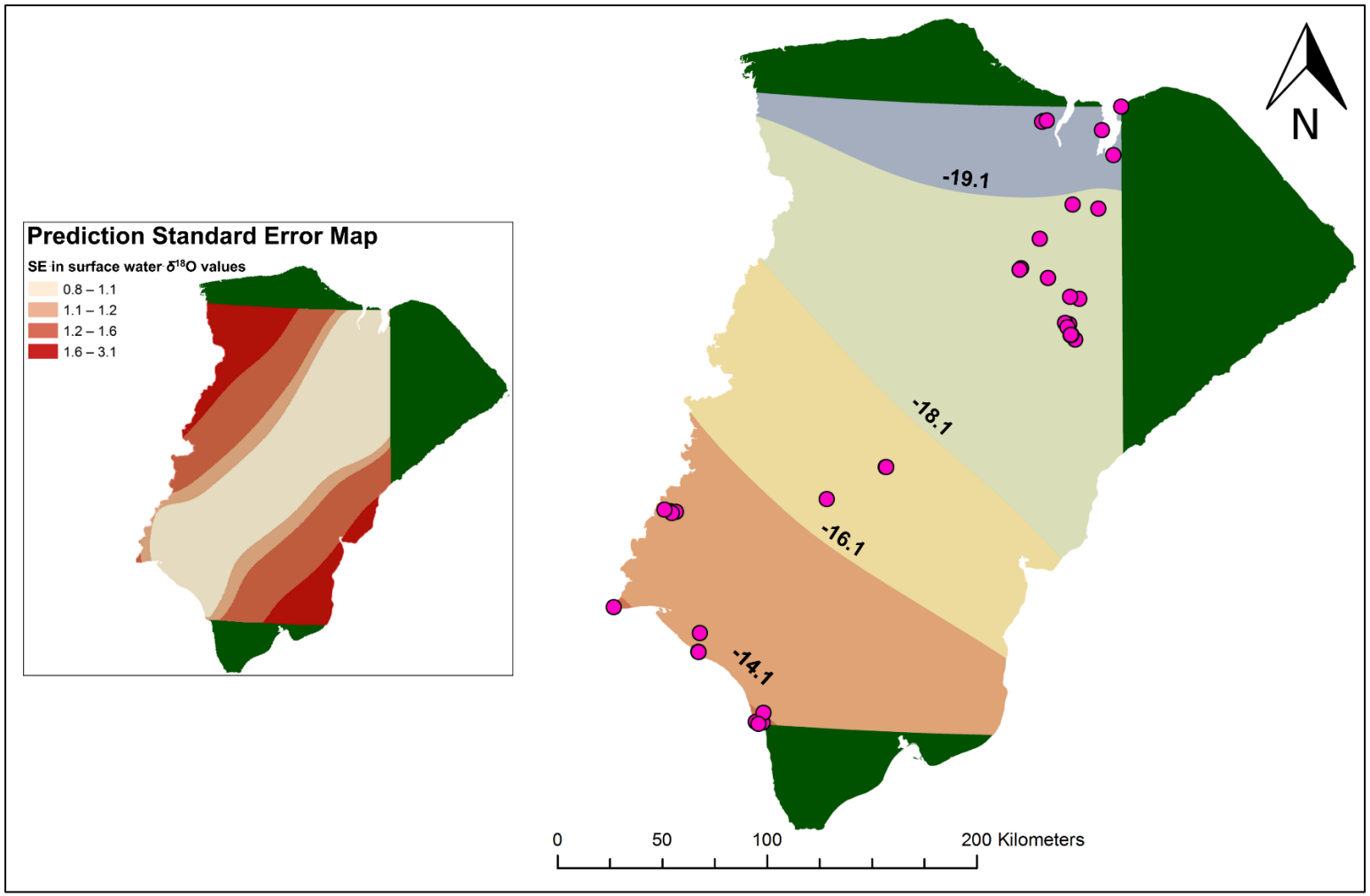


Figure 4.9. Isoscape of interpolated summer surface water $\delta^{18}O$ (‰, VSMOW) on Banks Island. The isoscape is based on our water sample data and created using empirical Bayesian Kriging (EBK) in ArcGIS®. Pink dots correspond to sampling locations. The Prediction Standard Error Map at left provides a measure of uncertainty around interpolated surface water $\delta^{18}O$.

4.4.2 FTIR Results

The infrared absorption spectra of tooth enamel samples are shown in Figure 4.10, and results for FTIR indices discussed in the following sections are presented in Table 4.6.

The crystallinity indices of modern and archaeological tooth samples were calculated following Weiner and Bar-Yosef (1990) (Table 4.4). The average CI of all enamel samples is 2.8 (min = 2.7, max = 3.0), with no statistically-significant difference in CI between teeth from different cultural periods. The FTIR crystallinity index of fresh bone bioapatite is typically between 2.5 and 3.3 (Weiner and Bar-Yosef 1990; Surovell and Stiner 2001; Webb et al. 2014). Reyes-Gasga et al. (2013) however, found that the CI of modern human tooth enamel not subjected to heating was 3.2±0.02, and decreased with heating; in fact, enamel heated to 400°C had CI values around 2.8. This discrepancy in enamel CI values is likely due to differences in the prism sizes of human and ungulate tooth enamel (e.g. Figure 13 in Tafforeau et al. 2007). One other possibility, however, is that the micromilled enamel powders used for FTIR were either not appropriately homogenized, or were smaller than the desired grain size (45-63 μm). Surovell and Stiner (2001) demonstrate that CI varies with grainsize and that smaller grain size is associated with lower CI values. We were not able to grind the enamel samples used for FTIR to a homogenous grain size because of their very small (~ 2 mg) weights and the potential for sample loss during sieving. Nevertheless, given their small range across modern and archaeological tooth enamel samples, their agreement with CI values for intact bone bioapatite, and the generally well-crystallized nature of tooth enamel (LeGeros 1991; Pucèat et al. 2004), the CI values of our tooth enamel samples indicate good preservation of the enamel apatite.

CO_3/PO_4 ratios average 0.5 (min = 0.4, max = 0.5) (Table 4.6). These CO_3/PO_4 ratios are higher than CO_3/PO_4 ratios for both modern suids, bovids, and camelids (average = 0.3, min = 0.2, max = 0.4) and archaeological mammals (average = 0.3, min = 0.2, max = 0.4) reported by Roche et al. (2010). This difference may be due to the fact that we observed only a single peak located at ~ 1418 cm^{-1}, rather than two carbonate peaks located at ~ 1415 and ~ 1425 cm^{-1}, as Roche et al. (2010) did, and we use this single peak in the

CO_3/PO_4 calculation. Additionally, the carbonyl peak expected at 1450 cm^{-1} is shifted closer to ~ 1457.5 cm^{-1} in our tooth enamel samples.

The CO/CO_3 ratio in all enamel samples is 2.1 (Table 4.6). Scorrano et al. (2016) suggest that CO/CO_3 ratios higher than 1.2 indicate that bone has been exposed to high temperatures. Given the significantly smaller fraction of organic content in enamel relative to bone, however, it is not surprising that the CO/CO_3 ratios of our enamel samples are significantly higher than those of bone. Further research is required to (1) establish expected CO/CO_3 ratios for well-preserved tooth enamel, and (2) determine whether sample grainsize also affects CO/CO_3 ratios in the same manner as the CI index.

BPI ratios of the samples average 0.5 (min = 0.4, max = 0.5) (Table 4.6). BPI and CO/CO_3 ratios are nearly identical (SD = 0.02), which is unsurprising given that both indices incorporate peaks at ~ 605 and ~ 1415 cm^{-1}, BPI indices reported by Sponheimer and Lee-Thorp (1999), Botha et al. (2004) and Roche et al. (2010) for extant and fossil mammals are lower on average than BPI values reported here. In fact, the BPI ratios of our enamel samples fall within the range of crocodile tooth enamel BPI ratios reported by both Botha et al. (2004) and Roche et al. (2010). Again, this discrepancy may have to do with the use of the carbonate peak located at ~ 1418 cm^{-1} in the BPI calculation, or the grainsize of the enamel powder created with the micromill. The inclusion of trace dentin in enamel samples analyzed via FTIR can also result in higher BPI ratios (Botha et al. 2004), although we were careful to avoid the DEJ while milling enamel, and BPI values are also high in samples where the milling area is well within the enamel. Additionally, if trace dentin was present in the FTIR enamel samples, this should have resulted in lower – not higher – CO/CO_3 ratios. Enamel structural carbonate contents (wt% CO_3) calculated using BPI (Table 4.6) average 5.4 (min = 4.7, max = 5.9), with no differences across cultural periods. These values fall within the expected range (~ 3-6%) of CO_3 in mammalian enamel (LeGeros 1991; Elliot 1997).

None of the enamel FTIR samples contain anomalous peaks associated with *post-mortem* chemical alteration, though two archaeological enamel samples (BIBS14-209 M1 and -409 M1) display small doublet peaks near 2350 cm^{-1} (red box, Figure 4.10d). Doublet peaks in

this wavenumber region are common in IR spectroscopy and can result from atmospheric CO_2 in FTIR spectrometers with unsealed sample chambers like the one used in this study (usually when some period of time has elapsed between acquisition of the baseline spectrum and the sample spectrum) (Sanati and Andersson 1993), or from vibrational overtones ("Fermi Resonance") in other wavenumber regions (Chang and Tanaka 2002; Sathyanarayana 2004; Figueiredo et al. 2012).

Although all the FTIR indices of both our modern and archaeological tooth enamel samples differ from data on other species reported in the literature, the lack of anomalous peaks, as well as the similarity between modern and archaeological FTIR indices suggests that, irrespective of effects due to sample collection and processing, the archaeological tooth enamel samples are unlikely to have experienced *post-mortem* chemical alteration.

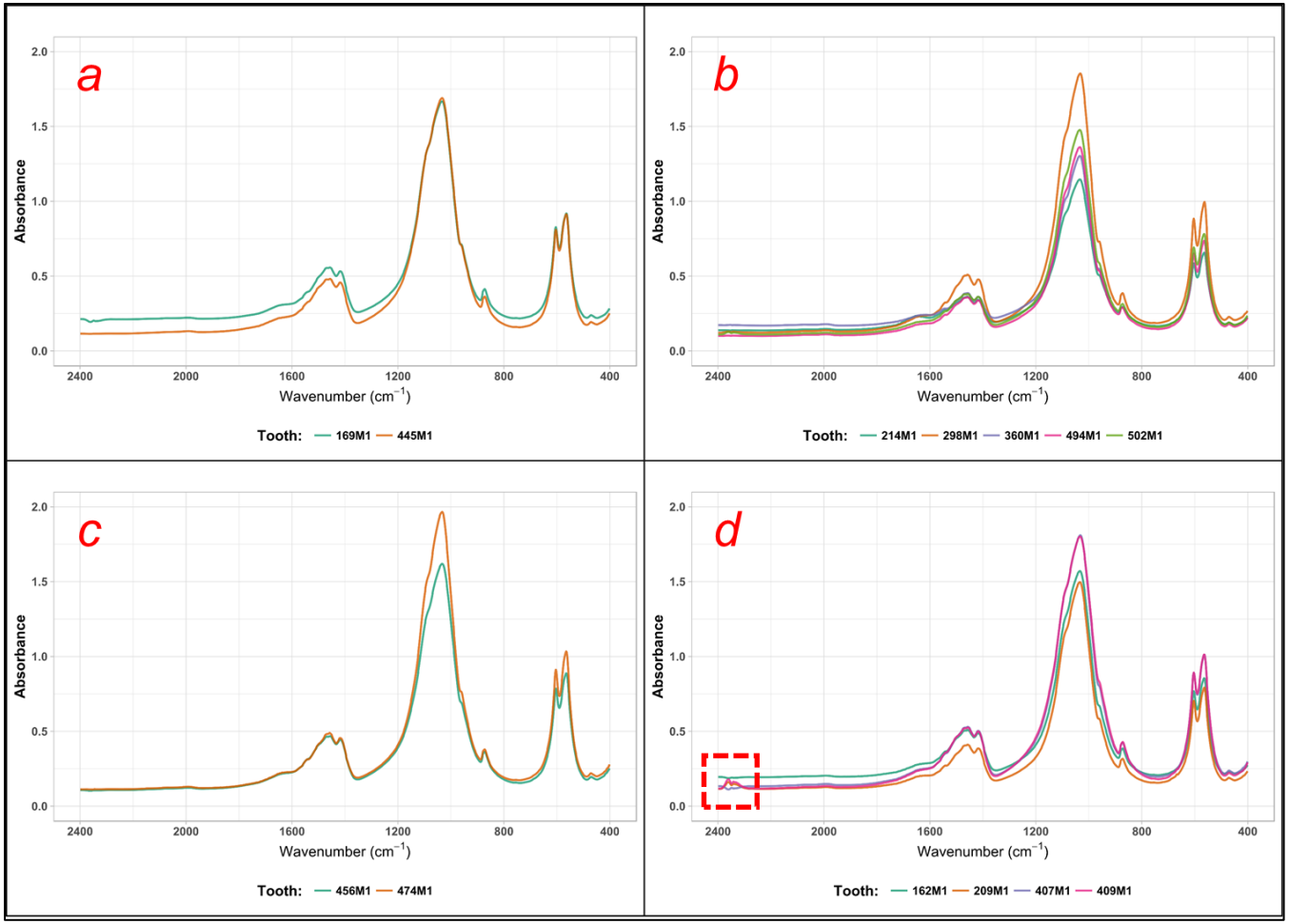


Figure 4.10. Infrared absorption spectra from: **(*a*)** modern muskox M1 enamel samples; **(*b*)** caribou tooth enamel samples from the Classic Thule and Inuit periods; **(*c*)** muskox M1 enamel samples from the Classic Thule and Inuit periods; **(*d*)** muskox M1 enamel samples from the Pre-Dorset and Lagoon periods. The red box in Figure 4.10d denotes small doublet-peaks caused by atmospheric CO_2 in the FTIR sample chamber. Due to scheduling we could not obtain FTIR spectra for all teeth analyzed in this study.

Table 4.6. Results of FTIR analysis of tooth enamel samples.

Sample ID	Cultural Period	Taxon	CI	CO_3/PO_4 Index	CO/CO_3 Ratio	BPI	wt% CO_3
BIBS14-298 M1	Classic Thule	Caribou	2.9	0.5	2.1	0.5	5.5
BIBS14-494 M1	Classic Thule	Caribou	2.9	0.4	2.1	0.4	5.0
BIBS14-502 M1	Classic Thule	Caribou	2.7	0.4	2.1	0.4	5.1
BIBS14-214 M1	Inuit	Caribou	2.8	0.5	2.1	0.5	5.4
BIBS14-360 M1	Inuit	Caribou	3.0	0.4	2.1	0.4	4.7
BIBS14-407 M1	Pre-Dorset	Muskox	2.7	0.5	2.1	0.5	5.6
BIBS14-409 M1	Pre-Dorset	Muskox	2.7	0.5	2.1	0.5	5.6
BIBS14-162 M1	Lagoon	Muskox	2.7	0.5	2.1	0.5	5.9
BIBS14-209 M1	Lagoon	Muskox	2.9	0.4	2.1	0.5	5.3
BIBS14-474 M1	Classic Thule	Muskox	2.8	0.4	2.1	0.4	5.0
BIBS14-456 M1	Inuit	Muskox	2.7	0.5	2.1	0.5	5.9
BIBS14-169 M1	Modern	Muskox	2.8	0.5	2.1	0.5	5.8
BIBS14-445 M1	Modern	Muskox	2.7	0.5	2.1	0.5	5.6

4.4.3 Tooth Enamel Structural Carbonate $\delta^{13}C$ and $\delta^{18}O$ ($\delta^{13}C_{sc}$ and $\delta^{18}O_{sc}$) Results

Across five analyses of NIST RM 8545 (accepted $\delta^{13}C$ and $\delta^{18}O$ –46.60‰ and –26.70‰, respectively), $\delta^{13}C$ was –46.60±0.06‰ and $\delta^{18}O$ was 4.02±0.11‰. Across nine analyses of WS-1 (mean $\delta^{13}C$ and $\delta^{18}O$ +0.76‰ and +26.23‰, respectively), $\delta^{13}C$ was +0.66‰ ±0.18 and $\delta^{18}O$ was 26.09‰ ±0.43. Because we did not treat enamel samples prior to analysis, and because tooth enamel microsamples are spatially-dependent, we did not produce methodological duplicates. The standard deviation of enamel samples analyzed as instrumental duplicates is $\delta^{13}C_{sc}$ = ±0.0‰ and $\delta^{18}O_{sc}$ = ±0.0‰.

Caribou $\delta^{13}C_{sc}$ and $\delta^{18}O_{sc}$ are presented in Table 4.7 and their sampling locations on each tooth thick section are shown in Appendix C, Supplemental Figure C1. Across four microsamples, the $\delta^{13}C_{sc}$ of modern caribou tooth enamel averaged –12.6‰ (min = –14.3‰, max = –11.7‰) and across 20 microsamples, the $\delta^{13}C_{sc}$ of archaeological caribou tooth enamel averaged –10.7‰ (min = –12.4‰, max = –8.5‰). The $\delta^{18}O_{sc}$ of all caribou tooth enamel samples averaged +14.5‰ (min = +12.2‰, max = +17.3‰).

Muskox $\delta^{13}C_{sc}$ and $\delta^{18}O_{sc}$ are presented in Table 4.8 and their sampling locations on each tooth thick section are shown in Appendix C, Supplemental Figure C2. Across three microsamples, the $\delta^{13}C_{sc}$ of modern muskox M1 enamel averaged –14.0‰ (min = –14.8‰, max = –13.3‰) and across thirteen microsamples, the $\delta^{13}C_{sc}$ of archaeological muskox M1 enamel averaged –12.4‰ (min = –14.2‰, max = –11.5‰). The $\delta^{18}O_{sc}$ of all muskox M1 enamel samples averaged +12.4‰ (min = +9.5‰, max = +15.5‰).

Table 4.7. Structural carbonate carbon and oxygen isotope results for micromilled caribou tooth enamel microsamples.

Sample ID	Taxon	Microbulk Sample	$\delta^{13}C_{sc}$ (‰, VPDB)	$\delta^{18}O_{sc}$ (‰, VSMOW)
Classic Thule				
BIBS14-298 M1	Caribou	MB1	–11.0	+16.1
		MB2	–9.5	+15.9
BIBS14-298 M2	Caribou	MB1	–8.8	+15.1
		MB2	–8.5	+13.9
BIBS14-298 M3	Caribou	MB1	–8.8	+13.4
		MB2	–9.4	+13.3
BIBS14-494 M1	Caribou	MB1	–12.4	+14.6
		MB2	–11.4	+14.5
BIBS14-502 M1	Caribou	MB1	–12.0	+17.3
		MB2	–10.9	+16.0
Inuit				
BIBS14-214 M1	Caribou	MB1	–11.8	+16.0
		MB2	–12.0	+15.5
BIBS14-214 M2	Caribou	MB1	–10.0	+13.5
		MB2	–10.2	+12.8
BIBS14-214 M3	Caribou	MB1	–10.8	+13.8
		MB2	–11.3	+14.3
BIBS14-214 P4	Caribou	MB1	–10.7	+13.3
		MB2	–10.5	+12.2
BIBS14-360 M1	Caribou	MB1	–12.3	+13.5
		MB2	–10.9	+13.3
Modern				
BIBS15-67 M2	Caribou	MB1	–11.7	+13.9
		MB2	–12.0	+14.4
BIBS16-19 M1	Caribou	MB1	–14.3	+16.2
BIBS16-19 M2	Caribou	MB2	–12.3	+15.0

Table 4.8. Structural carbonate carbon and oxygen isotope results for micromilled muskox tooth enamel microsamples.

Sample ID	Taxon	Microbulk Sample	$\delta^{13}C_{sc}$ (‰, VPDB)	$\delta^{18}O_{sc}$ (‰, VSMOW)
Pre-Dorset				
BIBS14-407 M1	Muskox	MB1	–11.8	+13.4
		MB2	–11.5	+11.4
BIBS14-409 M1	Muskox	MB1	–12.0	+15.2
		MB2	–11.5	+12.5
Lagoon				
BIBS14-162 M1	Muskox	MB1	–11.7	+11.2
		MB2	–11.5	+10.7
BIBS14-209 M1	Muskox	MB1	–11.8	+12.3
Early Thule				
BIBS16-30 M1	Muskox	MB1	–13.8	+10.7
		MB2	–12.9	+9.5
Classic Thule				
BIBS14-474 M1	Muskox	MB1	–13.6	+12.0
		MB2	–12.5	+9.9
Inuit				
BIBS14-456 M1	Muskox	MB1	–14.2	+14.7
		MB2	–12.4	+10.7
Modern				
BIBS14-169 M1	Muskox	MB1	–14.8	+15.5
	Muskox	MB2	–13.9	+14.4
BIBS14-445 M1	Muskox	MB1	–13.3	+14.2

4.4.4 Tooth Enamel Laser Ablation $\delta^{13}C$ and $\delta^{18}O$ ($\delta^{13}C_{LA}$ and $\delta^{18}O_{LA}$) Results

Isotopic results for ablation events where dentin adjacent to enamel was inadvertently contacted by the laser are excluded from this chapter. In some cases, a sample spot produced an abnormal[19] $\delta^{13}C_{LA}$ value, but a $\delta^{18}O_{LA}$ value similar to preceding and following sampling spots, and *vice versa*. In these cases, we have retained the acceptable isotopic data from the ablation event, but omit the abnormal results from all figures, tables, and calculations. Because the degree of occlusal wear in each tooth varies, the ablation spot closest to the root-enamel junction (REJ) of each enamel section is used as a common "anchor point" in all figures.

Caribou tooth enamel $\delta^{13}C_{LA}$ and $\delta^{18}O_{LA}$ data are presented in Table 4.9 and are represented graphically in Figures 4.11 and 4.12. Corresponding ablation spot locations on each tooth thick section are shown in Appendix C, Supplemental Figure C3. Intra-tooth variability in $\delta^{13}C_{LA}$ among the six caribou M1s averaged 1.5‰, with the highest intra-tooth variation (2.1‰) measured in BIBS14-502 M1. In the four caribou M2s analyzed, intra-tooth variability in $\delta^{13}C_{LA}$ averaged 0.9‰, with the highest intra-tooth variability (2.2‰) occurring in BIBS16-19 M2. Of the two caribou M3s analyzed, intra-tooth variability in $\delta^{13}C_{LA}$ in BIBS14-298 M3 was 1.6‰, while intra-tooth variability in $\delta^{13}C_{LA}$ in BIBS14-214 M3 was 0.5‰.

Intra-tooth variability in $\delta^{18}O_{LA}$ among the six caribou M1s averaged 1.4‰, with the highest intra-tooth variation (2.2‰) again occurring in BIBS14-502 M1. In the four caribou M2s, intra-tooth variability in $\delta^{18}O_{LA}$ averaged 1.8‰, with the highest intra-tooth variability (3.3‰) in BIBS14-298 M1. Of the two caribou M3s analyzed, intra-tooth variability in $\delta^{18}O_{LA}$ in BIBS14-298 M3 was 1.3‰, while intra-tooth variability in $\delta^{18}O_{LA}$ in BIBS14-214 M3 was 0.7‰. Tooth-averaged $\delta^{18}O_{LA}$ decreased across caribou molars (Figure 4.12) from +7.7‰ in M1s to +7.0‰ in M2s, to +6.3‰ in M3s.

---

[19] Although "abnormal" values were identified subjectively, they typically appeared as out-of-trend "spikes" exceeding ±1.5‰ of the $\delta^{13}C$ or $\delta^{18}O$ from preceding and following ablation spots.

The $\delta^{13}C_{LA}$ and $\delta^{18}O_{LA}$ of tooth enamel from muskox M1s are presented in Table 4.10 and are illustrated in Figures 4.13 and 4.14. Corresponding ablation spot locations on each tooth thick section are shown in Appendix C, Supplemental Figure C4. Overall, intra-tooth $\delta^{13}C_{LA}$ increases across the sample sequence in most of the muskox M1s. Intra-tooth variability in $\delta^{13}C_{LA}$ among the nine muskox M1s averaged 1.3‰, with the lowest intra-tooth variation (0.4‰) in BIBS14-209, and the highest (2.1‰) in both BIBS14-456 M1 and BIBS14-409 M1. Among archaeological muskox M1s, tooth-averaged $\delta^{13}C_{LA}$ was lowest in BIBS14-474 (–12.6‰) and BIBS14-456 M1 (–12.8‰), and highest in BIBS14-209 M1 (–10.8‰). Intra-tooth $\delta^{18}O_{LA}$ decreased across the sample sequence in most of the muskox M1s. Intra-tooth variability in $\delta^{18}O_{LA}$ among the nine muskox M1s averaged 2.1‰, with lowest intra-tooth variation (0.6‰) in BIBS14-162, and highest (4.5‰) in BIBS14-456.

Table 4.9. Values of $\delta^{13}C_{LA}$ and $\delta^{18}O_{LA}$ for caribou tooth enamel analyzed using LA-GC-IRMS.

Sample ID	Taxon	Spot	$\delta^{13}C_{LA}$ (‰, VPDB)	$\delta^{18}O_{LA}$ (‰, VSMOW)
Classic Thule				
BIBS14-298 M1	Caribou	1	–10.2	+8.1
		2	–10.4	+8.0
		3	–10.4	+9.0
		5	–10.4	+7.2
		6	–10.9	+7.7
		7	–10.3	+7.3
		8	–9.4	+8.1
BIBS14-298 M2	Caribou	1	–8.4	+8.3
		2	–8.5	+8.3
		3	–8.2	+8.1
		4	–8.2	+7.9
		5	–8.2	+7.9
		6	–8.2	+7.5
		7	–8.5	+6.3
		8	–8.6	+5.0
		9	–8.4	+6.7
		10	–8.4	+5.7
BIBS14-298 M3	Caribou	1	–8.8	+6.7
		2	–9.3	+7.3
		3	–9.6	+6.9
		4	–9.5	+6.6
		5	–9.4	+6.7
		6	–9.3	+6.6
		7	–9.5	+6.9
		8	–9.7	+6.4
		9	–9.3	+6.4
		10	–9.8	+6.0
		11	–10.2	+6.1
		12	–10.4	+6.1

BIBS14-494 M1	Caribou	1	–11.5	+7.2
		2	–12.1	+7.4
		3	–11.5	+7.4
		4	–12.7	+6.4
		5	–11.6	+6.7
BIBS14-502 M1	Caribou	1	–11.7	+9.8
		2	–13.2	+9.5
		3	–12.0	+9.2
		4	–11.8	+8.9
		5	–11.6	+8.2
		6	–11.4	+7.8
		7	–11.1	+7.6
Inuit				
BIBS14-214 M1	Caribou	1	–11.6	+7.6
		2	–10.8	+7.4
		3	–11.0	+6.9
BIBS14-214 M2	Caribou	1	–9.0	+4.9
		2	–9.2	+4.9
		3	–9.3	+4.6
		4	–9.0	+4.9
		5	–9.7	+5.0
		6		+4.7
BIBS14-214 M3	Caribou	1	–10.9	+6.3
		2	–10.8	+5.8
		3	–11	+6.0
		4	–11.2	+5.7
		5	–10.9	+5.6
		6	–10.7	+6.1
BIBS14-214 P4	Caribou	1	–11.0	+5.1
		2	–10.4	+4.5
		3	–10.6	+4.1
		4	–10.4	+4.3
		5	–10.4	+4.0
		6	–10.2	+4.0

		7	–10.2	+3.6
BIBS14-360 M1	Caribou	1	–11.4	+5.8
		2	–12.2	+6.6
		3	–12.3	+6.5
		4	–11.7	+6.5
		5	–11.4	+6.5
		6	–11.5	+6.4
		7	–11.3	+5.9
		8	–10.7	+5.9
		9	–10.7	+5.5
		10	–11.4	+5.2
Modern				
BIBS15-67 M2	Caribou	1	–11.2	+6.8
		2	–11.1	+6.8
		3	–11.3	+6.9
		4	–11.7	+7.3
BIBS16-19 dp4	Caribou	1	–12.5	+6.2
		2	–14.0	+6.5
		3	–14.8	+6.4
BIBS16-19 M1	Caribou	1	–14.4	+8.3
		2	–15.0	+9.3
		3	–14.7	+9.3
		4	–14.5	+8.9
		5	–14.4	+9.3
		6	–13.9	+9.4
		7	–13.4	+9.2
		8	–13.4	+8.7
BIBS16-19 M2	Caribou	1	–12.9	+9.7
		2	–12.7	+9.0
		3	–12.1	+9.0
		4	–11.9	+7.9
		5	–12.4	+8.1
		6	–12.9	+7.9
		7	–13.8	+7.4

	8	–14.1	+7.0
	9		+6.9

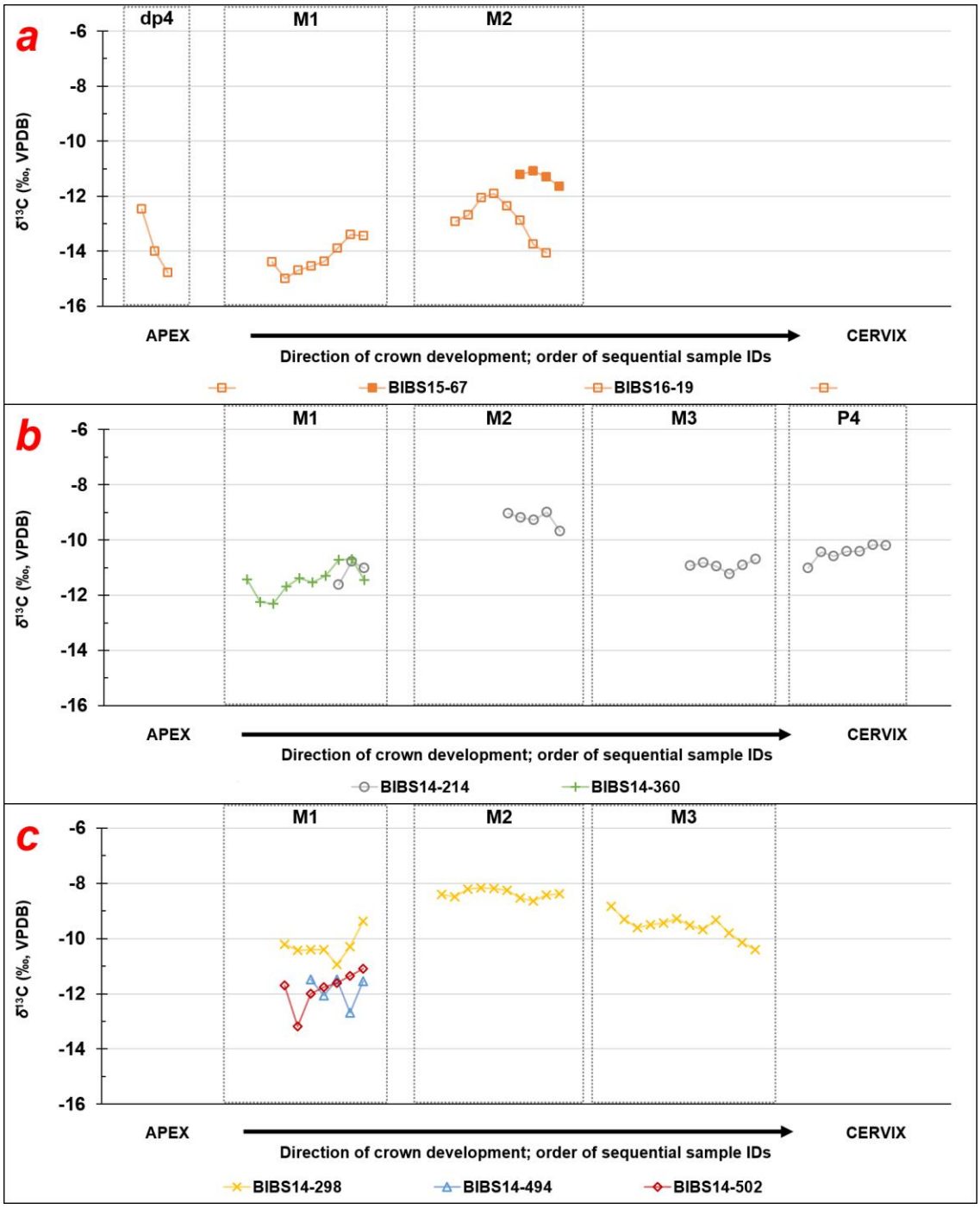


Figure 4.11. Values of $\delta^{13}C_{LA}$ for caribou tooth enamel from the: **(*a*)** modern, **(*b*)** Inuit; and **(*c*)** Classic Thule periods. Data are displayed in approximate order of tooth development (dp4, M1, M2, M3, P4).

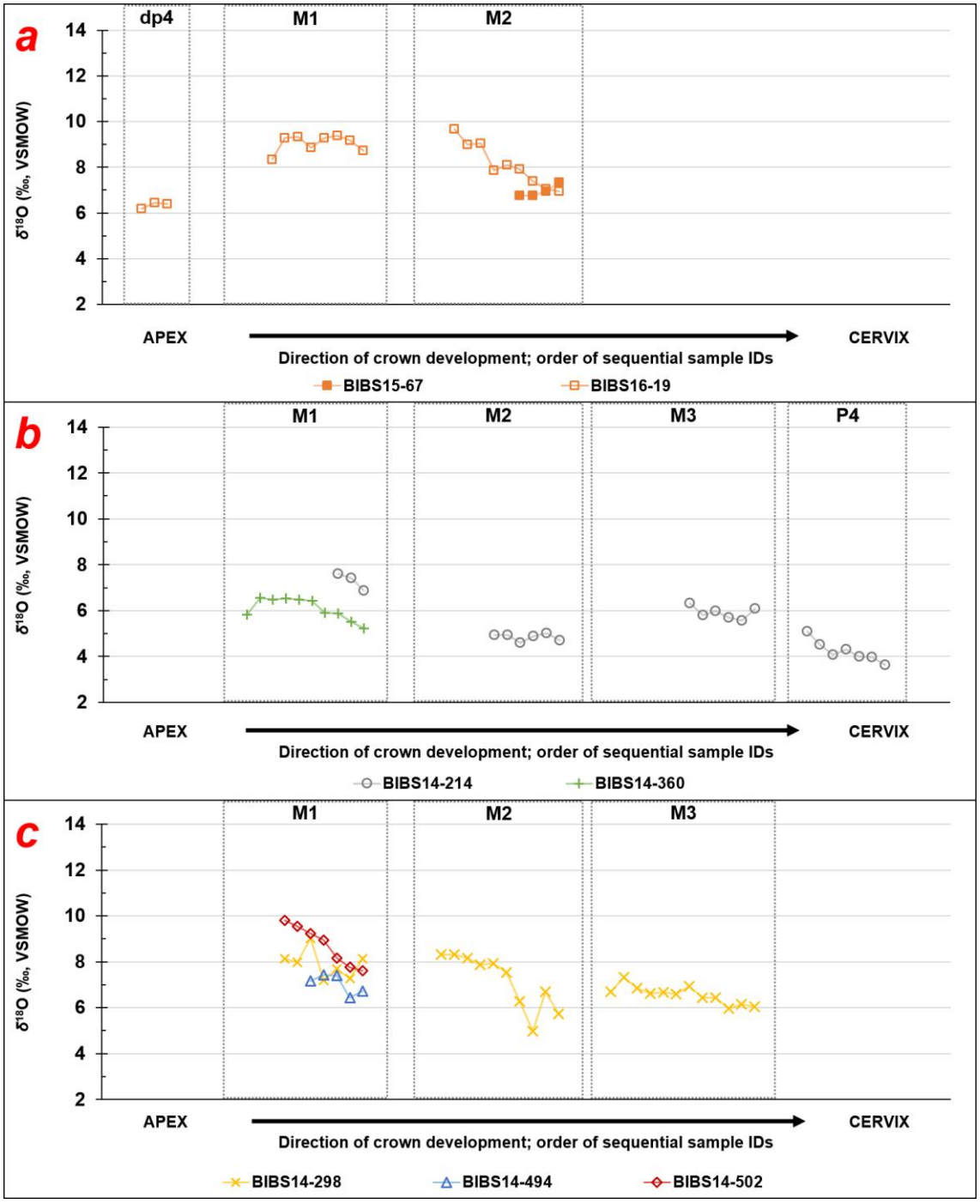


Figure 4.12. Values of $\delta^{18}O_{LA}$ for caribou tooth enamel from the: **(*a*)** modern, **(*b*)** Inuit; and **(*c*)** Classic Thule periods. Data are displayed in approximate order of tooth development (dp4, M1, M2, M3, P4).

Table 4.10. Values of $\delta^{13}C_{LA}$ and $\delta^{18}O_{LA}$ for muskox tooth enamel analyzed using LA-GC-IRMS.

Sample ID	Taxon	Spot	$\delta^{13}C_{LA}$ (‰, VPDB)	$\delta^{18}O_{LA}$ (‰, VSMOW)
Pre-Dorset				
BIBS14-407 M1	Muskox	1	–11.6	+5.6
		2	–11.6	+5.2
		3	–11.3	+5.2
		4	–11.9	+4.8
		5	–11.7	+4.9
		6	–11.4	+4.8
		7	–11.5	+4.5
		8	–12.1	+5.1
		9	–11.6	+4.7
		10	–11.5	+4.8
		11	–11.2	+4.5
		12	–11.1	+4.2
		13	–11.4	+3.6
		14	–11.3	+3.7
		15	–11.2	+3.8
		16	–11.6	+3.4
BIBS14-409 M1	Muskox	1	–12.4	+9.6
		2	–12.7	+9.4
		3	–12.8	+9.1
		4	–13.8	+9.0
		5		+7.9
		6	–12.3	+7.6
		7	–12.0	+7.7
		8	–12.1	+7.6
		9	–12.2	+7.4
		10	–12.0	+7.2
		11	–12.0	+7.5
		12	–11.7	+7.1
		13	–11.8	+7.1
		14	–12.0	+6.8

		15	–12.0	+6.4
		16	–12.1	+7.2
Lagoon				
BIBS14-162 M1	Muskox	1	–11.1	+3.1
		2	–11.1	+2.6
		3	–10.9	+2.7
		4	–10.9	+2.8
		5	–11.5	+3.1
		6	–10.9	+3.2
BIBS14-209 M1	Muskox	1	–10.8	+4.7
		2	–10.7	+4.5
		3	–10.6	+4.4
		4	–10.6	+4.4
		5	–10.7	+4.1
		6	–10.5	+3.9
		7	–10.8	+3.8
		8	–10.8	+3.9
		9	–10.9	+3.9
		10	–10.9	+3.9
		11	–10.9	+3.7
Early Thule				
BIBS16-30 M1	Muskox	1	–12.5	+5.6
		2	–12.7	+5.2
		3	–12.4	+5.2
		4	–13.1	+4.7
		5	–12.2	+5.0
		6	–12.0	+5.1
		7	–12.1	+5.0
		8	–12.0	+5.0
		9	–12.2	+4.8
		10	–13.5	+4.4
		11	–11.9	+5.0
		12	–12.0	+4.7
		13	–11.7	+4.4

		14	–12.0	+4.9
		15	–12.1	+4.9
Classic Thule				
BIBS14-474 M1	Muskox	1	–13.6	+6.3
		2	–12.5	+5.2
		3	–12.8	+5.1
		5	–12.5	+4.0
		6	–12.4	+3.9
		7	–12.1	+3.7
		8	–12.4	+3.7
		9	–12.6	+3.5
		10	–12.5	+3.8
Inuit				
BIBS14-456 M1	Muskox	1	–14.1	+8.2
		2	–14.2	+8.1
		3	–13.3	+7.7
		4	–13.3	+7.3
		5	–13.2	+7.1
		6	–13.0	+6.8
		7	–13.0	+6.5
		8	–13.1	+6.5
		9	–12.9	+6.5
		10	–12.9	+6.4
		11	–12.9	+6.4
		12	–13.0	+6.1
		13	–12.6	+5.4
		14	–12.9	+5.6
		15	–12.8	+5.3
		16	–12.9	+5.2
		17	–12.8	+5.0
		18	–12.3	+5.0
		19	–12.3	+4.9
		20	–12.4	+4.6
		21	–12.4	+4.6

		22	–12.3	+4.7
		23	–12.1	+4.4
		24	–12.3	+4.1
		25	–12.2	+3.7
		26	–12.4	+4.3
Modern				
BIBS14-169 M1	Muskox	1	–14.5	+6.2
		2	–14.5	+6.3
		3	–13.8	+6.5
		4	–13.8	+6.1
		5	–13.7	+6.1
		6	–13.6	+6.6
		7	–13.6	+6.5
		8	–13.7	+6.2
		9	–13.6	+5.6
		10	–13.2	+6.0
		11	–13.4	+6.2
		12	–13.3	+6.6
BIBS14-445 M1	Muskox	1	–13.3	
		2	–13.5	+8.2
		3	–13.3	+8.1
		4	–13.6	+7.8
		5	–13.4	+7.7
		6	–13.3	+7.1
		7	–14.4	
		10	–13.6	+6.2
		11	–13.9	+6.7
		12	–13.7	+6.5
		13	–13.5	+6.3
		14	–13.2	+5.6

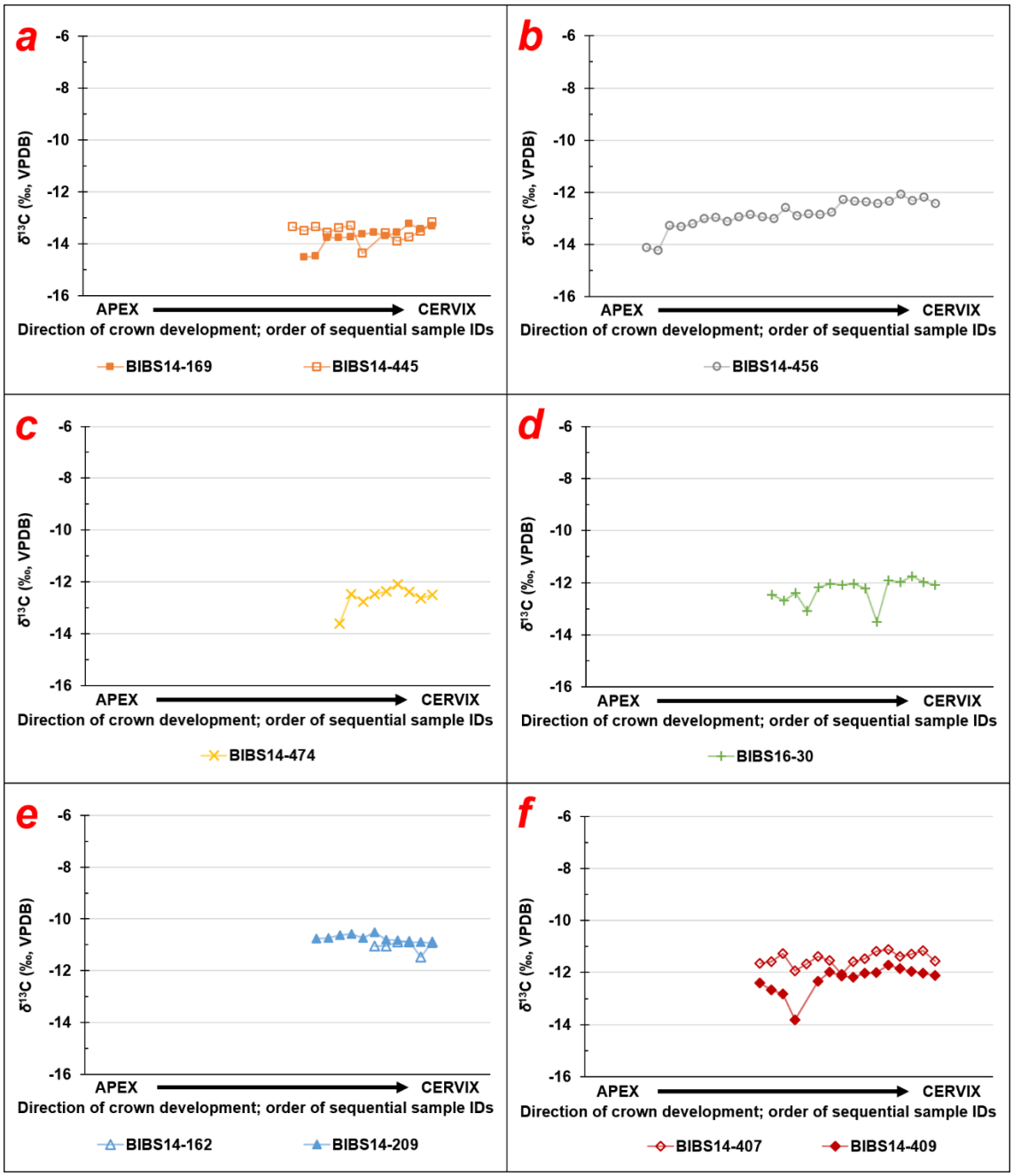


Figure 4.13. Values of $\delta^{13}C_{LA}$ for muskox tooth enamel from the: **(*a*)** modern, **(*b*)** Inuit, **(*c*)** Classic Thule **(*d*)** Early Thule, **(*e*)** Lagoon; and **(*f*)** Pre-Dorset periods.

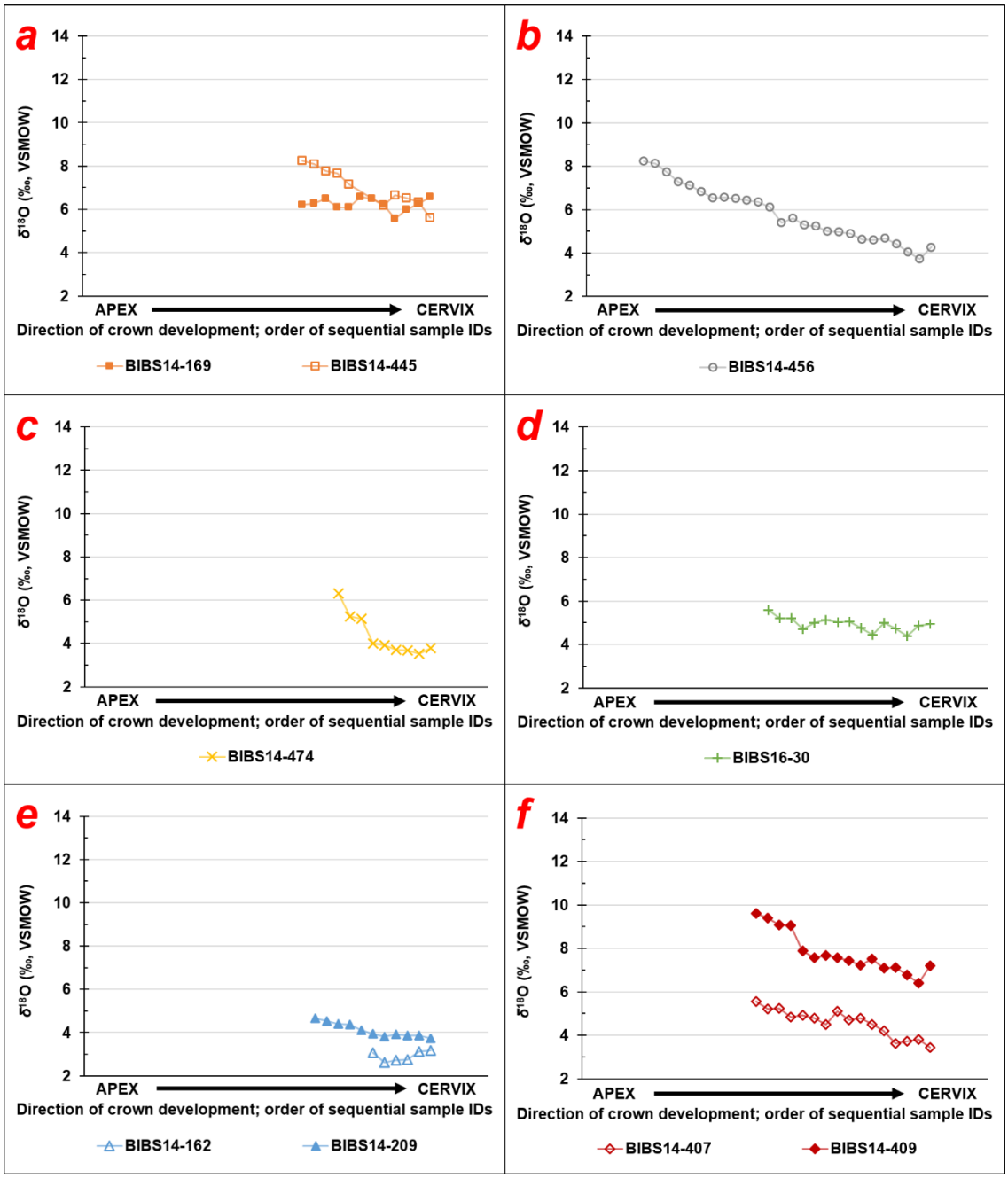


Figure 4.14. Values of $\delta^{18}O_{LA}$ for muskox tooth enamel from the: **(*a*)** modern, **(*b*)** Inuit, **(*c*)** Classic Thule, **(*d*)** Early Thule, **(*e*)** Lagoon; and **(*f*)** Pre-Dorset periods.

4.4.5 Comparison of Structural Carbonate and Laser Ablation $\delta^{13}C$ and $\delta^{18}O$ ($\Delta^{13}C_{sc\text{-}LA}$ and $\Delta^{18}O_{sc\text{-}LA}$)

Offsets between caribou and muskox tooth enamel $\delta^{13}C$ and $\delta^{18}O$ derived from structural carbonate and laser ablation of corresponding areas on A- and B-sections ($\Delta^{13}C_{sc\text{-}LA}$ and $\Delta^{18}O_{sc\text{-}LA}$) are listed in Tables 4.11 and 4.12, respectively. Out of 24 enamel microsamples from caribou A-sections, the $\delta^{13}C_{sc}$ of 12 were within ±0.4‰ of the $\delta^{13}C_{LA}$ from the same area on corresponding B-sections. Of the 16 enamel microsamples from muskox A-sections, the $\delta^{13}C_{sc}$ of 10 were within ±0.4‰ of the $\delta^{13}C_{LA}$ from the same area on the corresponding B-section. Instances where the $\Delta^{13}C_{sc\text{-}LA}$ offset was greater than ±0.4‰ are probably due to either differences in the sampling area, or the mixing of enamel from multiple micromilling locations to produce enough enamel powder.

Most of the structural carbonate $\delta^{13}C$ measurements from both species are slightly lower than those obtained by laser ablation from the same area on the corresponding thick section. This negative offset is contrary to expectation: the H_3PO_4 method should only produce CO_2 from the structural carbonate component of enamel, whereas laser ablation generates CO_2 from structural carbonate as well as the small organic component in enamel (LeGeros 1991), which is depleted of ^{13}C relative to structural carbonate. The negative $\delta^{13}C$ offset between most of the enamel structural carbonate $\delta^{13}C$ relative to laser ablation $\delta^{13}C$ may be the result of using only a constant (single-point) matrix correction for the laser ablation data. We found, for instance, that when the WS-1 calcite standard was used to perform a calibration correction for the laser data, $\Delta^{13}C_{sc\text{-}LA}$ offsets are larger, but the structural carbonate $\delta^{13}C$ was higher than laser ablation $\delta^{13}C$, as might have been expected.

In caribou tooth enamel samples, the mean offset between structural carbonate $\delta^{18}O$ and laser ablation $\delta^{18}O$ ($\Delta^{18}O_{sc\text{-}LA}$) from corresponding areas of the A- and B-sections is 7.8‰ (min = 6.7‰, max = 8.8‰) (Table 4.11). Similarly, the mean $\Delta^{18}O_{sc\text{-}LA}$ offset for muskox tooth enamel samples is 6.9‰ (min = 4.6‰, max = 9.3‰) (Table 4.12). The mean $\Delta^{18}O_{sc\text{-}LA}$ for both species are in line with the $\Delta^{18}O_{sc\text{-}LA}$ of our internal enamel standard (7.2‰), and Cerling and Sharp (1996), who arrived at a $\Delta^{18}O_{sc\text{-}LA}$ of 7.1‰ for tooth enamel from multiple taxa.

Table 4.11. Offsets between the $\delta^{13}C$ and $\delta^{18}O$ ($\Delta^{13}C_{sc\text{-}LA}$ and $\Delta^{18}O_{sc\text{-}LA}$) obtained from structural carbonate and laser ablation of caribou tooth enamel from corresponding areas on A- and B-sections. Where the area micromilled on the A-Section corresponds to multiple ablation spots on the B-section, $\Delta^{13}C_{sc\text{-}LA}$ and $\Delta^{18}O_{sc\text{-}LA}$ shown here reflect the averages of the ablation spots.

Sample ID	Taxon	Microbulk Sample	$\delta^{13}C_{sc}$ (‰, VPDB)	$\delta^{18}O_{sc}$ (‰, VSMOW)	Ablation Spot	$\delta^{13}C_{LA}$ (‰, VPDB)	$\delta^{18}O_{LA}$ (‰, VSMOW)	$\Delta^{13}C_{sc\text{-}LA}$ (‰, VPDB)	$\Delta^{18}O_{sc\text{-}LA}$ (‰, VSMOW)
Classic Thule									
BIBS14-298 M1	Caribou	MB1	–11.0	+16.1	1	–10.2	+8.1	–0.7	+8.0
					2	–10.4	+8.0		
		MB2	–9.5	+15.9	8	–9.4	+7.7	–0.1	+8.6
BIBS14-298 M2	Caribou	MB1	–8.8	+15.1	1	–8.4	+8.3	–0.4	+6.8
					2	–8.5	+8.3		
		MB2	–8.5	+13.9	9	–8.4	+6.7	–0.1	+7.2
					10	–8.4	+5.7		
BIBS14-298 M3	Caribou	MB1	–8.8	+13.4	1	–8.8	+6.7	+0.3	+6.7
					2	–9.3	+7.3		
		MB2	–9.4	+13.3	10	–9.8	+6.0	+0.7	+7.3
					11	–10.2	+6.1		
					12	–10.4	+6.1		
BIBS14-494 M1	Caribou	MB1	–12.4	+14.6	2	–12.1	+7.4	–0.3	+7.2
		MB2	–11.4	+14.5	3	–11.5	+7.4	+0.5	+7.1
					4	–12.7	+6.4		
					5	–11.6	+6.7		

BIBS14-502 M1	Caribou	MB1	–12.0	+17.3	1	–11.7	+9.8	+0.4	+7.5
					2	–13.2	+9.5		
		MB2	–10.9	+16	7	–11.1	+7.6	+0.2	+8.4
Inuit									
BIBS14-214 M1	Caribou	MB1	–11.8	+16.0	1	–11.6	+7.6	–0.2	+8.4
		MB2	–12.0	+15.5	3	–11.0	+6.9	–1.0	+8.6
BIBS14-214 M2	Caribou	MB1	–10.0	+13.5	1	–9.0	+4.9	–1.0	+8.6
		MB2	–10.2	+12.8	4	–9.0	+4.9	–0.9	+7.9
					5	–9.7	+5.0		
BIBS14-214 M3	Caribou	MB1	–10.8	+13.8	1	–10.9	+6.3	+0.1	+7.5
					2	–10.8	+5.8		
		MB2	–11.3	+14.3	5	–10.9	+5.6	–0.5	+8.7
					6	–10.7	+6.1		
BIBS14-214 P4	Caribou	MB1	–10.7	+13.3	2	–10.4	+4.5	–0.3	+8.8
		MB2	–10.5	+12.2	6	–10.2	+4.0	–0.3	+8.2
					7	–10.2	+3.6		
BIBS14-360 M1	Caribou	MB1	–12.3	+13.5	1	–11.4	+5.8	–0.5	+7.7
					2	–12.2	+6.6		
		MB2	–10.9	+13.3	10	–11.4	+5.2	+0.5	+8.1
Modern									
BIBS15-67 M2	Caribou	MB1	–11.7	+13.9	1	–11.2	+6.8	–0.6	+7.1
					2	–11.1	+6.8		

		MB2	–12.0	+14.4	3	–11.3	+6.9	–0.5	+7.5
					4	–11.7	+7.3		
BIBS16-19 M1	Caribou	MB1	–14.3	+16.2	1	–14.4	+8.3	+0.4	+7.9
					2	–15.0	+9.3		
BIBS16-19 M2	Caribou	MB2	–12.3	+15.0	8	–14.1	+7.0	+1.8	+8.0

Table 4.12. Offsets between the $\delta^{13}C$ and $\delta^{18}O$ ($\Delta^{13}C_{sc\text{-}LA}$ and $\Delta^{18}O_{sc\text{-}LA}$) obtained from structural carbonate and laser ablation of muskox tooth enamel from corresponding areas on A- and B-sections. Where the area micromilled on the A-Section corresponds to multiple ablation spots on the B-section, $\Delta^{13}C_{sc\text{-}LA}$ and $\Delta^{18}O_{sc\text{-}LA}$ shown here reflect the averages of the ablation spots.

Sample ID	Taxon	Microbulk Sample	$\delta^{13}C_{sc}$ (‰, VPDB)	$\delta^{18}O_{sc}$ (‰, VSMOW)	Ablation Spot	$\delta^{13}C_{LA}$ (‰, VPDB)	$\delta^{18}O_{LA}$ (‰, VSMOW)	$\Delta^{13}C_{sc\text{-}LA}$ (‰, VPDB)	$\Delta^{18}O_{sc\text{-}LA}$ (‰, VSMOW)
Pre-Dorset									
BIBS14-407 M1	Muskox	MB1	–11.8	+13.4	1	–11.6	+5.6	–0.2	+7.8
		MB2	–11.5	+11.4	14	–11.3	+3.7	–0.2	+7.7
					15	–11.2	+3.8		
					16	–11.6	+3.4		
BIBS14-409 M1	Muskox	MB1	–12.0	+15.2	1	–12.4	+9.6	+0.4	+5.6
		MB2	–11.5	+12.5	15	–12.0	+6.4	+0.5	+6.1
Lagoon									
BIBS14-162 M1	Muskox	MB1	–11.7	+11.2	1	–11.1	+3.1	–0.6	+8.4
					2	–11.1	+2.6		
		MB2	–11.5	+10.7	5	–11.5	+3.1	–0.3	+7.5
					6	–10.9	+3.2		
BIBS14-209 M1	Muskox	MB1	–11.8	+12.3	2	–10.7	+4.5	–1.1	+7.8
					3	–10.6	+4.4		
Early Thule									
BIBS16-30 M1	Muskox	MB1	–13.8	+10.7	1	–12.5	+5.6	–1.3	+5.1
		MB2	–12.9	+9.5	15	–12.1	+4.9	–0.8	+4.6

Classic Thule									
BIBS14-474 M1	Muskox	MB1	–13.6	+12.0	1	–13.6	+6.3	0.0	+5.7
		MB2	–12.5	+9.9	9	–12.6	+3.5	+0.1	+6.3
					10	–12.5	+3.8		
Inuit									
BIBS14-456 M1	Muskox	MB1	–15.9	+14.7	1	–14.1	+8.2	–0.1	+6.5
		MB2	–14.1	+10.7	12	–12.3	+4.1	–0.1	+6.7
					13	–12.2	+3.7		
					14	–12.4	+4.3		
Modern									
BIBS14-169 M1	Muskox	MB1	–14.8	+15.5	1	–14.5	+6.2	–0.3	+9.3
		MB2	–13.9	+14.4	11	–13.4	+6.2	–0.5	+8.0
					12	–13.3	+6.6		
BIBS14-445 M1	Muskox	MB1	–13.3	+14.2	1	–13.3	+6.1	+0.1	+7.1
					2	–13.5	+8.2		

4.5 Discussion

4.5.1 Caribou Tooth Enamel $\delta^{13}C$ Derived via Laser Ablation ($\delta^{13}C_{LA}$)

When compared to sequential dentin collagen $\delta^{13}C$ from the same caribou teeth (Chapter 3), the spatial resolution of $\delta^{13}C$ data obtain from tooth enamel using laser ablation is much higher. This affords greater insight into the relationship between the eruption schedule for caribou teeth (Figure 4.2) and their development. Sequential $\delta^{13}C_{LA}$ from the teeth of the modern caribou, BIBS16-19, (Figure 4.11a) provide a useful example of this relationship. Because the fourth deciduous premolar (dp4) in caribou is present and erupting upon birth (Banfield 1954; Miller 1974), its isotopic composition reflects variation in maternal diet, which is passed on to the developing calf *in utero*. Consequently, the ~ 2‰ decrease in $\delta^{13}C_{LA}$ from –12.5 to –14.8‰ across ablation spots of BIBS16-19 dp4 likely corresponds to a shift from maternal dietary signals from late winter forage (with higher $\delta^{13}C$) passed on to the calf *in utero* to summer forage (with lower $\delta^{13}C$) during the period of enamel mineralization. Intra-tooth variation in $\delta^{13}C_{LA}$ in BIBS16-19 M1 reflects a shift from summer forage with lower $\delta^{13}C$ to winter forage with higher $\delta^{13}C$, which corresponds with the approximate period of formation and eruption in this tooth (Figure 4.2). Likewise, intra-tooth variation in $\delta^{13}C_{LA}$ in BIBS16-19 M2 probably records a shift towards forage with higher $\delta^{13}C$ during the first winter of life, and the subsequent shift towards forage with lower $\delta^{13}C$ during the second summer of life (Figure 4.2). In short, the intra-tooth sequence of $\delta^{13}C_{LA}$ from the dp4, M1 and M2 of BIBS16-19 describe a near-continuous sequence of dietary variation starting at the winter or spring prior to birth and ending near the second summer of life.

The ~ 2‰ variation in intra-tooth $\delta^{13}C_{LA}$ in BIBS16-19 suggests that this caribou probably switched to a different forage resource with higher $\delta^{13}C$ in winter, rather than simply eating desiccated or lignified tissues from typical summer forage species. If the latter was the

case, we would expect $\delta^{13}C_{LA}$, which essentially represents structural carbonate $\delta^{13}C$, to decrease during the winter due to the greater proportion of ^{13}C-depleted lignin in diet[20].

Dentin collagen $\delta^{13}C$, and its slightly positive offset relative to bulk bone collagen $\delta^{13}C$ (Chapter 2 and 3) also suggests that milk proteins, rather than lipids, influence dentin collagen carbon isotope compositions. The strong intra-tooth variation in $\delta^{13}C_{LA}$ in the teeth of the modern caribou BIBS16-19, however, suggest that any influence on $\delta^{13}C_{LA}$ due to milk consumption is probably offset by other forage sources. If milk was the dominant dietary input during the period in which the teeth of this caribou formed, we would expect relatively homogenous intra-tooth $\delta^{13}C_{LA}$. The $\delta^{13}C_{LA}$ of teeth from BIBS16-19 therefore support our conclusion in Chapter 2 that this caribou started and completed the weaning process relatively early.

Although the tooth sample dataset is limited, where we obtained data from more than one caribou in a single cultural period, sequential carbon isotope compositions tend to fall within a similar range, or trend in a similar direction. Consequently, the $\delta^{13}C_{LA}$ of caribou teeth across cultural periods (Figure 4.11) may provide some information about variability in seasonal diet over the last several hundred years. For instance, the intra-tooth pattern of $\delta^{13}C_{LA}$ from the M1 of BIBS14-360, from the Inuit period, resembles that of the modern caribou (BIBS16-19), with a small decrease early in the sequence followed by gradually increasing $\delta^{13}C_{LA}$. As discussed above, this quasi-sinusoidal pattern is consistent with a shift toward summer forage with lower $\delta^{13}C$, followed by a gradual change towards winter forage with higher $\delta^{13}C$. Conversely, the relatively steep decrease from –11.7‰ to –13.2‰, and then an increase to –12.0‰ in the first three ablation spots of BIBS14-502 M1 (Classic Thule period, red diamonds in Figure 4.11c) may suggest that summer forage availability was comparatively brief. Likewise, there is no strong decrease apparent in intra-tooth $\delta^{13}C_{LA}$ from the M1 of BIBS14-298 (Classic Thule period, yellow X's in Figure 4.11c),

[20]Tahmasebi (2015) for instance, found either no changes or slight decreases in $\delta^{13}C$ in modern grass samples from the Yukon allowed to decompose in experimental treatments replicating surface conditions. The $\delta^{13}C$ of one sample of *Cyclamen purpurascens*, however, increased by ~ 2.5‰ in the first 150 days, and then remained the same.

and hence no indication of a shift towards summer forage. The intra-tooth sequence of $\delta^{13}C_{LA}$ in the M2 of BIBS14-298 is also relatively flat, which suggests that the first winter of life was relatively long, in agreement with archaeological caribou dentin collagen $\delta^{13}C$ from the Inuit and Classic Thule periods (Chapter 3).

4.5.2 Muskox Tooth Enamel $\delta^{13}C$ Derived via Laser Ablation ($\delta^{13}C_{LA}$)

Unlike those of caribou teeth, the intra-tooth sequences of $\delta^{13}C_{LA}$ from muskox M1s (Figure 4.13) lack any strong sinusoidal patterning that might relate to large seasonal variations in forage items. Most of the muskox M1s we analyzed display a ~ 1‰ increase in ^{13}C across ablation spots. We suggest, based on eruption indices (Tener 1965; Henrichsen and Grue 1980), that this change corresponds to a shift from mid-summer to winter diet. We also observe increases in ^{13}C across sequential crown dentin collagen samples (Chapter 3) in the teeth discussed here, which suggests that, although significantly taller than those of caribou, the tooth enamel of muskox M1s mineralizes relatively quickly, such that there is limited lag between the isotopic signals integrated into dentin and enamel.

Though the intra-tooth variability in $\delta^{13}C_{LA}$ of muskox M1s across cultural periods is more limited than in caribou, it is notable that the two teeth dating to the Lagoon period (~ 2700-2100 calibrated ^{14}C BP), BIBS14-162 M1 and -209 M1, have the highest tooth-averaged $\delta^{13}C_{LA}$ of all archaeological muskox M1s (intra-tooth average $\delta^{13}C_{LA}$ = –11.0‰ and –10.8‰, respectively) (Figure 4.13e, Table 4.10). During the Lagoon period, average annual air temperature in the Canadian Arctic was considerably lower than today (Kaufman et al. 2004; Gajewski 2015; Navarro et al. 2016; Lecavalier et al. 2017). The higher $\delta^{13}C_{LA}$ in tooth enamel from both Lagoon period muskoxen, and the homogeneity of intra-tooth $\delta^{13}C_{LA}$ in BIBS14-209 M1, suggests that phytomass diversity may have been reduced during this period, limiting seasonal dietary variation. This interpretation is consistent with palynological evidence (Gajewski 1995; Gajewski et al. 2000; Gajewski and MacDonald 2004; Peros and Gajewski 2009), which suggests that around 3000 BP, shrub phytomass in the Canadian Arctic started declining while sedge and grass phytomass productivity increased. Given that sedges compose a significant portion of muskox diet year-round (Oakes et al. 1992; Larter and Nagy 1997, 2004), muskoxen may have had a nutritional

advantage over caribou during these cold centuries. This relationship between diet, phytomass productivity, and faunal productivity may also explain why caribou remains appear less frequently than muskoxen at Lagoon period sites on Banks Island.

4.5.3 $\Delta^{13}C_{LA\text{-}bc}$ Spacings in Caribou and Muskox Teeth

Spacings between tooth-averaged $\delta^{13}C_{LA}$ and bulk bone collagen $\delta^{13}C$ ($\Delta^{13}C_{LA\text{-}bc}$) for caribou and muskoxen are presented in Tables 4.13 and 4.14, respectively. The average $\Delta^{13}C_{LA\text{-}bc}$ spacings across archaeological and modern caribou (+9.0‰ and +8.6‰, respectively), and archaeological and modern muskoxen (+8.9‰ and +9.4‰, respectively) are all typical of enamel structural carbonate-bulk bone collagen $\delta^{13}C$ spacings in large-bodied herbivores (Krueger and Sullivan 1984; Lee-Thorp et al. 1989). We can go further and combine the respective $\Delta^{13}C_{LA\text{-}bc}$ spacings for caribou and muskoxen with their respective Bayesian-derived bone collagen-diet trophic discrimination factors ($\Delta^{13}C_{coll\text{-}diet}$; Chapter 2) to estimate the total structural carbonate-diet spacings ($\Delta^{13}C_{LA\text{-}diet}$). Doing so results in average $\Delta^{13}C_{LA\text{-}diet}$ spacings of +13.7‰ and +13.3‰ for archaeological and modern caribou, respectively (Table 4.13), and +11.5‰ and +12.0‰ for archaeological and modern muskoxen, respectively (Table 4.14).

In modern caribou and muskoxen, these $\Delta^{13}C_{LA\text{-}diet}$ spacings yield dietary $\delta^{13}C$ estimates of –26.4‰ and –25.7‰, respectively, which are in line with mean dietary $\delta^{13}C$ estimates for modern caribou and muskoxen on Banks Island (Chapter 2). When corrected by –1.7‰ to account for the depletion of ^{13}C in atmospheric CO_2 over the last ~ 150 years (i.e. the "Suess Effect") (Keeling et al. 1979, 2005; Francey et al. 1999; Long et al. 2005; Verburg 2007), the $\delta^{13}C_{diet}$ estimates for archaeological caribou and muskoxen yield modern dietary $\delta^{13}C$ estimates of –25.9‰ and –25.1‰, respectively (Table 4.13 and 4.14, respectively), which is in line with the average dietary $\delta^{13}C$ for modern caribou and muskoxen on Banks Island.

Although the $\Delta^{13}C_{LA\text{-}diet}$ of both species falls within the range expected from highly methanogenic animals feeding exclusively on C_3 plants (+12 to 14‰, Cerling and Harris 1999), we might predict based solely on rumen size (Staaland and Thing 1991) that methanogenic activity, and hence $\Delta^{13}C_{LA\text{-}diet}$ spacings, would be higher in muskoxen than

caribou. Data on methanogenic activity in caribou and muskoxen (Hackstein and van Alen 1996), however, suggests that caribou produce more than double the amount of methane per hour than muskoxen, and that the passage time for ingesta is relatively slow in muskoxen (Adamczewski et al. 1994). Additionally, data from Cerling and Harris (1999) indicates that, of ruminants feeding on C_3 plants, those with more dicots (e.g. legumes, shrubs, and non-leguminous forbs) in their diet will have slightly higher $\Delta^{13}C_{LA\text{-}diet}$ spacings, and Bayesian mixing models (Chapter 2) suggest that modern caribou consume significantly greater quantities of dicots than muskoxen on Banks Island. In short, the respective $\Delta^{13}C_{LA\text{-}diet}$ spacings for caribou and muskoxen make sense given the differences both in their typical diets and methanogenic activity, and support the Bayesian-derived trophic discrimination factors used in Chapters 2 and 3.

Table 4.13. Caribou intratooth-averaged $\delta^{13}C_{LA}$ (column A) vs. bulk bone collagen $\delta^{13}C$ ($\delta^{13}C_{bc}$, see chapter 3) from the same individual (column B). The isotopic fractionation of ^{13}C between tooth enamel and bulk bone collagen ($\Delta^{13}C_{LA\text{-}bc}$, column C) is calculated by subtracting column B values from column A. Using Bayesian-derived estimates of isotopic fractionation of ^{13}C between bulk bone collagen and diet ($\Delta^{13}C_{bc\text{-}diet}$, here +4.7‰), the total spacing between tooth enamel $\delta^{13}C$ and dietary $\delta^{13}C$ is estimated (column D). By simply subtracting column D from column A, the average $\delta^{13}C$ of diet is estimated (column E). Finally, archaeological $\delta^{13}C_{diet}$ in column E can be compared to modern forage $\delta^{13}C$ by subtracting 1.7‰ (column F).

			A	B	C	D	E	F
Lab Sample ID	**Taxon**	**Tooth**	**Intratooth Average $\delta^{13}C_{LA}$**	**$\delta^{13}C_{bc}$**	**$\Delta^{13}C_{LA\text{-}bc}$ Spacing**	**$\Delta^{13}C_{LA\text{-}diet}$ Spacing**	**Inferred $\delta^{13}C_{diet}$**	**Inferred Modern $\delta^{13}C_{diet}$**
			(‰, VPDB)	**(‰, VPDB)**	**(A – B)**	**(C + 4.7)**	**(A – D)**	**(E – 1.7)**
Classic Thule								
BIBS14-298	Caribou	M1	–10.3	–18.9	+8.6	+13.3	–23.6	–25.3
		M2	–8.4		+10.5	+15.2	–23.6	–25.3
		M3	–9.6		+9.3	+14.0	–23.6	–25.3
BIBS14-494	Caribou	M1	–11.9	–19.3	+7.4	+12.1	–24.0	–25.7
BIBS14-502	Caribou	M1	–11.8	–19.2	+7.4	+12.1	–23.9	–25.6
Inuit								
BIBS14-214	Caribou	M1	–11.1	–20.2	+9.1	+13.8	–24.9	–26.6
		M2	–9.2		+11.0	+15.7	–24.9	–26.6
		M3	–10.9		+9.3	+14.0	–24.9	–26.6
		P4	–10.5		+9.7	+14.4	–24.9	–26.6
BIBS14-360	Caribou	M1	–11.5	–19.3	+7.8	+12.5	–24.0	–25.7
Mean			–10.5	–19.4	+9.0	+13.7	–24.2	–25.9

Modern							
BIBS15-67	Caribou	M2	–11.3	–22.1	+10.8	+15.5	–26.8
		dp4	–13.8		+7.7	+12.4	–26.2
BIBS16-19	Caribou	M1	–14.2	–21.5	+7.3	+12.0	–26.2
		M2	–12.8		+8.7	+13.4	–26.2
	Mean		–13.0	–21.8	+8.6	+13.3	–26.4

Table 4.14. Muskox intratooth-averaged $\delta^{13}C_{LA}$ (column A) vs. bulk bone collagen $\delta^{13}C$ ($\delta^{13}C_{bc}$, see chapter 3) from the same individual (column B). The isotopic fractionation of ^{13}C between tooth enamel and bulk bone collagen ($\Delta^{13}C_{LA\text{-}bc}$, column C) is calculated by subtracting column B values from column A. Using Bayesian-derived estimates of isotopic fractionation of ^{13}C between bulk bone collagen and diet ($\Delta^{13}C_{bc\text{-}diet}$, here +2.6‰), the total spacing between tooth enamel $\delta^{13}C$ and dietary $\delta^{13}C$ is estimated (column D). By simply subtracting column D from column A, the average $\delta^{13}C$ of diet is estimated (column E). Finally, archaeological $\delta^{13}C_{diet}$ in column E can be compared to modern forage $\delta^{13}C$ by subtracting 1.7‰ (column F).

			A	B	C	D	E	F
Lab Sample ID	**Taxon**	**Tooth**	**Intratooth Average $\delta^{13}C_{LA}$**	**$\delta^{13}C_{bc}$**	**$\Delta^{13}C_{LA\text{-}bc}$ Spacing**	**$^{\Delta 13}C_{LA\text{-}diet}$ Spacing**	**Inferred $\delta^{13}C_{diet}$**	**Inferred Modern $\delta^{13}C_{diet}$**
			(‰, VPDB)	**(‰, VPDB)**	**(A – B)**	**(C + 2.6)**	**(A – D)**	**(E – 1.7)**
Pre-Dorset								
BIBS14-407	Muskox	M1	–11.5	–20.3	+8.8	+11.4	–22.9	–24.6
BIBS14-409	Muskox	M1	–12.3	–20.9	+8.6	+11.2	–23.5	–25.2
Lagoon								
BIBS14-162	Muskox	M1	–11.0	–20.4	+9.4	+12.0	–23.0	–24.7
BIBS14-209	Muskox	M1	–10.8	–20.8	+10.0	+12.6	–23.4	–25.1
Early Thule								
BIBS16-30	Muskox	M1	–12.3	–20.5	+8.2	+10.8	–23.1	–24.8
Classic Thule								
BIBS14-474	Muskox	M1	–12.6	–21	+8.4	+11.0	–23.6	–25.3
Inuit								
BIBS14-456	Muskox	M1	–12.8	–21.8	+9.0	+11.6	–24.4	–26.1
	Mean		–11.9	–20.8	+8.9	+11.5	–23.4	–25.1

Modern							
BIBS14-169	Muskox	M1	–13.7	–23.4	+9.7	+12.3	–26.0
BIBS14-445	Muskox	M1	–13.6	–22.7	+9.1	+11.7	–25.3
	Mean		–13.7	–23.1	+9.4	+12.0	–25.7

4.5.4 Tooth Enamel $\delta^{18}O$ Derived via Laser Ablation ($\delta^{18}O_{LA}$)

In both caribou and muskoxen, seasonal climatic variation, rather than geographic variation in growing-season plant water $\delta^{18}O$, appears to dominate tooth enamel $\delta^{18}O_{LA}$. For instance, we conclude based on eruption indices and intra-tooth $\delta^{13}C_{LA}$ that – in caribou – enamel from the first molar reflects isotopic signals between birth (and/or the first summer of life depending on occlusal wear) and the first fall of life, while the second molar reflects isotopic signals from the first fall of life (again depending on occlusal wear) to the second spring of life. All but one of the caribou M1s we analyzed also depict quasi-sinusoidal patterns in intra-tooth $\delta^{18}O_{LA}$ (Figure 4.12), with higher $\delta^{18}O_{LA}$ earlier in the sequence and lower $\delta^{18}O_{LA}$ later in the sequence. Likewise, sequential $\delta^{18}O_{LA}$ from muskox M1s appears to capture seasonal climatic signals between the first summer and mid-winter of life. All but three of the muskox M1s we analyzed display declines in $\delta^{18}O_{LA}$ across the sample sequence on the order of ~ 3‰ (Figure 4.14).

Of the four caribou M2s we analyzed, two also display declines in $\delta^{18}O_{LA}$ across the sequence consistent with a continued decline in temperature, and consequently precipitation $\delta^{18}O$, through the winter and spring. Of the other two M2s, one (BIBS14-214 M2) has very low $\delta^{18}O_{LA}$ across the entire sampling sequence (Figure 4.12b), potentially indicating a long and cold winter. The other (BIBS15-67 M2) is a modern tooth, and shows a ~ 1‰ increase in $\delta^{18}O_{LA}$ across the relatively short sequence (Figure 4.12a), potentially indicating an early summer during the year the tooth developed, consistent with recent temperature trends on Banks Island (Trevor Lucas 2016, personal communication). In both cases, variation in $\delta^{18}O_{LA}$ along the sample sequence conforms to expected seasonal variation in precipitation $\delta^{18}O$ (Fricke and O'Neil 1996; Fricke et al. 1998), where higher $\delta^{18}O_{LA}$ corresponds to warmer air temperatures and *vice versa*. If $\delta^{18}O_{LA}$ was dominated by geographic variation, we would expect the opposite, particularly in caribou: lower $\delta^{18}O$ in enamel corresponding to summers spent in northern calving grounds, and higher $\delta^{18}O$ in enamel corresponding to winters spent farther south, either on Banks Island or elsewhere.

It is also unlikely that we have simply misinterpreted the enamel developmental schedule in the teeth, such that we are relating tooth development, and consequently, intra-tooth

$\delta^{18}O_{LA}$, to the wrong parts of the year. Since oxygen isotope measurements obtained via laser ablation are ~ 1.2‰ higher than phosphate $\delta^{18}O$ (Cerling and Sharp 1996) due to the influence of structural carbonate $\delta^{18}O$, we can adjust our $\delta^{18}O_{LA}$ by –1.2‰, then use Equation 4.2 (Huertas et al. 1995) to approximate the $\delta^{18}O$ of water ingested during enamel mineralization:

$$\delta^{18}O_{bw/dw} = \frac{\delta^{18}O_p - 24.1}{0.88}$$

[Equation 4.2]

where $\delta^{18}O_{bw/dw}$ represents the oxygen isotope composition of drinking or body water, and $\delta^{18}O_p$ represents the $\delta^{18}O$ of tooth enamel phosphate.

As demonstrated in Figure 4.15, $\delta^{18}O_{bw/dw}$ estimates from modern caribou and muskox $\delta^{18}O_{LA}$, respectively, have maxima near ~ –18.5‰ and minima near –22‰. Maximum $\delta^{18}O_{bw/dw}$ estimates are within the range of month-averaged precipitation $\delta^{18}O$ ($\delta^{18}O_{pw}$) in late summer and early fall on Banks Island calculated using the OIPC (Bowen 2017) (Figure 4.16). They likewise align with long-term records of monthly variation in $\delta^{18}O_{pw}$ in late summer and early fall recorded at Mould Bay, Northwest Territories, Canada, which is the GNIP station nearest Banks Island (IAEA/WMO 2017) (Figure 4.16). The minimum $\delta^{18}O_{bw/dw}$ estimates are between 7‰ and 10‰ higher than month-averaged $\delta^{18}O_{pw}$ data from the OIPC and GNIP datasets. This discrepancy could be due to isotopic signal attenuation during the enamel mineralization process, but another likely possibility is that higher-than-expected $\delta^{18}O_{bw/dw}$ estimates corresponding to winter reflect the influence of ingested water from plant tissues enriched in ^{18}O due to transpiration during the growing season, or evaporative enrichment in ^{18}O during freezing.

Still, transpiration is known to cause enrichment in leaf water ^{18}O on the order of 15-27‰ depending on factors such as air temperature and relative humidity (Sternberg and DeNiro 1983; Sternberg 1988; Yakir and DeNiro 1990; Flanagan and Ehleringer 1991; Flanagan 1993; Yakir et al. 1993; Barbour and Farquhar 2000; Cernusak et al. 2003; Barbour et al. 2007), and the fact that $\delta^{18}O_{bw/dw}$ estimates obtained using phosphate-corrected $\delta^{18}O_{LA}$ are

only 7-10‰ higher than precipitation data therefore suggests that either the enrichment of ^{18}O in leaves is not particularly extreme on Banks Island, or that the contribution of plant water to caribou and muskox body water is limited. The strong precipitation signal in the caribou and muskox enamel $\delta^{18}O_{LA}$ data further suggests that both species may consume water, as liquid during summer and snow or ice during winter, with greater frequency than we and other researchers (e.g. Gray 1973; Bocherens et al. 1996; Britton et al. 2009) have hypothesized. It is also likely that some amount of snow or ice is inadvertently consumed along with forage during the winter, which may be enough to dominate body water $\delta^{18}O$ compositions.

Finally, we must consider the potential role of lichens in determining the $\delta^{18}O$ of caribou and muskox tooth enamel. Based on dietary mixing model results and sequential dentin collagen $\delta^{13}C$, we suggest in Chapter 2 that yellow lichen (*Cetraria tilesii*) is an important forage resource for both caribou and muskoxen on Banks Island, with particular importance during the winter. Lichens, unlike vascular plants, cannot utilize soil moisture because they have no roots and instead rely on precipitation and atmospheric water vapor for their water requirements. Further, because they lack vasculature and stomata, the water status of green foliose/fruticose lichens like *C. tilesii* varies with environmental conditions (Lange et al. 1988; Máguas et al. 1993). A set of experiments by Lakatos et al. (2007) and Hartard et al. (2008, 2009) demonstrate that because lichen cannot control water loss via stomatal closure, the water in their thalli is constantly equilibrating isotopically with atmospheric water vapor. Therefore, the $\delta^{18}O$ of lichens during summer should reflect the $\delta^{18}O$ of atmospheric water vapor.

Experimental work (Lakatos et al. 2007; Hartard et al. 2008, 2009) demonstrates that desiccating lichens experience an enrichment in ^{18}O of ~ 7‰, and it is conceivable that lichens on high, snow-free ridges experience such enrichment in ^{18}O via sublimation during winter. The $\delta^{18}O$ of lichens during winter would therefore be higher than the $\delta^{18}O$ of winter precipitation, and their consumption by caribou and muskoxen might drive $\delta^{18}O_{LA}$ corresponding to winter upwards. This topic, however, deserves further consideration, and growth chamber experiments replicating winter field conditions may yield useful

information on the metabolic and water status of foliose/fruticose lichens in the Arctic, and seasonal variation in their $\delta^{18}O$.

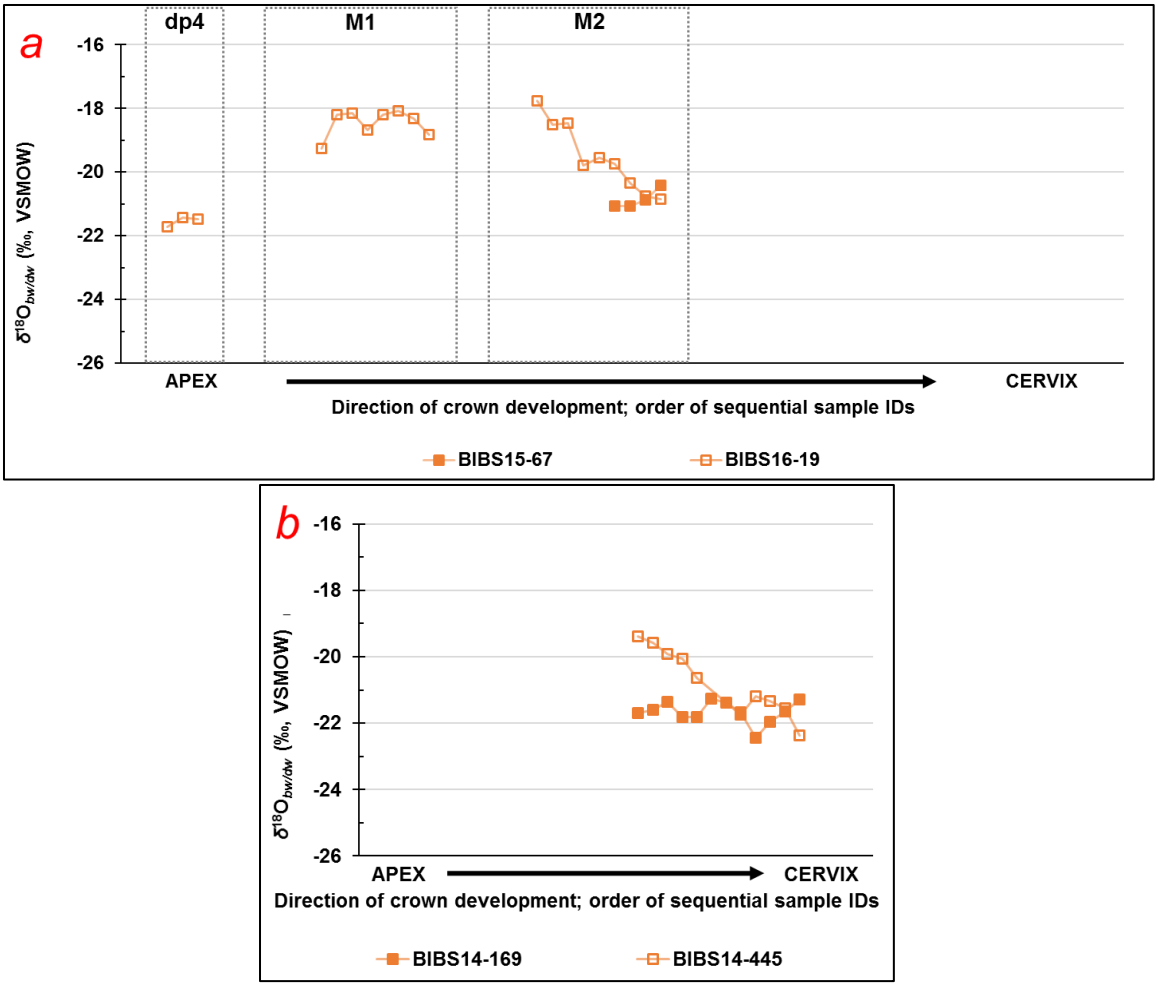


Figure 4.15. Estimated $\delta^{18}O_{dw/bw}$ calculated from modern **(*a*)** caribou; and **(*b*)** muskox tooth enamel $\delta^{18}O_{LA}$ using Equation 4.2.

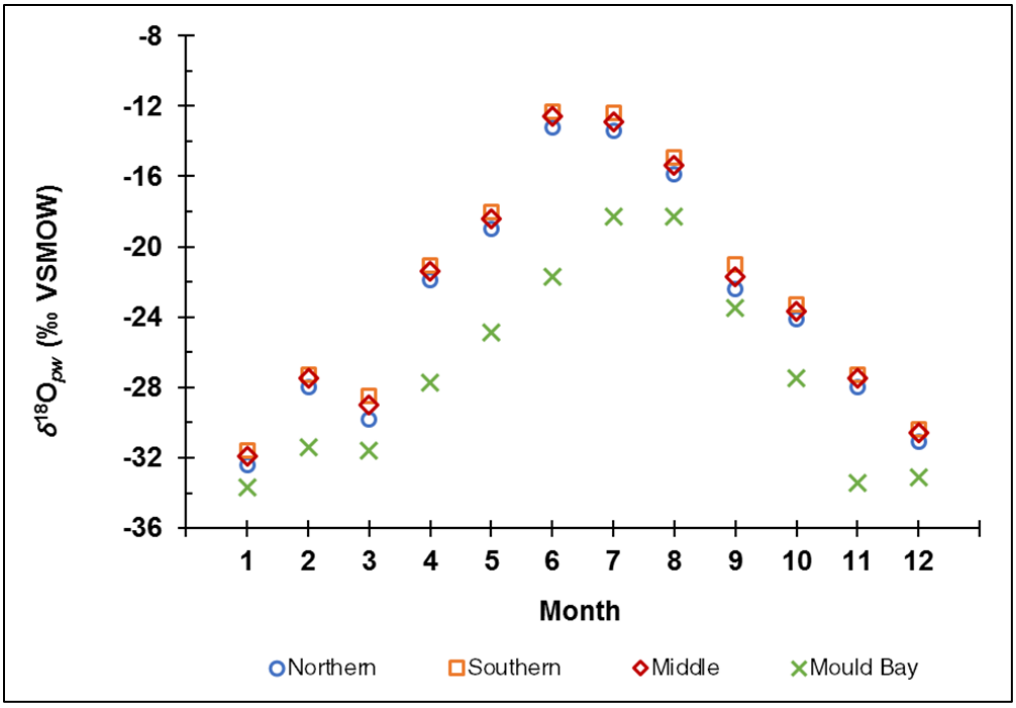


Figure 4.16. Monthly-averaged $\delta^{18}O_{pw}$ calculated using the OIPC (Bowen 2017) and randomly-chosen coordinates near the northern, southern, and middle portions of Banks Island (closed shapes), and monthly-averaged $\delta^{18}O_{pw}$ measured at Mould Bay, NWT, Canada from 1989 to 1993 (green X's) (IAEA/WMO 2017).

4.6 Conclusion

In both caribou and muskoxen, sequential tooth enamel $\delta^{13}C_{LA}$ predominately reflects shifts between summer forage with lower $\delta^{13}C$ and winter forage with higher $\delta^{13}C$. As with enamel $\delta^{18}O_{LA}$, there are also temporal variations in the patterning of intra- and inter-tooth $\delta^{13}C_{LA}$ consistent with shorter, cooler summers during the Lagoon, Early Thule, and Classic Thule periods on Banks Island. The $\Delta^{13}C_{LA\text{-}diet}$ spacings that integrate Bayesian-derived $\Delta^{13}C_{coll\text{-}diet}$ spacings for caribou and muskoxen (Chapter 2 and 3) conform with expectations from published data on $\Delta^{13}C_{LA\text{-}diet}$ spacings in large ungulate herbivores with dicot/grass-, and grass-dominated diets, respectively.

Our FTIR results demonstrate that enamel preservation in the Arctic is very good, even for relatively ancient teeth. Our hypothesis that the $\delta^{18}O_{LA}$ of caribou and muskox teeth are dominated by geographic variation in plant water $\delta^{18}O$, however, is not supported. This study suggests that tooth enamel $\delta^{18}O$ is not ideal – by itself – as a tracer for the seasonal movements of caribou and muskoxen on Banks Island. Instead, sequential $\delta^{18}O_{LA}$ appears to closely track seasonal variation in precipitation $\delta^{18}O$. Given that caribou and muskoxen are commonly the only species represented at smaller, ancient campsites found in the Canadian Arctic, the $\delta^{18}O$ of caribou and muskox tooth enamel, at larger sample sizes, should prove useful as proxies for annual or sub-annual paleoclimatic variation during the middle and late Holocene.

4.7 References

Adamczewski JZ, Kerr WM, Lammerding EF, Flood PF. 1994. Digestion of Low-Protein Grass Hay by Muskoxen and Cattle. Journal of Wildlife Management 58(4): 679-685.

Allessio ML, Tieszen LL. 1975. Patterns of Carbon Allocation in an Arctic Tundra Grass, Dupontia Fischeri (Gramineae), at Barrow, Alaska. American Journal of Botany 62(8): 797-807.

Alstad KP, Welker JM, Williams SA, Trlica MJ. 1999. Carbon and Water Relations of *Salix monticola* in Response to Winter Browsing and Changes in Surface Water Hydrology: An Isotopic Study Using $\delta^{13}C$ and $\delta^{18}O$. Oecologia 120: 375-385.

Arnason B. 1981. Ice and Snow Hydrology. In: Gat JR, Gonfiatini R, editors. Stable Isotope Hydrology, Deuterium and Oxygen-18 in the Water Cycle. IAEA Technical Reports Series 210. Vienna: IAEA. Pp. 143-176.

Arsenault AL, Robinson BW. 1989. The Dentino-enamel Junction: A Structural and Microanalytical Study of Early Mineralization. Calcified Tissue International 45: 111-121.

Ayliffe LK, Chivas AR. 1990. Oxygen Isotope Composition of the Bone Phosphate of Australian Kangaroos: Potential as a Palaeoenvironmental Recorder. Geochimica et Cosmochimica Acta 54: 2603-2609.

Balasse M, Ambrose SH, Smith AB, Price TD. 2002. The Seasonal Mobility Model for Prehistoric Herders in the South-western Cape of South Africa Assessed by Isotopic Analysis of Sheep Tooth Enamel. Journal of Archaeological Science 29: 917-932.

Balasse M. 2002. Reconstructing Dietary and Environmental History from Enamel Isotopic Analysis: Time Resolution of Intra-tooth Sequential Sampling. International Journal of Osteoarchaeology 12: 155-165.

Balasse M, Smith AB, Ambrose SH, Leigh SR. 2003. Determining Sheep Birth Seasonality by Analysis of Tooth Enamel Oxygen Isotope Ratios: The Late Stone Age Site of Kasteelberg (South Africa). Journal of Archaeological Science 30: 205-215.

Banfield AWF. 1954. Preliminary Investigation of the Barren-ground Caribou. Canadian Wildlife Service Wildlife Management Bulletin Series 1, Numbers 10A and 10B.

Barbour MM, Farquhar GD. 2000. Relative Humidity- and ABA-induced Variation in Carbon and Oxygen Isotope Ratios of Cotton Leaves. Plant, Cell and Environment 23: 473-485.

Barbour MM, Farquhar GD, Hanson DT, Bickford CP, Powers H, McDowell NG. 2007. A New Measurement Technique Reveals Temporal Variation in $\delta^{18}O$ of Leaf-respired CO_2. Plant, Cell and Environment 30: 456-468.

Behnke RH. 2000. Equilibrium and Non-equilibrium Models of Livestock Population Dynamics in Pastoral Africa: Their Relevance to Arctic Grazing Systems. Rangifer 20(3): 141-152.

Berden G, Peeters R, Meijer G. 2000. Cavity Ring-down Spectroscopy: Experimental Schemes and Applications. International Reviews in Physical Chemistry 19(4): 565-607.

Bigeleisen J, Perlman ML, Prosser HC. 1952. Conversion of Hydrogenic Materials to Hydrogen for Isotopic Analysis. Analytical Chemistry 24: 1356-1357.

Bliss LC, Courtin GM, Pattie DL, Riewe RR, Whitfield DWA, Widden P. 1973. Arctic Tundra Ecosystems. Annual Review of Ecology and Systematics 4: 359-399.

Bocherens H, Pacaud G, Lazarev PA, Mariotti A. 1996. Stable Isotope Abundances (13C, 15N) in Collagen and Soft Tissues from Pleistocene Mammals from Yakutia: Implications for the Palaeobiology of the Mammoth Steppe. Palaeogeography, Palaeoclimatology, Palaeoecology 126: 31-44.

Bocherens H, Machkour M, Billiou D, Pelle E, Mariotti A. 2001. A New Approach for Studying Prehistoric Herd Management in Arid Areas: Intra-tooth Isotopic Analyses of Archaeological Caprine from Iran. Earth and Planetary Science 332: 67-74.

Botha J, Lee-Thorp J, Sponheimer M. 2004. An Examination of Triassic Cynodont Tooth Enamel Chemistry Using Fourier Transform Infrared Spectroscopy. Calcified Tissue International 74: 162-169.

Bowen GJ, Wilkinson B. 2002. Spatial Distribution of $\delta^{18}O$ in Meteoric Precipitation. Geology 30(4): 315-318.

Bowen GJ, Revenaugh J. 2003. Interpolating the Isotopic Composition of Modern Meteoric Precipitation. Water Resources Research 39(10): 1299.

Bowen GJ, Wassenaar LI, Hobson KA. 2005. Global Application of Stable Hydrogen and Oxygen Isotopes to Wildlife Forensics. Oecologia 143: 337-348.

Bowen GJ. 2008. Spatial Analysis of the Intra-annual Variation of Precipitation Isotope Ratios and Its Climatological Corollaries. Journal of Geophysical Research 113: D05113.

Bowen GJ. 2017. The Online Isotopes in Precipitation Calculator, Version 3.1. Available from: http://www.waterisotopes.org.

Boyar H, Zorlu F, Melike M, Severcan F. 2004. The Effects of Chronic Hypoperfusion on Rat Cranial Bone Mineral and Organic Matrix. Analytical and Bioanalytical Chemistry 379: 433-438.

Brady AL, White CD, Longstaffe FJ, Southam G. 2008. Investigating Intra-bone Isotopic Variations in Bioapatite Using IR-laser Ablation and Micromilling: Implications for Identifying Diagenesis? Palaeogeography, Palaeoclimatology, Palaeoecology 266: 190-199.

Britton K, Grimes V, Dau J, Richards MP. 2009. Reconstructing Faunal Migrations Using Intra-tooth Sampling and Strontium and Oxygen Isotope Analyses: a Case Study of Modern Caribou (*Rangifer tarandus granti)*. Journal of Archaeological Science 36: 1163-1172.

Bryant JD, Froelich PN. 1995. A Model of Oxygen Isotope Fractionation in Body Water of Large Mammals. Geochimica et Cosmochimica Acta 59(21): 4523-4537.

Bryant JD, Koch PL, Froelich PN, Showers WJ, Genna BJ. 1996. Oxygen Isotope Partitioning Between Phosphate and Carbonate in Mammalian Apatite. Geochimica et Cosmochimica Acta 60(24): 5145-5148.

Bursey GG, Edwards TWD, Frape SK. 1990. Hydrology and Geochemistry studies, District of Keewatin, Northwest Territories, Canada. Nordicana 54: 159-165.

Caughley G, Gunn A. 1993. Dynamics of Large Herbivores in Deserts: Kangaroos and Caribou. Oikos 67: 47-55.

Cerling TE, Sharp ZD. 1996. Stable Carbon and Oxygen Isotope Analysis of Fossil Tooth Enamel Using Laser Ablation. Palaeogeography, Palaeoclimatology, Palaeoecology 126: 173-186.

Cerling TE, Harris JM. 1999. Carbon Isotope Fractionation Between Diet and Bioapatite in Ungulate Mammals and Implications for Ecological and Paleoecological Studies. Oecologia 120: 347-363.

Cernusak LA, Wong S-C, Farquhar GD. 2003. Oxygen Isotope Composition of Phloem Sap in Relation to Leaf Water in *Ricinus communis*. Functional Plant Biology 30: 1059-1070.

Chang MC, Tanaka J. 2002. FT-IR Study for Hydroxyapatite/Collagen Nanocomposite Cross-linked by Glutaraldehyde. Biomaterials 23: 4811-4818.

Christensen R. 1991. Linear Models for Multivariate Time Series and Spatial Data. Berlin: Springer.

Cooper LW, Solis C, Kane DL, Hinzman LD. 1993. Application of Oxygen-18 Tracer Techniques to Arctic Hydrological Processes. Arctic and Alpine Research 25(3): 247-255.

Coplen TB, Wildman JD, Chen J. 1991. Improvements in the Gaseous Hydrogen-water Equilibration Technique for Hydrogen Isotope Ratio Analysis. Analytical Chemistry 63: 910-912.

Coplen TB, Brand WA, Gehre M, Gröning M, Meijer HAJ, Toman B, Verkouteren RM. 2006. New Guidelines for δ^{13}C Measurements. Analytical Chemistry 78: 2439-2441.

COSEWIC. 2004. COSEWIC Assessment and Update Status Report in the Peary caribou *Rangifer tarandus Pearyi* and the barren-ground caribou *Rangifer tarandus groenlandicus* (Dolphin and Union Population) in Canada. Ottawa: Committee on the Status of Endangered Wildlife in Canada.

Craig H, Gordon LI. 1965. Deuterium and Oxygen 18 Variations in the Ocean and the Marine Atmosphere. In: Tongiorgi E, editor. Stable Isotopes in Oceanographic Studies and Paleotemperatures. Pisa: Consiglio Nazionale delle Richerche Laboratorio di Geologia Nucleare. Pp. 9-130.

Cuntz M, Ogée J, Farquhar GD, Peylin P, Cernusak LA. 2007. Modeling Advection and Diffusion of Water Isotopologues in Leaves. Plant, Cell and Environment 30: 892-909.

Dansgaard W. 1964. Stable Isotopes in Precipitation. Tellus 16(4): 436-468.

Darling WG, Bath AH, Gibson JJ, Rozanski K. 2005. Isotopes in Water. In: Leng MJ, editor. Isotopes in Palaeoenvironmental Research. New York: Springer. Pp. 1-66.

Dawson TE. 1998. Fog in the California Redwood Forest: Ecosystem Inputs and Use by Plants. Oecologia 117: 476-485.

Dongmann G, Nurnberg HW, Forstel H, Wagener K. 1974. On the Enrichment of $H_2{}^{18}O$ in the Leaves of Transpiring Plants. Radiation and Environmental Biophysics 11: 41-52.

Dutton A, Wilkinson BH, Welker JM, Bowen GJ, Lohmann KC. 2005. Spatial Distribution and Seasonal Variation in $^{18}O/^{16}O$ of Modern Precipitation and River Water Across the Conterminous USA. Hydrological Processes 19: 4121-4146.

Edlund SA. 1986. Modern Arctic Vegetation Distribution and Its Congruence with Summer Climate Patterns. In: French HM, editor. Climate Change Impacts in the Canadian Arctic, Proceedings of a Canadian Climate Program Workshop, March 3-5, 1986, Geneva Park, Ontario.

Ehleringer JR, Roden J, Dawson TE. 2000. Assessing Ecosystem-level Water Relations Through Stable Isotope Ratio Analyses. In: Sala OE, Jackson RB, Mooney HA, Howarth RW, editors. Methods in Ecosystem Science. New York: Springer. Pp. 181-198.

Eller CB, Lima AL, Oliveira RS. 2013. Foliar Uptake of Fog Water and Transport Belowground Alleviates Drought Effects in the Cloud Forest Tree Species, *Drimys brasiliensis* (Winteraceae). New Phytologist 199: 151-162.

Elliott JC. 1997. Structure, Crystal Chemistry and Density of Enamel Apatites. In: Chadwick DJ, Cardew G, editors. Dental Enamel. Chichester: John Wiley & Sons. Pp. 54-67.

Elliott JC. 2002. Calcium Phosphate Biominerals. In: Kohn MJ, Rakovan J, Hughes JM, editors. Phosphates – Geochemical, Geobiological, and Materials Importance. Reviews in Mineralogy and Geochemistry 48. Chantilly: Mineralogical Society of America. Pp. 427-453.

Epstein S, Mayeda T. 1953. Variation in O^{18} Content of Waters from Natural Sources. Geochimica et Cosmochimica Acta 4: 213-224.

Epstein S, Thompson P, Yapp CJ. 1977. Oxygen and Hydrogen Isotopic Ratios in Plant Cellulose. Science New Series 198(4323): 1209-1215.

ESRI. 2016. ArcGIS Help 10.1 – What's New in ArcGIS Geostatistical Analyst 10.1. Available from: http://desktop.arcgis.com/en/arcmap/latest/extensions/geostatistical-analyst/what-is-empirical-bayesian-kriging-.htm.

Figueiredo MM, Gamelas JAF, Martins AG. 2012. Characterization of Bone and Bone-based Graft Materials Using FTIR Spectroscopy. In: Theophanides T, editor. Infrared Spectroscopy – Life and Biomedical Sciences. Pp. 315-338.

Flanagan LB, Ehleringer JR. 1991. Stable Isotope Composition of Stem and Leaf Water: Applications to the Study of Plant Water Use. Functional Ecology 5(2): 270-277.

Flanagan LB. 1993. Environmental and Biological Influences on the Stable Oxygen and Hydrogen Isotopic Composition of Leaf Water. In: Ehleringer JR, Hall AE, Farquhar GD, editors. Stable Isotopes and Plant Carbon-water Relations. San Diego: Academic Press. Pp. 71-92.

Francey RJ, Allison CE, Etheridge DM, Trudinger CM, Enting IG, Leuenberger M, Langenfelds RL, Michel E, Steele LP. 1999. A 1000-year High Precision Record of $\delta^{13}C$ in Atmospheric CO_2. Tellus 51B: 170-193.

Fricke HC, O'Neil JR. 1996. Inter- and Intra-tooth Variation in the Oxygen Isotope Composition of Mammalian Tooth Enamel Phosphate: Implications for Palaeoclimatological and Palaeobiological Research. Palaeogeography, Palaeoclimatology, Palaeoecology 126: 91-99.

Fricke HC, Clyde WC, O'Neil JR. 1998. Intra-tooth Variations in $\delta^{18}O$ (PO_4) of Mammalian Tooth Enamel as a Record of Seasonal Variations in Continental Climate Variables. Geochimica et Cosmochimica Acta 62(11): 1839-1850.

Friedman I. 1953. Deuterium Content of Natural Waters and Other Substances. Geochimica et Cosmochimica Acta 4: 89-103.

Gajewski K. 1995. Modern and Holocene Pollen Assemblages from Some Small Arctic Lakes on Somerset Island, NWT, Canada. Quaternary Research 44: 228-236.

Gajewski K, Mott RJ, Ritchie JC, Hadden K. 2000. Holocene Vegetation History of Banks Island, Northwest Territories, Canada. Canadian Journal of Botany 78: 430-436.

Gajewski K, MacDonald GM. 2004. Palynology of North American Arctic Lakes. In: Pienitz R, Douglas MSV, Smol JP, editors. Long-term Environmental Change in Arctic and Antarctic Lakes. Dordrecht: Springer. Pp. 89-116.

Gajewski K. 2015. Quantitative Reconstruction of Holocene Temperatures Across the Canadian Arctic and Greenland. Global and Planetary Change 128: 14-23.

Garvie-Lok SJ, Varney TL, Katzenberg MA. 2004. Preparation of Bone Carbonate for Stable Isotope Analysis: The Effects of Treatment Time and Acid Concentration. Journal of Archaeological Science 31: 763-776.

Gat JR. 1981a. Properties of the Isotopic Species of Water: the 'Isotope Effect'. In: Gat JR, Gonfiatini R, editors. Stable Isotope Hydrology, Deuterium and Oxygen-18 in the Water Cycle. IAEA Technical Reports Series 210. Vienna: IAEA. Pp. 7-19.

Gat JR. 1981b. Isotopic Fractionation. In: Gat JR, Gonfiatini R, editors. Stable Isotope Hydrology, Deuterium and Oxygen-18 in the Water Cycle. IAEA Technical Reports Series 210. Vienna: IAEA. Pp. 21-33.

Gat JR. 1981c. Groundwater. In: Gat JR, Gonfiatini R, editors. Stable Isotope Hydrology, Deuterium and Oxygen-18 in the Water Cycle. IAEA Technical Reports Series 210. Vienna: IAEA. Pp. 223-240.

Gat JR, Mook WG, Meijer AJ. 2001. Atmospheric Water. In: Mook WG, editor. Environmental Isotopes in the Hydrological Cycle: Principles and Applications. IHP-V Technical Documents in Hydrology 39(2). Paris: International Hydrological Programme.

Gibson JJ, Edwards TWD, Bursey GG. 1993. Estimating Evaporation Using Stable Isotopes: Quantitative Results and Sensitivity Analysis for Two Catchments in Northern Canada. Nordic Hydrology 24: 79-94.

Gibson JJ. 2001. Forest-tundra Water Balance Signals Traced by Isotopic Enrichment in Lakes. Journal of Hydrology 251: 1-13.

Gibson JJ. 2002. Short-term Evaporation and Water Budget Comparisons in Shallow Arctic Lakes Using Non-steady Isotope Mass Balance. Journal of Hydrology 264: 242-261.

Gibson JJ, Edwards TWD. 2002. Regional Water Balance Trends and Evaporation-Transpiration Partitioning from a Stable Isotope Survey of Lakes in Northern Canada. Global Biogeochemical Cycles 16(2): 1026.

Gibson JJ, Prepas EE, McEachern P. 2002. Quantitative Comparison of Lake Throughflow, Residency, and Catchment Runoff Using Stable Isotopes: Modelling and Results from a Regional Survey of Boreal Lakes. Journal of Hydrology 262: 128-144.

Gibson JJ, Edwards TWD, Birks SJ, St Amour NA, Buhay WM, McEachern P, Wolfe BB, Peters DL. 2005. Progress in Isotope Tracer Hydrology in Canada. Hydrological Processes 19: 303-327.

Gibson JJ, Fekete BM, Bowen GJ. 2010. Stable Isotopes in Large Scale Hydrological Applications. In: West JB, Bowen GJ, Dawson TE, Tu KP, editors. Isoscapes: Understanding Movement, Pattern, and Process on Earth Through Isotope Mapping. Springer Science+Business. Pp. 389-405.

Godfrey JD. 1962. The Deuterium Content of Hydrous Minerals from the East-central Sierra Nevada and Yosemite National Park. Geochimica et Cosmochimica Acta 26: 1215-1245.

Gonfiatini R, Gratziu S, Tongiorgi E. 1965. Oxygen Isotopic Composition of Water in Leaves. In: Isotopes and Radiation in Soil-Plant Nutrition Studies: Proceedings of the Symposium on the Use of Isotopes and Radiation in Soil-Plant Nutrition Studies Jointly Organized by the International Atomic Energy Agency and the Food and Agricultural Organization of the United Nations and Held in Ankara, 28 June-2 July 1965. Pp. 405-412.

Gould WA, Raynolds M, Walker DA. 2003. Vegetation, Plant Biomass, and Net Primary Productivity Patterns in the Canadian Arctic. Journal of Geophysical Research 108(D2): 8167.

Gray DR. 1973. Social Organization and Behaviour of Muskoxen (Ovibos moschatus) on Bathurst Island, N.W.T.. [Dissertation]. [Edmonton (AB)]: University of Alberta.

Gray DR. 1997a. Climate. In: The Natural and Cultural Resources of Aulavik National Park. Report on file at Parks Canada Western Service Centre, Winnipeg, Manitoba.

Gray DR. 1997b. Vegetation. In: The Natural and Cultural Resources of Aulavik National Park. Report on file at Parks Canada Western Service Centre, Winnipeg, Manitoba.

Grimes V, Pellegrini M. 2013. A Comparison of Pretreatment Methods for the Analysis of Phosphate Oxygen Isotope Ratios in Bioapatite. Rapid Communications in Mass Spectrometry 27: 375-390.

Hackstein JHP, van Alen T. 1996. Fecal Methanogens and Vertebrate Evolution. Evolution 50(2): 559-572.

Halevy E. 1970. The Relationship Between Isotopic Composition of Precipitation and Lysimeter Percolates. In: Interpretation of Environmental Isotope Data in Hydrology: Report of a Panel Sponsored by the International Atomic Energy Agency and Held in Vienna, 24-28 June 1968. Pp. 10-13.

Hartard B, Máguas C, Lakatos M. 2008. δ^{18}O Characteristics of Lichens and Their Effects on Evaporative Processes of the Subjacent Soil. Isotopes in Environmental and Health Studies 44(1): 111-128.

Hartard B, Cuntz M, Máguas C, Lakatos M. 2009. Water Isotopes in Desiccating Lichens. Planta 231: 179-193.

Hedges REM, Millard AR. 1995. Bones and Groundwater: Towards the Modelling of Diagenetic Processes. Journal of Archaeological Science 22: 155-164.

Hedges REM, Millard AR, Pike AWG. 1995. Measurements and Relationships of Diagenetic Alteration of Bone from Three Archaeological Sites. Journal of Archaeological Science 22: 201-209.

Hedges REM, van Klinken GJ. 2000. "Consider a Spherical Cow…"—on Modeling and Diet. In: Ambrose SH, Katzenberg MA, editors. Biogeochemical Approaches to Paleodietary Analysis. New York: Kluwer Academic Publishers. Pp. 211-242.

Hedges REM. 2003. On Bone Collagen – Apatite-Carbonate Isotopic Relationships. International Journal of Osteoarchaeology 13: 66-79.

Henrichsen P, Grue H. 1980. Age Criteria in the Muskox (*Ovibos moschatus*) from Greenland. Danish Review of Game Biology 11(4): 1-18.

Hillson S. 2000. Teeth. Cambridge: Cambridge University Press.

Hoppe KA, Stover SM, Pascoe JR, Amundson R. 2004. Tooth Enamel Biomineralization in Extant Horses: Implications for Isotopic Microsampling. Palaeogeography, Palaeoclimatology, Palaeoecology 206: 355-365.

Hoppe KA. 2006. Correlation Between the Oxygen Isotope Ratio of North American Bison Teeth and Local Waters: Implication for Paleoclimatic Reconstructions. Earth and Planetary Science Letters 244: 408-417.

Horita J. 1988. Hydrogen Isotope Analysis of Natural Waters Using an H_2-water Equilibration Method: A Special Implication to Brines. Chemical Geology (Isotope Geosciences Section) 72: 89-94.

Horita J, Wesoloski DJ. 1994. Liquid-vapor Fractionation of Oxygen and Hydrogen Isotopes of Water from the Freezing to the Critical Temperature. Geochimica et Cosmochimica Acta 58(16): 3425-3437.

Huertas AD, Iacumin P, Stenni B, Chillón BS, Longinelli A. 1995. Oxygen Isotope Variations of Phosphate in Mammalian Bone and Tooth Enamel. Geochimica et Cosmochimica Acta 59(20): 4299-4305.

Hughes JM, Rakovan J. 2002. The Crystal Structure of Apatite, $Ca_5(PO_4)_3(F,OH,Cl)$. In: Kohn MJ, Rakovan J, Hughes JM, editors. Phosphates – Geochemical, Geobiological, and Materials Importance. Reviews in Mineralogy and Geochemistry 48. Chantilly: Mineralogical Society of America. Pp. 1-12.

Hummel M, Ray JC. 2008. Caribou and the North: A Shared Future. Toronto: Dundurn Press.

Iacumin P, Longinelli A. 2002. Relationship Between $\delta^{18}O$ Values for Skeletal Apatite from Reindeer and Foxes and Yearly Mean $\delta^{18}O$ Values of Environmental Water. Earth and Planetary Science Letters 201: 213-219.

IAEA/WMO. 2017. Global Network of Isotopes in Precipitation. The GNIP Database. Available from: https://nucleus.iaea.org/wiser.

Ingraham NL, Matthews RA. 1988. Fog Drip as a Source of Groundwater Recharge in Northern Kenya. Water Resources Research 24: 1406-1410.

Ingraham NL, Matthews RA. 1990. A Stable Isotopic Study of Fog: The Point Reyes Peninsula, California, USA. Chemical Geology (Isotope Geoscience Section) 80: 281-290.

Johnston K, Ver Hoef JM, Krivoruchko K, Lucas N. 2003. ArcGIS 9: Using ArcGIS Geostatistical Analyst. ESRI Press.

Kaufman DS, Ager TA, Anderson NJ, Anderson PM, Andrews JT, Bartlein PJ, Brubaker LB, Coats LL, Cwynar LC, Duvall ML, Dyke AS, Edwards ME, Eisner WR, Gajewski K, Geirsdottir A, and fifteen others. 2004. Holocene Thermal Maximum in the Western Arctic (0-180°W). Quaternary Science Reviews 23: 529-560.

Kauppinen JK, Moffatt DJ, Mantsch HH, Cameron DG. 1981. Fourier Self-deconvolution: A Method for Resolving Intrinsically Overlapped Bands. Applied Spectroscopy 35: 271-276.

Keeling CD, Mook WG, Tans PP. 1979. Recent Trends in the $^{13}C/^{12}C$ Ratio of Atmospheric Carbon Dioxide. Nature 277(11): 121-122.

Keeling CD, Piper SC, Bacastow RB, Wahlen M, Whorf TP, Heimann M, Meijer HA. 2005. Atmospheric CO_2 and $^{13}CO_2$ Exchange with the Terrestrial Biosphere and Oceans from 1978 to 2000: Observations and Carbon Cycle Implications. In: Baldwin IT, Caldwell MM, Heldmaier G, Jackson RB, Lange OL, Mooney HA, Schulze E-D, Sommer U, Ehleringer JR, Dearing MD, Cerling TE, editors. A History of Atmospheric CO_2 and Its Effects on Plants, Animals, and Ecosystems. Ecological Studies Volume 177. Springer Science+Business. Pp. 83-113.

Kendall C, Coplen TB. 1985. Multisample Conversion of Water to Hydrogen by Zinc for Stable Isotope Determination. Analytical Chemistry 57: 1437-1440.

Kelsall JP. 1968. The Migratory Barren-ground Caribou of Canada. Ottawa: Canadian Wildlife Service, Department of Northern Affairs and National Resources, Natural and Historic Resources Branch.

Kelvin LE. 2016. There Is More Than One Way to Do Something Right: Applying Community-Based Approaches to an Archaeology of Banks Island, NWT. [Dissertation]. [London (ON)]: University of Western Ontario.

Kierdorf H, Kierdorf U, Frölich K, Witzel C. 2013. Lines of Evidence-Incremental Markings in Molar Enamel of Soay Sheep as Revealed by a Fluorochrome Labeling and Backscattered Electron Imaging Study. PLoS One 8(9): e74597.

Kirshenbaum I. 1951. Physical Properties and Analysis of Heavy Water. New York: McGraw Hill.

Koch PL, Tuross N, Fogel ML. 1997. The Effects of Sample Treatment and Diagenesis on the Isotopic Integrity of Carbonate in Biogenic Hydroxylapatite. Journal of Archaeological Science 24: 417-429.

Kohn MJ. 1996. Predicting Animal ^{18}O: Accounting for Diet and Physiological Adaptation. Geochimica et Cosmochimica Acta 60(23): 4811-4829.

Kohn MJ, Schoeninger MJ, Valley JW. 1998. Variability in Oxygen Isotope Compositions of Herbivore Teeth: Reflections of Seasonality or Developmental Physiology. Chemical Geology 152: 97-112.

Kohn MJ, Cerling TE. 2002. Stable Isotope Compositions of Biological Apatite. In: Kohn MJ, Rakovan J, Hughes JM, editors. Phosphates. Geochemical, Geobiological, and Materials Importance. Reviews in Mineralogy and Geochemistry, v. 48. Washington D.C.: Mineralogical Society of America. Pp. 455-488.

Kohn MJ. 2004. Comment: Tooth Enamel Mineralization in Ungulates: Implications for Recovering a Primary Isotopic Time-series, by B.H. Passey and T.E. Cerling (2002). Geochimica et Cosmochimica Acta 68(2): 403-405.

Krivoruchko K. 2012. Empirical Bayesian Kriging Implemented in ArcGIS Geostatistical Analyst. ARCUSER 15(4): 6-10.

Krueger HW, Sullivan CH. 1984. Models for Carbon Isotope Fractionation Between Diet and Bone. In: Turnlund JR, Johnson PE, editors. ACS Symposium Series Number 258 Stable Isotopes in Nutrition. Pp. 205-220.

Kolodny Y, Luz B, Navon O. 1983. Oxygen Isotope Variations in Phosphate of Biogenic Apatites: I. Fish Bone Apatite-Rechecking the Rules of the Game. Earth and Planetary Science Letters 64: 398-404.

Lakatos M, Hartard B, Máguas C. 2007. The Stable Isotopes $\delta^{13}C$ and $\delta^{18}O$ of Lichens Can Be Used as Tracers of Microenvironmental Carbon and Water Sources. In: Dawson TE, Siegwolf RTW, editors. Stable Isotopes as Indicators of Ecological Change. New York: Elsevier. Pp. 77-92.

Land LS, Lundelius EL, Valastro, S Jr. 1980. Isotopic Ecology of Deer Bones. Palaeogeography, Palaeoclimatology, Palaeoecology 32: 143-151.

Lange OL, Green TGA, Ziegler H. 1988. Water Status Related Photosynthesis and Carbon Isotope Discrimination in Species of the Lichen Genus *Pseudocyphellaria* with Green or Blue-green Photobionts and in Photosynthesis. Oecologia 75: 494-501.

Larson TE, Longstaffe FJ. 2007. Deciphering Seasonal Variations in the Diet and Drinking Water of Modern White-tailed Deer by In Situ Analysis of Osteons in Cortical Bone. Journal of Geophysical Research 112: G4003.

Larter NC, Nagy JA. 1997. Peary Caribou and Banks Island Forage: Assessing Seasonal Diet Similarities. Rangifer 17(1): 9-16.

Larter NC, Nagy JA. 2001. Seasonal and Annual Variability in the Quality of Important Forage Plants on Banks Island, Canadian High Arctic. Applied Vegetation Science 4: 115-128.

Larter NC, Nagy JA. 2004. Seasonal Changes in the Composition of the Diets of Peary Caribou and Muskoxen on Banks Island. Polar Research 23(2): 131-140.

Lecavalier BS, Fisher DA, Milne GA, Vinther BM, Tarasov L, Huybrechts P, Lacelle D, Main B, Zheng J, Bourgeois J, Dyke AS. 2017. High Arctic Holocene Temperature Record from the Agassiz Ice Cap and Greenland Ice Sheet Evolution. Proceedings of the National Academy of Sciences 114(23): 5952-5957.

Lechler AR, Niemi NA. 2012. The Influence of Snow Sublimation on the Isotopic Composition of Spring and Surface Waters in the Southwestern United States: Implications for Stable Isotope-Based Paleoaltimetry and Hydrologic Studies. Geological Society of America Bulletin 124(3/4): 318-334.

Lécuyer C, Grandjean P, Emig CC. 1996. Determination of Oxygen Isotope Fractionation Between Water and Phosphate from Living Lingulids: Potential Application to Palaeoenvironmental Studies. Palaeogeography, Palaeoclimatology, Palaeoecology 126: 101-108.

Lee-Thorp JA, van der Merwe NJ. 1987. Carbon Isotope Analysis of Fossil Bone Apatite. South African Journal of Science 83: 71-74.

Lee-Thorp JA, Sealy JC, van der Merwe NJ. 1989. Stable Carbon Isotope Ratio Differences Between Bone Collagen and Bone Apatite, and Their Relationship to Diet. Journal of Archaeological Science 16: 585-599.

Lee-Thorp HA, van der Merwe NJ. 1991. Aspects of the Chemistry of Modern and Fossil Biological Apatites. Journal of Archaeological Science 18: 343-354.

LeGeros RZ. 1981. Apatites in Biological Systems. Progress in Crystal Growth Characterization 4: 1-45.

LeGeros RZ, LeGeros JP. 1984. Phosphate Minerals in Human Tissues. In: Nriagu JO, Moore PB, editors. Phosphate Minerals. Berlin: Springer Verlag. Pp. 351-385.

LeGeros RZ. 1991. Calcium Phosphates in Oral Biology and Medicine, Volume 15. Paris: Karger Press.

Lent PC. 1999. Muskoxen and Their Hunters: A History. Norman: University of Oklahoma Press.

Long ES, Sweitzer RA, Diefenbach DR, Ben-David M. 2005. Controlling for Anthropogenically Induced Atmospheric Variation in Stable Carbon Isotope Studies. Oecologia 146(1): 148-156.

Longinelli A, Nuti S. 1973. Revised Phosphate-water Isotopic Temperature Scale. Earth and Planetary Science Letters 19: 373-376.

Longinelli A. 1984. Oxygen Isotopes in Mammal Bone Phosphate: A New Tool for Paleohydrological and Paleoclimatological Research? Geochimica et Cosmochimica Acta 48: 385-390.

Lowenstam HA, Weiner S. 1989. On Biomineralization. New York: Oxford University Press.

Luz B, Kolodny Y, Horowitz M. 1984. Fractionation of Oxygen Isotopes Between Mammalian Bone-phosphate and Environmental Drinking Water. Geochimica et Cosmochimica Acta 48: 1689-1693.

Luz B, Cormie AB, Schwarcz HP. 1990. Oxygen Isotope Variations in Phosphate of Deer Bones. Geochimica et Cosmochimica Acta 54: 1723-1728.

Máguas C, Griffiths H, Ehleringer J, Serôdio J. 1993. Characterization of Photobiont Associations in Lichens Using Carbon Isotope Discrimination Techniques. In: Ehleringer JR, Hall AE, Farquhar GD, editors. Stable Isotopes and Plant Carbon-water Relations. San Diego: Academic Press. Pp. 201-212.

Manning TH, MacPherson AH. 1958. The Mammals of Banks Island. Arctic Institute of North America Technical Papers 2: 5-74.

Matthews CJD, Longstaffe FJ, Ferguson SH. 2016. Dentine Oxygen Isotopes (δ^{18}O) as a Proxy for Odonocete Distributions and Movements. Ecology and Evolution 6(14): 4643-4653.

Maxwell MS. 1980. Archaeology of the Arctic and Subarctic Zones. Annual Review of Anthropology 9: 161-185.

McArthur JM, Coleman ML, Bremmer JM. 1980. Carbon and Oxygen Isotopic Composition of Structural Carbonate in Sedimentary Francolite. Journal of the Geological Society of London 137: 669-673.

Metcalfe JZ, Longstaffe FJ, White CD. 2009. Method-dependent Variations in Stable Isotope Results for Structural Carbonate in Bone Bioapatite. Journal of Archaeological Science 36: 110-121.

Metges C, Kempe K, Schmidt H-L. 1990. Dependence of the Carbon-isotope Contents of Breath Carbon Dioxide, Milk, Serum, and Rumen Fermentation Products on the $\delta^{13}C$ Value of Food in Dairy Cows. British Journal of Nutrition 63: 187-196.

Miller FL. 1974. Biology of the Kaminuriak Population of Barren-ground Caribou. Park 2: Dentition as an Indicator of Age and Sex; Composition and Socialisation of the Population. Canadian Wildlife Service Report Series 31.

Miller FL. 1990. Inter-island Movements of Peary Caribou: A Review and Appraisement of Their Ecological Importance. In: Harington CR, editor. Canada's Missing Dimension: Science and History in the Canadian Arctic Islands. Ottawa: Canadian Museum of Nature. Pp. 608-632.

Miller FL, Gunn A. 2003. Catastrophic Die-off of Peary Caribou on the Western Queen Elizabeth Islands, Canadian High Arctic. Arctic 56(4): 381-390.

Miller FL, Barry SJ, Calvert WA. 2005. Sea-ice Crossings by Caribou in the South-central Canadian Arctic Archipelago and Their Ecological Importance. Rangifer Special Issue 16: 77-88.

Mills A, Urey HC. 1940. The Kinetics of Isotopic Exchange Between Carbon Dioxide, Bicarbonate Ion, Carbonate Ion, and Water. Journal of the America Chemical Society 62: 1019-1026.

Nagy M. 1999. Aulavik Oral History Project on Banks Island, NWT: Final Report. Prepared for Inuvialuit Social Development Program.

Navarro JCA, Varma V, Riipinen I, Seland Ø, Kirkevåg A, Struthers H, Iversen T, Hansson H-C, Ekman AML. 2016. Amplification of Arctic Warming by Past Air Pollution Reductions in Europe. Nature Geoscience 9: 277-282.

Nieminen M. 1980. Nutritional and Seasonal Effects on the Haematology and Blood Chemistry in Reindeer (*Rangifer Tarandus Tarandus L.*). Comparative Biochemistry and Physiology 66A: 399-413.

Oakes EJ, Harmsen R. 1992. Sex, Age, and Seasonal Differences in the Diets and Activity Budgets of Muskoxen (*Ovibos moschatus*). Canadian Journal of Zoology 70: 605-616.

O'Keefe A, Deacon DAG. 1988. Cavity Ring-down Optical Spectrometer for Absorption-measurements Using Pulsed Laser Sources. Review of Scientific Instruments 59: 2544-2551.

Passey BH, Cerling TE. 2002. Tooth Enamel Mineralization in Ungulates: Implications for Recovering a Primary Isotopic Time Series. Geochimica et Cosmochimica Acta 66(18): 3225-3234.

Passey BH, Cerling TE, Schuster GT, Robinson TF, Roeder BL, Krueger SK. 2005. Inverse Methods for Estimating Primary Input Signals from Time-averaged Isotope Profiles. Geochimica et Cosmochimica Acta 69(16): 4101-4116.

Passey BH, Cerling TE. 2006. In Situ Stable Isotope Analysis (δ^{13}C, δ^{18}O) of Very Small Teeth Using Laser Ablation GC/IRMS. Chemical Geology 235: 238-249.

Pasteris JD, Wopenka B, Freeman JJ, Rogers K, Valsami-Jones E, van der Houwen JAM, Silva MJ. 2004. Lack of OH in Nanocrystalline Apatite as a Function of Degree of Atomic Order: Implications for Bone and Biomaterials. Biomaterials 25: 229-238.

Pearson J, Grove M. 2013. Counting Sheep: Sample Size and Statistical Inference in Stable Isotope Analysis and Palaeodietary Reconstruction. World Archaeology 45(3): 373-387.

Pellegrini M, Snoeck C. 2016. Comparing Bioapatite Carbonate Pre-treatments for Isotopic Measurements: Part 2 – Impact on Carbon and Oxygen Isotope Compositions. Chemical Geology 420: 88-96.

Penel G, Leroy G, Rey C, Bres E. 1998. MicroRaman Spectral Study of the PO4 and CO3 Vibrational Modes in Synthetic and Biological Apatites. Calcified Tissue International 63: 475-481.

Peros MC, Gajewski K. 2009. Pollen-based Reconstructions of Late Holocene Climate from the Central and Western Canadian Arctic. Journal of Paleolimnology 41: 161-175.

Person A, Bocherens H, Mariotti A, Renard M. 1996. Diagenetic Evolution and Experimental Heating of Bone Phosphate. Palaeogeography, Palaeoclimatology, Palaeoecology 126: 135-149.

Pilz J, Spöck G. 2008. Why Do We Need and How Should We Implement Bayesian Kriging Methods. Stochastic Environmental Research and Risk Assessment 22: 621-632.

Pucéat E, Reynard B, Lécuyer C. 2004. Can Crystallinity Be Used to Determine the Degree of Chemical Alteration of Biogenic Apatites? Chemical Geology 205: 83-97.

Rey C, Shimizu M, Collins B, Glimcher MJ. 1990. Resolution-enhanced Fourier Transform Infrared Spectroscopy Study of the Environment of the Phosphate Ions in the Early Deposits of a Solid Phase of Calcium-Phosphate in Bone and Enamel, and Their Evolution with Age. 1: Investigations in the υ_4 PO_4 Domain.

Rey C, Miquel JL, Facchini L, LeGrand AP, Glimcher MJ. 1995. Hydroxyl Groups in Bone Mineral. Bone 16(5): 583-586.

Reyes-Gasga J, Martínez-Piñeiro EL, Rodríguez-Álvarez G, Tiznado-Orozco GE, García-García R, Brès EF. 2013. XRD and FTIR Crystallinity Indices in Sound Human Tooth Enamel and Synthetic Hydroxyapatite. Materials Science and Engineering C 33: 4568-4574.

Roche D, Ségalen L, Balan E, Delattre S. 2010. Preservation Assessment of Miocene-Pliocene Tooth Enamel from Tugen Hills (Kenyan Rift Valley) Through FTIR, Chemical and Stable-isotope Analyses. Journal of Archaeological Science 37: 1690-1699.

Rozanski K, Araguás-Araguás L, Gonfiatini R. 1993. Isotopic Patterns in Modern Global Precipitation. Climate Change in Continental Isotopic Records Geophysical Monograph 78. Washington DC: American Geophysical Union.

Rozanski K, Froehlich K, Mook WG. 2001. Surface Water. In: Mook WG, editor. Environmental Isotopes in the Hydrological Cycle: Principles and Applications. International Hydrological Programme Technical Documents in Hydrology 39, Volume 3.

Sakai S, Kodan T. 2011. Micropowder Collecting Technique for Stable Isotope Analysis of Carbonates. Rapid Communications in Mass Spectrometry 25: 1205-1208.

Sanati M, Andersson A. 1993. DRIFT Study of the Oxidation and the Ammoxidation of Toluene Over a TiO_2(B)-supported Vanadia Catalyst. Journal of Molecular Catalysis 81: 51-62.

Sathyanarayana DN. 2004. Vibrational Spectroscopy: Theory and Applications. New Delhi: New Age International.

Scorrano G, Mazzuca C, Valentini F, Scano G, Buccolieri A, Giancane G, Manno D, Valli L, Mallegni F, Serra A. 2016. The Tale of Henry VII: A Multidisciplinary Approach to Determining the Post-mortem Practice. Archaeological and Anthropological Science. doi:10.1007/s12520-016-0321-4.

Sharp ZD, Cerling TE. 1996. A Laser GC-IRMS Technique for In Situ Stable Isotope Analyses of Carbonates and Phosphates. Geochimica et Cosmochimica Acta 60(15): 2909-2916.

Shemesh A. 1990. Crystallinity and Diagenesis of Sedimentary Apatite. Geochimica et Cosmochimica Acta 54: 2433-2438.

Silverman DN. 1982. Carbonic Anhydrase: Oxygen-18 Exchange Catalyzed by an Enzyme with Rate-contributing Proton-transfer Steps. Methods in Enzymology 87: 732-752.

Smith CI, Nielsen-Marsh CM, Jans MME, Collins MJ. 2007. Bone Diagenesis in the European Holocene I: Patterns and Mechanisms. Journal of Archaeological Science 34: 1485-1493.

Snoeck C, Pellegrini M. 2015. Comparing Bioapatite Carbonate Pre-treatments for Isotopic Measurements: Part 1 – Impact on Structure and Chemical Composition. Chemical Geology 417: 394-403.

Sponheimer M, Lee-Thorp JA. 1999. Oxygen Isotopes in Enamel Carbonate and Their Ecological Significance. Journal of Archaeological Science 26: 723-728.

Staaland H, Thing H. 1991. Distribution of Nutrients and Minerals in the Alimentary Tract of Muskoxen, *Ovibos moschatus*. Comparative Biochemistry and Physiology 98A(3/4): 543-549.

Sternberg L, DeNiro MJ. 1983. Bio-geochemical Implications of the Isotopic Equilibrium Fractionation Factor Between Oxygen Atoms of Acetone and Water. Geochimica et Cosmochimica Acta 47: 2271-2274.

Sternberg LSL. 1988. Oxygen and Hydrogen Isotope Ratios in Plant Cellulose: Mechanisms and Applications. In: Rundel PW, Ehleringer JR, Nagy JA, editors. Stable Isotopes in Ecological Research. Berlin: Springer-Verlag. Pp. 124-141.

Suga S, Murayama Y, Musashi T. 1970. A Study of the Mineralization Process in the Developing Enamel of Guinea Pigs. Archives of Oral Biology 15: 597-612.

Suga S. 1979. Comparative Histology of Progressive Mineralization Patterns of Developing Incisor Enamel in Rodents. Journal of Dental Research 58: 1025-1026.

Suga S. 1982. Progressive Mineralization Pattern of Developing Enamel During the Maturation Stage. Journal of Dental Research 61: 1532-1542.

Suga S. 1983. Comparative Histology of the Progressive Mineralization Pattern of Developing Enamel. In: Suga S, editor. Mechanisms of Tooth Enamel Formation. Tokyo: Quintessence Publishing. Pp. 167-203.

Sullivan PF, Welker JM. 2007. Variation in Leaf Physiology of *Salix arctica* Within and Across Ecosystems in the High Arctic: Test of a Dual Isotope ($\Delta^{13}C$ and $\Delta^{18}O$) Conceptual Model. Oecologia 151: 372-386.

Surovell TA, Stiner MC. 2001. Standardizing Infra-red Measures of Bone Mineral Crystallinity: An Experimental Approach. Journal of Archaeological Science 28: 633-642.

Tafforeau P, Bentaleb I, Jaeger J-J, Martin C. 2007. Nature of Laminations and Mineralization in Rhinoceros Enamel Using Histology and X-ray Synchrotron Microtomography: Potential Implications for Palaeoenvironmental Isotopic Studies. Palaeogeography, Palaeoclimatology, Palaeoecology 246: 206-227.

Tahmasebi F. 2015. Carbon and Nitrogen Isotopic Investigations of the Late Pleistocene Paleoecology of Eastern Beringia, Yukon Territory, Using Soils, Plants, and Rodent Bones. [Dissertation]. [London (ON)]: University of Western Ontario.

Tener JS. 1965. Muskoxen in Canada: A Biological and Taxonomic Review. Ottawa: Canadian Wildlife Service, Department of Northern Affairs and National Resources, Natural and Historic Resources Branch.

Thompson TJU, Gauthier M, Islam M. 2009. The Application of a New Method of Fourier Transform Infrared Spectroscopy to the Analysis of Burned Bone. Journal of Archaeological Science 36: 910-914.

Usher PJ. 1965. Banks Island: An Area Economic Survey. Report on file at Industrial Division, Department of Northern Affairs and National Resources, Ottawa, Ontario.

Verburg P. 2007. The Need to Correct for the Suess Effect in the Application of $\delta^{13}C$ in Sediment of Autotrophic Lake Tanganyika, as a Productivity Proxy in the Anthropocene. Journal of Paleolimnology 37: 591-602.

Walker DA. 2000. Hierarchical Subdivision of Arctic Tundra Based on Vegetation Response to Climate, Parent Material and Topography. Global Change Biology 6: 19-34.

Webb EC, White CD, Longstaffe FJ. 2014. Investigating Inherent Differences in Isotopic Composition Between Human Bone and Enamel Bioapatite: Implications for Reconstructing Residential Histories. Journal of Archaeological Science 50: 97-107.

Weiner S, Bar-Yosef O. 1990. States of Preservation of Bones from Prehistoric Sites in the Near East: A Survey. Journal of Archaeological Science 17(2): 187-196.

Welker JM, Rayback S, Henry GHR. 2005. Arctic and North Atlantic Oscillation Phase Changes are Recorded in the Isotopes ($\delta^{18}O$ and $\delta^{13}C$) of *Cassiope tetragona* Plants. Global Change Biology 11: 997-1002.

Wheeler MD, Newman SM, Orr-Ewing AJ, Ashfold MNR. 1998. Cavity Ring-down Spectroscopy. Journal of the Chemical Society, Faraday Transactions 94(3): 337-351.

White JWC, Cook ER, Lawrence JR, Broecker WS. 1985. The D/H Ratios of Sap in Trees: Implications for Water Sources and Tree Ring D/H Ratios. Geochimica et Cosmochimica Acta 49: 237-246.

Wright LE, Schwarcz HP. 1996. Infrared and Isotopic Evidence for Diagenesis of Bone Apatite at Dos Pilas, Guatemala: Paleodietary Implications. Journal of Archaeological Science 23: 933-944.

Yakir D, DeNiro MJ. 1990. Oxygen and Hydrogen Isotope Fractionation During Cellulose Metabolism in *Lemna gibba* L. Plant Physiology 93: 325-332.

Yakir D, DeNiro MJ, Gat JR. 1990. Natural Deuterium and Oxygen-18 Enrichment in Leaf Water of Cotton Plants Grown Under Wet and Dry Conditions: Evidence for Water Compartmentation and Its Dynamics. Plant, Cell, and Environment 13: 49-56.

Yakir D, Berry JA, Giles L, Osmond CB. 1993. The ^{18}O of Water in the Metabolic Compartment of Transpiring Leaves. In: Ehleringer JR, Hall AE, Farquhar GD, editors. Stable Isotopes and Plant Carbon-water Relations. San Diego: Academic Press. Pp. 529-540.

Yakir D, da Silveira Lobo Sternberg L. 2000. The Use of Stable Isotopes to Study Ecosystem Gas Exchange. Oecologia 123(3): 297-311.

Yi Y, Gibson JJ, Cooper LW, Hélie J-F, Birks SJ, McClelland JW, Holmes RM, Peterson BJ. 2012. Isotopic Signals (^{18}O, ^{2}H, ^{3}H) of Six Major Rivers Draining the Pan-Arctic Watershed. Global Biogeochemical Cycles 26: GB1027.

Young RA. 1975. Biological Apatite vs. Hydroxyapatite at the Atomic Level. Clinical Orthopaedics and Related Research 113: 249-262.

Yurtsever Y, Gat JR. 1981. Atmospheric Waters. In: Stable Isotope Hydrology, Deuterium and Oxygen-18 in the Water Cycle. IAEA Technical Reports Series 210. Vienna: IAEA. Pp. 103-142.

Chapter 5

5 General Discussion and Conclusion

5.1 The Importance of Baseline Isotopic Data in Understanding Tissue Isotopic Compositions

One of the primary goals of this dissertation was to investigate how shifts in caribou and muskox ecology may have influenced the subsistence choices of hunters on Banks Island over the last 4000 years, primarily using bone collagen as the analyte. Small bone fragments are often the only zooarchaeological remains present at archaeological sites on Banks Island, and bone collagen carbon and nitrogen isotope compositions ($\delta^{13}C$ and $\delta^{15}N$, respectively) record information about resource and environment variables during life.

Given the number of ecological and physiological factors that influence bulk bone collagen $\delta^{13}C$ and $\delta^{15}N$, these data, on their own, are typically inadequate to answer specific research questions, except where there are large differences in the isotopic compositions and/or trophic positions of relatively few dietary sources. In all other cases, we can make only general inferences about ecological questions of interest based on basic stable isotopic theory. Caribou and muskoxen on Banks Island provide a useful example: both species are large-bodied ruminants whose diets consist exclusively of C_3 plants. We can estimate their bone collagen $\delta^{13}C$ based on general knowledge of the $\delta^{13}C$ of modern C_3 plants as a group (typically ~ –27 to –28‰, Park and Epstein 1960; Smith and Epstein 1971; Deines 1981; O'Leary 1981, 1988), and their bone collagen $\delta^{15}N$ based on the trophic relationships among terrestrial nitrogen sources, primary producers, and herbivores (Hoering and Ford 1960; DeNiro and Epstein 1981; Virginia and Delwiche 1982; Minagawa and Wada 1984; Schoeninger and DeNiro 1984). Aside from this relatively basic information, however, we can say very little without knowing the actual isotopic compositions of forage vegetation.

Likewise, dietary mixing models, which are increasingly utilized to make inferences about dietary compositions and ecological niche relationships, require specific source (i.e. dietary) isotopic data. On Banks Island, as in many cases, it is not possible to obtain archaeological vegetation samples in any significant quantities, and microbial activity may alter the isotopic compositions of any archaeological plant samples that are obtained

(Macko and Estep 1984; DeNiro and Hastorf 1985; Macko et al. 1987; Lehmann et al. 2002; Tahmasebi 2015). One partial solution, which we employ here, is to quantify relationships between modern consumer tissues and their dietary sources using a dietary mixing model, and then use this information to make interpretations about the significance of archaeological tissue isotope compositions. This approach is less useful, however, where environmental isotopic baselines have shifted significantly due, for example, to the effects of artificial fertilization, or where the diets of consumers have changed significantly (e.g. a shift from herbivory to omnivory, or the introduction of dietary items with unique isotopic compositions). As mixing models increase in availability and sophistication, researchers will be able to explore increasingly specific research questions. Without high-quality baseline data, however, these mixing models provide misleading results that are obscured by – or overlooked because of – their mathematical complexity. Unless they already exist at site- or region-specific scales, researchers should plan to collect and incorporate baseline data into any project where mixing models are used. The plant isotopic data presented here will be useful for researchers tracking future changes in the terrestrial carbon and nitrogen cycles of the Western North American Arctic, as well as future studies of niche relationships between caribou and muskoxen on Banks Island.

5.2 Potential Disparities Between Ellipse Metrics and Mixing Models

Our investigation of caribou and muskox niche relationships on Banks Island over the last 4000 years (Chapter 3) also highlights a potential methodological, and therefore interpretive, disjunction between paleoecological and ecological research. Most mixing models, including the one we use in Chapter 2 ("MixSIAR", see Semmens et al. 2013; Stock and Semmens 2013) require an additional input besides source (dietary) and consumer (tissue) isotopic data: the enrichments in ^{13}C and ^{15}N between the source and consumer trophic levels, which we refer to as the "trophic discrimination factor" or "TDF". If the TDFs for two species under comparison are the same, then overlap or separation in their tissue isotope compositions will directly reflect overlap or separation in their dietary resources. If, however, the TDFs of the species under comparison are different, then their tissue isotope compositions alone will mischaracterize their ecological relationships. This

difference must also be accounted for when using "shape-based metrics" (Newsome et al. 2012) such as multivariate ellipses to quantify the overlap in "isotopic niche" between two species. Again, caribou and muskoxen from Banks Island provide a salient example. Because no controlled feeding studies have been performed on either species, we employ a mathematical model ("SIDER", see Healy et al. 2016) in Chapter 2 to estimate carbon and nitrogen TDFs. Significantly, the SIDER model suggests that the carbon TDF for caribou is nearly twice as large as that of muskoxen. When caribou and muskox bone collagen δ^{13}C and δ^{15}N from each archaeological period on Banks Island are plotted, they suggest that the isotopic niches of caribou and muskoxen are typically separated, but overlap strongly during periods associated with climatic instability. When the difference in carbon isotope TDFs is accounted for, however, the isotopic data instead suggest that caribou and muskoxen tend towards niche expansion with separation during cold or climatically-unstable periods.

Where specific source isotopic data can be obtained, we agree with Newsome et al. (2007, 2012) that consumer isotopic data should be presented in "DietSpace" (i.e. as source posterior probability distributions; see for instance Figure 2.15 in Chapter 2). Paleoecologists face a greater challenge because source isotopic data are generally not available and controlled feeding studies cannot be performed on extinct species. In this case, statistical approaches to TDF estimation like SIDER should be used and developed further.

5.3 Relationships Between Caribou, Muskoxen, and Ancient Hunters on Banks Island

One of the original questions motivating this project is the extent to which human occupational hiatuses on Banks Island over the last 4000 years were related to declines in the availability of caribou and particularly muskoxen, which were brought about by overexploitation from hunters, *de facto* niche competition, or niche competition caused by ecological changes. Although we cannot explore the motivations of ancient hunters with faunal stable isotope compositions alone, these data demonstrate two important points. First, as evidenced by bone collagen isotopic data from the Pre-Dorset period, caribou and muskoxen, under certain ecological conditions, are able to persist in the same ecological

niche. The number of muskox remains at the Umingmak (PjRa-2) site during the Pre-Dorset period also suggests that muskoxen were abundant during this period. Second, there appears to be a strong positive correlation between the proportion of muskox and caribou remains present at archaeological sites during an archaeological period, the proximity of caribou and muskox niches, and average annual air temperature.

These findings suggest that niche overlap in caribou and muskoxen on Banks Island probably does not relate to population declines in either species. Further, that the ecological niches of caribou and muskoxen appear to expand and separate during climatically-unstable periods (e.g. the Lagoon and Early Thule periods, see Figure 3.9 in Chapter 3) suggests that decreased availability of preferred forage, rather than increased forage competition may cause demographic declines, particularly in caribou, which have nutritional requirements more specific than those of muskoxen. Still, the significant shifts in muskox niche characteristics during the Lagoon and Early Thule periods, and the decreased presence of muskox remains relative to marine resources at Lagoon and Early Thule sites suggests that there is a relationship between the ecological status of muskoxen and the level of utilization by human hunters.

5.4 Contributions to Isotopic Baseline Development at Northern Latitudes

Independent of our interpretations, the isotopic data presented in this dissertation will also be useful for other researchers working at high northern latitudes. Although there is a growing body of vegetation isotopic data from Alaska (Barnett 1994; Ben-David et al. 2001; Baltensperger et al. 2015), data from the Canadian High Arctic is limited (Blake 1991). Our vegetation dataset includes $\delta^{13}C$ and $\delta^{15}N$ for individual plant tissues from 49 samples of 18 genera collected across Banks Island in 2014 and 2015. This is currently the largest published dataset of this kind, from this region, of which we know. Similarly, isotopic data from Holocene caribou and muskoxen, both archaeological and modern, are limited (Bocherens et al. 1996; Coltrain et al. 2004; Drucker et al. 2012; Bocherens et al. 2016), even though both species represent a unique ecological link between the Pleistocene mammoth steppe and the modern Arctic tundra ecosystem. Our bone collagen dataset expands the number of data points significantly, and among other topics, will be useful for

investigating relationships between primary producers, herbivores, and consumers at higher trophic levels. Finally, our meteoric surface water dataset extends the reach of existing surface water isotopic data from northern Canada (Gibson 2002; Gibson and Edwards 2002; Gibson et al. 2005; Yi et al. 2012), complementing the valuable but relatively limited set of precipitation isotope data from GNIP collection stations across the North American Arctic.

5.5 Further Research

Although this dissertation addresses several longstanding hypotheses concerning caribou and muskox ecology on Banks Island, it also generates several other questions that could be addressed through future isotopic investigations.

5.5.1 The Relationship Between Caribou and Muskox Niche Variation and Population Size

An important goal moving forward will be determining the relationship between the presence of caribou and muskoxen at archaeological sites on Banks Island, their niche characteristics, and genetic diversity in each species. Mitochondrial DNA analysis of many bone samples used in this project is currently underway (Rodrigues, Yang, and Hodgetts, unpublished data). When this research is complete, it will provide additional evidence with which to evaluate the relationship between dietary changes observed through time via stable isotope analyses and variation in caribou and muskox population size.

5.5.2 Traditional Hunting Knowledge on Banks Island

Several researchers (Nagy 1999; Kelvin 2016) have worked with the community of Sachs Harbour to document traditional knowledge of Banks Island's history and cultural practices. Although knowledge about caribou and muskoxen is an important part of these documents, future work can and should focus specifically on canvassing hunters for their experiential knowledge of caribou and muskox diet and behavior. This knowledge base will supplement the growing body of observational and experimental data specific to Banks Island.

5.5.3 Systematic Study of Vegetation Isotopic Compositions on Banks Island

The posterior probability distributions of some forage sources in our dietary mixing models are relatively large and overlapping, even when the source data are aggregated to reduce the total number of source divisions. Large, overlapping posterior probability distributions are less informative because there are a broad number of possible dietary contributions (Phillips et al. 2014). It is not yet clear, however, whether the mixing models produce such large posterior probability distributions because of the limited isotopic variability of arctic vegetation species, which all utilize the C_3 photosynthetic pathway, or because the source dataset is inadequate in size. The former issue is intractable, but the latter is simply a matter of collecting and analyzing more vegetation samples. Relatively speaking, the isotopic analysis of bulk vegetation samples is inexpensive, and additional samples could be collected opportunistically by Parks Canada researchers visiting Banks Island for other purposes.

Non-isotopic studies of plant species distributions in the Eastern Arctic (e.g. Ferguson 1991; Oakes et al. 1992; Larter and Nagy 2001) generally divide the landscape into different habitats (e.g. “upland barren”, “hummock tundra”, “wet sedge meadow”) and obtain vegetation samples from each. Kristensen et al. (2011) also sampled vegetation from different habitats in Greenland, and incorporated differences in the $\delta^{13}C$ and $\delta^{15}N$ of each functional group (e.g. graminoids, willow, and forbs) between habitats to provide additional structure in their dietary mixing model. Although our research demonstrates statistically significant geographic variation in the $\delta^{13}C$ and $\delta^{15}N$ of certain forage species or functional groups collected on Banks Island, helicopter travel is extremely expensive, and our time at each collection area was generally limited. Further research may benefit from structured, systematic studies of isotopic variation in vegetation from different habitats on Banks Island. While tooth enamel $\delta^{18}O$ appears not to be informative of seasonal movements in caribou or muskoxen, a vegetation “isoscape” of sufficient resolution may prove useful for this purpose.

5.5.4 The Role of Glycine and Microflora in Caribou and Muskox Bone Collagen Isotopic Compositions

Contrary to most existing research (Oakes et al. 1992; Larter and Nagy 1997, 2004), our mixing models suggest that yellow lichen (*Cetraria tilesii*) may be an important dietary resource for muskoxen on Banks Island. As discussed above, this finding may be an artifact of low sample size or limited isotopic variation in vegetation samples, though existing studies of muskox diet on Banks Island are based on analyses of rumen and fecal content. Multiple studies (Gill et al. 1983; Holechek and Valdez 1985; Thing et al. 1987; Bartolomé et al. 1995) demonstrate that, while useful, both approaches to dietary reconstruction tend to be biased towards poorly-digestible forage. The possibility also exists, however, that bulk bone collagen carbon isotope compositions are influenced by those of glycine routed without deamination from comparatively small amounts of ingested yellow lichen. The most straightforward approach for evaluating this "lichen hypothesis" is to simply compare the $\delta^{13}C$ of glycine extracted from yellow lichen and muskox bone collagen samples using a compound-specific approach.

Another possibility is that gut microflora constitute a significant protein source for ruminants exposed to seasonal declines in forage availability. Consequently, the isotopic compositions of gut microflora may also influence consumer tissue isotopic composition. To our knowledge, there is little published research in this area (but see Schwartz-Narbonne 2016) though many researchers (Sillen et al. 1989; Bocherens et al. 1996; Dewhurst et al. 2001; Sponheimer et al. 2003; Atasoglu et al. 2004) have discussed the topic. Approaching this problem would be challenging: obtaining rumen microfloral samples from harvested muskoxen is not feasible because of the rapid decomposition of digestive contents (Cuthbert 1857; Peary 1910; Tener 1965; Lent 1999). Likewise, there are methodological, and certainly ethical, impediments to field-sampling rumen microflora from wild muskoxen. One potential approach is to obtain rumen microfloral samples from muskoxen kept at research stations and temporarily placed on deprivation diets, which would then be preserved and prepared using established methods (Adamczewski et al. 1988), and analyzed for their isotopic compositions, again using GC-C-IRMS (Boschker and Middelburg 2002) or similar systems (Eek et al. 2007).

5.5.5 Controlled Feeding Studies in Captive/Domesticated Caribou and Muskoxen

Another point of significant uncertainty in our dietary mixing models, and in our interpretation of archaeological caribou and muskox $\delta^{13}C_{bc}$ and $\delta^{15}N_{bc}$, are their trophic discrimination factors (TDFs). As discussed in Chapters 2 and 3, researchers typically either utilize TDFs from published data, or derive TDFs from controlled feeding studies. Although our Bayesian-derived TDFs are reasonable for large-bodied ruminants, they could be partially "ground-truthed" by placing captive or domesticated caribou and muskoxen on controlled diets (but see Chapter 2 for a discussion of difficulties associated with this approach), and then sampling different tissues for isotopic analysis after the animals are harvested. Given their environment and unique evolutionary trajectories, both species likely possess physiological adaptations unique from ruminants that dwell in temperate or arid environments. Such a study could consequently provide unique insight into our general understanding of the relationships among diet, physiology, and tissue isotopic compositions.

5.5.6 Development of Matrix-Matched Tooth Enamel Standards for LA-GC-IRMS

The development of the laser ablation-GC-IRMS method represents a major advancement in the isotopic analysis of inorganic and biogenic carbonates and phosphates. For the sequential sampling and analysis of microbulk tooth enamel, cycle time per sample is approximately 10 minutes – several orders of magnitude shorter than the traditional approach of offline sampling and preparation – and analysis for structural carbonate and phosphate isotopic compositions. Currently, the quality of tooth enamel isotopic data obtained via LA-GC-IRMS is limited by the lack of matrix-matched reference and check standards. Our solution in Chapter 4 is to use intact enamel segments from a single muskox 4th premolar (P4) that exhibited limited intratooth isotopic variability, and for which structural carbonate $\delta^{13}C$ and $\delta^{18}O$, and phosphate $\delta^{18}O$ were independently determined, as a reference standard. As we discuss in Chapter 4, this single enamel standard provides better calibration of the data than an internal inorganic carbonate standard (WS-4). Still, because only a single reference standard is used, and the isotopic composition of this

internal standard is similar to those of our samples, the sample isotopic data are susceptible to scale contraction (Meijer et al. 2000; Sharp 2007). Ideally, at least two matrix-matched standards should be developed with carbon and oxygen isotope compositions at extreme ends of the VPDB and VSMOW scales. While there would be ethical challenges to negotiate, these standards could conceivably be developed by providing small laboratory animals with isotopically-labeled food and water, and then harvesting them for their teeth. Such standards would be of considerable value to researchers applying LA-GC-IRMS to the isotopic analysis of teeth.

5.5.7 $^{87}Sr/^{86}Sr$ as a Tool for Investigating Caribou and Muskox Movements on Banks Island

Our hypothesis that tooth enamel $\delta^{18}O$ could be used to investigate seasonal movements in caribou and muskoxen was not supported. This is unfortunate because changes in seasonal movement patterns, and in the case of caribou, temporary migrations to other islands or the mainland could play an important role in the subsistence choices of hunters on Banks Island over the last 4000 years. Elsewhere, researchers have applied radiogenic strontium isotope ($^{87}Sr/^{86}Sr$) analysis to tooth enamel to investigate seasonal movements (Hoppe et al. 1999; Balasse et al. 2002; Price et al. 2002; Schweissing and Grupe 2003; Copeland et al. 2008; Britton et al. 2009, 2011). Radiogenic strontium isotope analysis, as applied to herbivore movements, rests on differences in the $^{87}Sr/^{86}Sr$ ratio of ions from soil and water taken up by vegetation (Sillen and Kavanagh 1982; Graustein 1989; Slovak and Paytan 2011), which are in turn influenced by the age of the parent material (Dasch 1969; Faure and Powell 1972). Since ^{87}Sr is produced by the radioactive decay of rubidium, older geologic formations will have higher ^{87}Sr contents than younger ones. Given that Banks Island's tectonic assemblage is composed of Proterozoic, Devonian, Mesozoic, and Cenozoic formations (Tedrow and Douglas 1964; Miall 1976, 1979; Fyles et al. 1994), there is some potential for geographic variation in the $^{87}Sr/^{86}Sr$ of forage plants. Still, such a project would require some idea of variation in the $^{87}Sr/^{86}Sr$ of plants, surface soils, and surface waters on Banks Island, and to our knowledge these data, the collection of which would constitute a major project within itself, do not yet exist.

5.6 Summary

The papers in this dissertation utilize stable isotope analysis to investigate the Holocene ecology of caribou and muskoxen on Banks Island, NWT, Canada, with the aim of contextualizing both ecological and archaeological research in the Western Canadian Arctic. Specifically, we characterize modern caribou and muskox dietary ecology in Chapter 2, and use this information to interpret caribou and muskox niche relationships over the last 4000 years on Banks Island in Chapter 3. Finally, we explore the potential of caribou and muskox tooth enamel as indices of seasonal movements and migrations in Chapter 4. Our research highlights several important themes including potential ecological changes which may have affected the use of caribou and muskoxen by people on Banks Island over time, and issues related to the use of isotopic data for reconstructing modern and ancient faunal ecology. Additionally, this project has generated novel baseline isotopic data that will be useful for other research focused on wildlife biology and terrestrial ecology at high latitudes.

5.7 References

Adamczewski JZ, Gates CC, Soutar BM, Hudson RJ. 1988. Limiting Effects of Snow on Seasonal Habitat Use and Diets of Caribou (*Rangifer tarandus groenlandicus*) on Coats Island, Northwest Territories, Canada. Canadian Journal of Zoology 66: 1986-1996.

Atasoglu C, Guliye AY, Wallace RJ. 2004. Use of Stable Isotopes to Measure *de novo* Synthesis and Turnover of Amino Acid-C and -N in Mixed Micro-Organisms from the Sheep rumen *in vitro*. British Journal of Nutrition 91: 253-261.

Balasse M, Ambrose SH, Smith AB, Price TD. 2002. The Seasonal Mobility Model for Prehistoric Herders in the South-western Cape of South Africa Assessed by Isotopic Analysis of Sheep Tooth Enamel. Journal of Archaeological Science 29: 917-932.

Baltensperger AP, Huettmann F, Hagelin JC, Welker JM. 2015. Quantifying Trophic Niche Spaces of Small Mammals Using Stable Isotopes (δ^{15}N and δ^{13}C) at Two Scales Across Alaska. Canadian Journal of Zoology 93: 579-588.

Barnett BA. 1994. Carbon and Nitrogen Isotope Ratios of Caribou Tissues, Vascular Plants, and Lichens from Northern Alaska. [Dissertation]. [Fairbanks (AK)]: University of Alaska, Fairbanks.

Bartolomé J, Franch J, Gutman M, Seligman NAG. 1995. Technical Note: Physical Factors That Influence Fecal Analysis Estimates of Herbivore Diets. Journal of Range Management 48: 267-270.

Ben-David M, Shochat E, Adams LG. 2001. Utility of Stable Isotope Analysis in Studying Foraging Ecology of Herbivores: Examples from Moose and Caribou. Alces 37(2): 421-434.

Blake W. 1991. Ratios of Stable Carbon Isotopes in Some High Arctic Plants and Lake Sediments. Journal of Paleolimnology 6: 157-166.

Bocherens H, Pacaud G, Lazarev PA, Mariotti A. 1996. Stable Isotope Abundances (^{13}C, ^{15}N) in Collagen and Soft Tissues from Pleistocene Mammals from Yakutia: Implications for the Palaeobiology of the Mammoth Steppe. Palaeogeography, Palaeoclimatology, Palaeoecology 126: 31-44.

Bocherens H, Drucker DG, Haidle MN, Müller-Beck H, Münzel SC, Naito YI. 2016. Isotopic Evidence (C, N, S) for a High Aquatic Dietary Contribution for a Pre-Dorset Muskox Hunter from Umingmak (Banks Island, Canada). Journal of Archaeological Science: Reports 6: 700-708.

Boschker HTS, Middelburg JJ. 2002. Stable Isotopes and Biomarkers in Microbial Ecology. FEMS Microbiology Ecology 40: 85-95.

Britton K, Grimes V, Dau J, Richards MP. 2009. Reconstructing Faunal Migrations Using Intra-tooth Sampling and Strontium and Oxygen Isotope Analyses: a Case Study of Modern Caribou (*Rangifer tarandus granti)*. Journal of Archaeological Science 36: 1163-1172.

Britton K, Grimes V, Niven L, Steele TE, McPherron S, Soressi M, Kelly TE, Jaubert J, Hublin J-J, Richards MP. 2011. Strontium Isotope Evidence for Migration in Late Pleistocene Rangifer: Implications for Neanderthal Hunting Strategies at the Middle Palaeolithic Site of Jonzac, France. Journal of Human Evolution 61: 176-185.

Coltrain JB, Hayes MG, O'Rourke DH. 2004. Sealing, Whaling and Caribou: The Skeletal Isotope Geochemistry of Eastern Arctic Foragers. Journal of Archaeological Science 31: 39-57.

Copeland SR, Sponheimer M, le Roux PJ, Grimes V, Lee-Thorp JA, de Ruiter DJ, Richards MP. 2008. Strontium Isotope Ratios ($^{87}Sr/^{86}Sr$) of Tooth Enamel: A Comparison of Solution and Laser Ablation Multicollector Inductively Coupled Plasma Mass Spectrometry Methods. Rapid Communications in Mass Spectrometry 22: 3187-3194.

Cuthbert WJ. 1857. The Effects of the Exposure of Animals to a Low Temperature and to Moisture. The Farmer's Magazine 11(3): 90-93.

Dasch EJ. 1969. Strontium Isotopes in Weathering Profiles, Deep-sea Sediments and Sedimentary Rocks. Geochimica et Cosmochimica Acta 33: 1521-1522.

Deines P. 1980. The Isotopic Composition of Reduced Organic Carbon. In: Fritz P, Fontes JC, editors. Handbook of Environmental Isotope Geochemistry. New York: Elsevier Scientific. Pp. 329-406.

DeNiro MJ, Epstein S. 1981. Influence of Diet on the Distribution of Nitrogen Isotopes in Animals. Geochimica et Cosmochimica Acta 45: 341-351.

DeNiro MJ, Hastorf CA. 1985. Alteration of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ Ratios of Plant Matter During the Initial Stages of Diagenesis: Studies Utilizing Archaeological Specimens from Peru. Geochimica et Cosmochimica Acta 49: 97-115.

Dewhurst RJ, Davies DR, Merry RJ. 2000. Microbial Protein Supply from the Rumen. Animal Feed Science and Technology 85: 1-21.

Drucker DG, Hobson KA, Münzel SC, Pike-Tay A. 2012. Intra-individual Variation in Stable Carbon ($\delta^{13}C$) and Nitrogen ($\delta^{15}N$) Isotopes in Mandibles of Modern Caribou of Qamanirjuaq (*Rangifer tarandus groenlandicus*) and Banks Island (*Rangifer tarandus pearyi*): Implications for Tracing Seasonal and Temporal Changes in Diet. International Journal of Osteoarchaeology 22: 494-504.

Eek KM, Sessions AL, Lies DP. 2007. Carbon-isotopic Analysis of Microbial Cells Sorted by Flow Cytometry. Geobiology 5: 85-95.

Faure G, Powell T. 1972. Strontium Isotope Geology. New York: Springer-Verlag.

Ferguson RS. 1991. Detection and Classification of Muskox Habitat on Banks Island, Northwest Territories, Canada, Using Landsat Thematic Mapper Data. Arctic 44(S1): 66-74.

Fyles JG, Hills LV, Matthews JV Jr., Barendregt R, Baker J, Irving E, Jetté H. 1994. Ballast Brook and Beaufort Formations (Late Tertiary) on Northern Banks Island, Arctic Canada. Quaternary International 22/23: 141-171.

Gibson JJ. 2002. Short-term Evaporation and Water Budget Comparisons in Shallow Arctic Lakes Using Non-steady Isotope Mass Balance. Journal of Hydrology 264: 242-261.

Gibson JJ, Edwards TWD. 2002. Regional Water Balance Trends and Evaporation-Transpiration Partitioning from a Stable Isotope Survey of Lakes in Northern Canada. Global Biogeochemical Cycles 16(2): 1026.

Gibson JJ, Edwards TWD, Birks SJ, St Amour NA, Buhay WM, McEachern P, Wolfe BB, Peters DL. 2005. Progress in Isotope Tracer Hydrology in Canada. Hydrological Processes 19: 303-327.

Gill RB, Carpenter LH, Bartmann RM, Baker DL, Schoonveld GG. 1983. Fecal Analysis to Estimate Mule Deer Diets. Journal of Wildlife Management 47: 902-915.

Graustein WC. 1989. $^{87}Sr/^{86}Sr$ Ratios Measure the Sources and Flow of Strontium in Terrestrial Ecosystems. In: Rundel PW, Ehleringer JR, Nagy KA, editors. Stable Isotopes in Ecological Research. New York: Springer-Verlag. Pp. 491-512.

Healy K, Kelly SBA, Guillerme T, Inger R, Bearhop S, Jackson AL. 2016. Predicting Trophic Discrimination Factor Using Bayesian Inference and Phylogenetic, Ecological and Physiological Data. DEsIR: Discrimination Estimation in R. PeerJ Preprints 4: e1950v1.

Hoering TC, Ford HT. 1960. The Isotope Effects in the Fixation of Nitrogen by *Azotobacter*. Journal of the American Chemical Society 82(2): 376-378.

Holechek JL, Valdez R. 1985. Magnification and Shrub Stemmy Material Influences on Fecal Analysis Accuracy. Journal of Range Management 38(4): 350-352.

Hoppe KA, Koch PL, Carlson RW, Webb SD. 1999. Tracking Mammoths and Mastodons: Reconstruction of Migratory Behavior Using Strontium Isotope Ratios. Geology 27(5): 439-442.

Kelvin LE. 2016. There Is More Than One Way to Do Something Right: Applying Community-Based Approaches to an Archaeology of Banks Island, NWT. [Dissertation]. [London (ON)]: University of Western Ontario.

Kristensen DK, Kristensen E, Forchhammer MC, Michelsen A, Schmidt NM. 2011. Arctic Herbivore Diet Can Be Inferred from Stable Carbon and Nitrogen Isotopes in C_3 Plants, Faeces, and Wool. Canadian Journal of Zoology 89: 892-899.

Larter NC, Nagy JA. 1997. Peary Caribou and Banks Island Forage: Assessing Seasonal Diet Similarities. Rangifer 17(1): 9-16.

Larter NC, Nagy JA. 2001. The Distribution of Forage Types Among Four Terrestrial Habitats on Southern Banks Island. Department of Resources, Wildlife & Economic Development, Government of the Northwest Territories, Manuscript Report Number 142. Northwest Territories: Inuvik.

Larter NC, Nagy JA. 2004. Seasonal Changes in the Composition of the Diets of Peary Caribou and Muskoxen on Banks Island. Polar Research 23(2): 131-140.

Lehmann MF, Bernasconi SM, Barbieri A, McKenzie JA. 2002. Preservation of Organic Matter and Alteration of Its Carbon and Nitrogen Isotope Composition During Simulated and In Situ Early Sedimentary Diagenesis. Geochimica et Cosmochimica Acta 66(20): 3573-3584.

Lent PC. 1999. Muskoxen and Their Hunters: A History. Norman: University of Oklahoma Press.

Macko SA, Estep MLF. 1984. Microbial Alteration of Stable Nitrogen and Carbon Isotopic Compositions of Organic Matter. Organic Geochemistry 6: 787-790.

Macko SA, Fogel Estep ML, Hare PE, Hoering TC. 1987. Isotopic Fractionation of Nitrogen and Carbon in the Synthesis of Amino Acids by Microorganisms. Chemical Geology 65: 79-92.

Meijer HAJ, Neubert REM, Visser GH. 2000. Cross Contamination in Dual Inlet Isotope Ratio Mass Spectrometers. International Journal of Mass Spectrometry 198: 45-61.

Miall AD. 1976. Proterozoic and Paleozoic Geology of Banks Island, Arctic Canada. Geological Survey of Canada Bulletin 258. Ottawa: Geological Survey of Canada.

Miall AD. 1979. Mesozoic and Tertiary Geology of Banks Island, Arctic Canada: The History of an Unstable Craton Margin. Geological Survey of Canada Memoir 387. Ottawa: Geological Survey of Canada.

Minagawa M, Wada E. 1984. Stepwise Enrichment of ^{15}N Along Food Chains: Further Evidence and the Relation Between δ^{15}N and Animal Age. Geochimica et Cosmochimica Acta 48: 1135-1140.

Nagy M. 1999. Aulavik Oral History Project on Banks Island, NWT: Final Report. Prepared for Inuvialuit Social Development Program.

Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL. 2007. A Niche for Isotopic Ecology. Frontiers in Ecology and the Environment 5(8): 429-436.

Newsome SD, Yeakel JD, Wheatley PV, Tinker MT. 2012. Tools for Quantifying Isotopic Niche Space and Dietary Variation at the Individual and Population Level. Journal of Mammalogy 93(2): 329-341.

Oakes EJ, Harmsen R. 1992. Sex, Age, and Seasonal Differences in the Diets and Activity Budgets of Muskoxen (*Ovibos moschatus*). Canadian Journal of Zoology 70: 605-616.

O'Leary MH. 1981. Carbon Isotope Fractionation in Plants. Phytochemistry 20(4): 553-567.

O'Leary MH. 1988. Carbon Isotopes in Photosynthesis. BioScience 38(5): 328-336.

Park R, Epstein S. 1960. Carbon Isotope Fractionation During Photosynthesis. Geochimica et Cosmochimica Acta 21: 110-126.

Peary RE. 1910. The North Pole. London: Hodder and Stoughton.

Phillips DL, Inger R, Bearhop S, Jackson AL, Moore JW, Parnell AC, Semmens BX, Ward EJ. 2014. Best Practices for Use of Stable Isotope Mixing Models in Food-Web Studies. Canadian Journal of Zoology 92: 823-835.

Price TD, Burton JH, Bentley RA. 2002. The Characterization of Biologically Available Strontium Isotope Ratios for the Study of Prehistoric Migration. Archaeometry 44(1): 117-135.

Schoeninger MJ, DeNiro MJ. 1984. Nitrogen and Carbon Isotopic Composition of Bone Collagen from Marine and Terrestrial Animals. Geochimica et Cosmochimica Acta 48: 625-639.

Schwartz-Narbonne RE. 2016. Reframing the Mammoth Steppe: Examining Mammoth Steppe Ecology Using Carbon and Nitrogen Isotopic Compositions of Megafauna Collagen. [Dissertation]. [London (ON)]: University of Western Ontario.

Schweissing MM, Grupe G. 2003. Tracing Migration Events in Man and Cattle by Stable Strontium Isotope Analysis of Appositionally Grown Mineralized Tissue. International Journal of Osteoarchaeology 13: 96-103.

Semmens BX, Ward EJ, Parnell AC, Phillips DL, Bearhop SB, Inger R, Jackson A, Moore JW. 2013. Statistical Basis and Outputs of Stable Isotope Mixing Models: Comments on Fry (2013). Marine Ecology Progress Series 490: 285-289.

Sharp Z. 2007. Principles of Stable Isotope Geochemistry. Upper Saddle River: Pearson Prentice Hall.

Sillen A, Kavanagh M. 1982. Strontium and Paleodietary Research: a Review. Yearbook of Physical Anthropology 25: 67-90.

Sillen A, Sealy JC, van der Merwe NJ. 1989. Chemistry and Paleodietary Research: No More Easy Answers. American Antiquity 54(3): 504-512.

Slovak NM, Paytan A. 2011. Applications of Sr Isotopes in Archaeology. In: Baskaran M, editor. Handbook of Environmental Isotope Geochemistry, Advances in Isotope Geochemistry. Heidelberg: Springer-Verlag. Pp. 743-767.

Smith BN, Epstein S. 1971. Two Categories of $^{13}C/^{12}C$ Ratios for Higher Plants. Plant Physiology 47: 380-384.

Sponheimer M, Robinson T, Ayliffe L, Roeder B, Hammer J, Passey B, West A, Cerling T, Dearing D, Ehleringer J. 2003. Nitrogen Isotopes in Mammalian Herbivores: Hair $\delta^{15}N$ Values from a Controlled Feeding Study. International Journal of Osteoarchaeology 13: 80-87.

Stock BC, Semmens BX. 2013. MixSIAR GUI User Manual. Version 3.1. Available from: https://github.com/brianstock/MixSIAR.

Tahmasebi F. 2015. Carbon and Nitrogen Isotopic Investigations of the Late Pleistocene Paleoecology of Eastern Beringia, Yukon Territory, Using Soils, Plants, and Rodent Bones. [Dissertation]. [London (ON)]: University of Western Ontario.

Tedrow JCF, Douglas LA. 1964. Soil Investigations on Banks Island. Soil Science 98: 53-65.

Tener JS. 1965. Muskoxen in Canada: A Biological and Taxonomic Review. Ottawa: Canadian Wildlife Service, Department of Northern Affairs and National Resources, Natural and Historic Resources Branch.

Thing H, Klein DR, Jingfors K, Holt S. 1987. Ecology of Muskoxen in Jameson Land, Northeast Greenland. Holarctic Ecology 10(2): 95-103.

Virginia RA, Delwiche CC. 1982. Natural ^{15}N Abundance of Presumed N_2-Fixing and Non-N_2-Fixing Plants from Selected Ecosystems. Oecologia 54(3): 317-325.

Yi Y, Gibson JJ, Cooper LW, Hélie J-F, Birks SJ, McClelland JW, Holmes RM, Peterson BJ. 2012. Isotopic Signals (^{18}O, ^{2}H, ^{3}H) of Six Major Rivers Draining the Pan-Arctic Watershed. Global Biogeochemical Cycles 26: GB1027.

Appendices

Appendix A

Table A1. Mean and median, and 95% credible intervals of the posterior probability distributions of all forage sources to caribou bone collagen from Banks Island using carbon and nitrogen TDFs from Szpak et al. (2012): $\Delta^{13}C_{bc\text{-}diet}$ = 3.7±1.6; $\Delta^{15}N_{bc\text{-}diet}$ = 3.6±1.3. Values correspond to the histograms in Figure A1.

Forage Source	Median (%)	Mean (%)	95% CI (%)
Rose/Heath	0.01	0.02	0.00 – 0.07
Northern Dwarf Willow	0.02	0.03	0.00 – 0.09
Northern Non-leguminous Forb	0.02	0.03	0.00 – 0.10
Moss	0.02	0.03	0.00 – 0.10
Northern Leguminous Forb	0.02	0.03	0.00 – 0.11
Southern Dwarf Willow	0.02	0.03	0.00 – 0.12
Thamnolia vermicularis	0.03	0.04	0.00 – 0.14
Southern Non-leguminous Forb	0.03	0.04	0.00 – 0.15
Grass	0.04	0.05	0.00 – 0.16
Northern Sedge	0.04	0.05	0.00 – 0.18
Southern Legume	0.06	0.08	0.00 – 0.30
Southern Sedge	0.17	0.16	0.06 – 0.26
Cetraria tilesii	0.41	0.40	0.20 – 0.53

Table A2. Mean and median, and 95% credible intervals of the posterior probability distributions of all forage sources to muskox bone collagen from Banks Island using carbon and nitrogen TDFs from Szpak et al. (2012): $\Delta^{13}C_{bc\text{-}diet}$ = 3.7±1.6; $\Delta^{15}N_{bc\text{-}diet}$ = 3.6±1.3. Values correspond to the histograms in Figure A2.

Forage Source	Median (%)	Mean (%)	95% CI (%)
Rose/Heath	0.02	0.03	0.00 – 0.09
Moss	0.02	0.03	0.00 – 0.11
Northern Dwarf Willow	0.02	0.03	0.00 – 0.11
Northern Non-leguminous Forb	0.02	0.03	0.00 – 0.11
Northern Leguminous Forb	0.03	0.04	0.00 – 0.12
Southern Dwarf Willow	0.03	0.04	0.00 – 0.14
Southern Non-leguminous Forb	0.04	0.05	0.00 – 0.17
Thamnolia vermicularis	0.04	0.05	0.00 – 0.17
Grass	0.05	0.07	0.00 – 0.21
Northern Sedge	0.05	0.07	0.00 – 0.23
Southern Legume	0.07	0.09	0.00 – 0.28
Southern Sedge	0.22	0.22	0.10 – 0.32
Cetraria tilesii	0.25	0.25	0.08 – 0.37

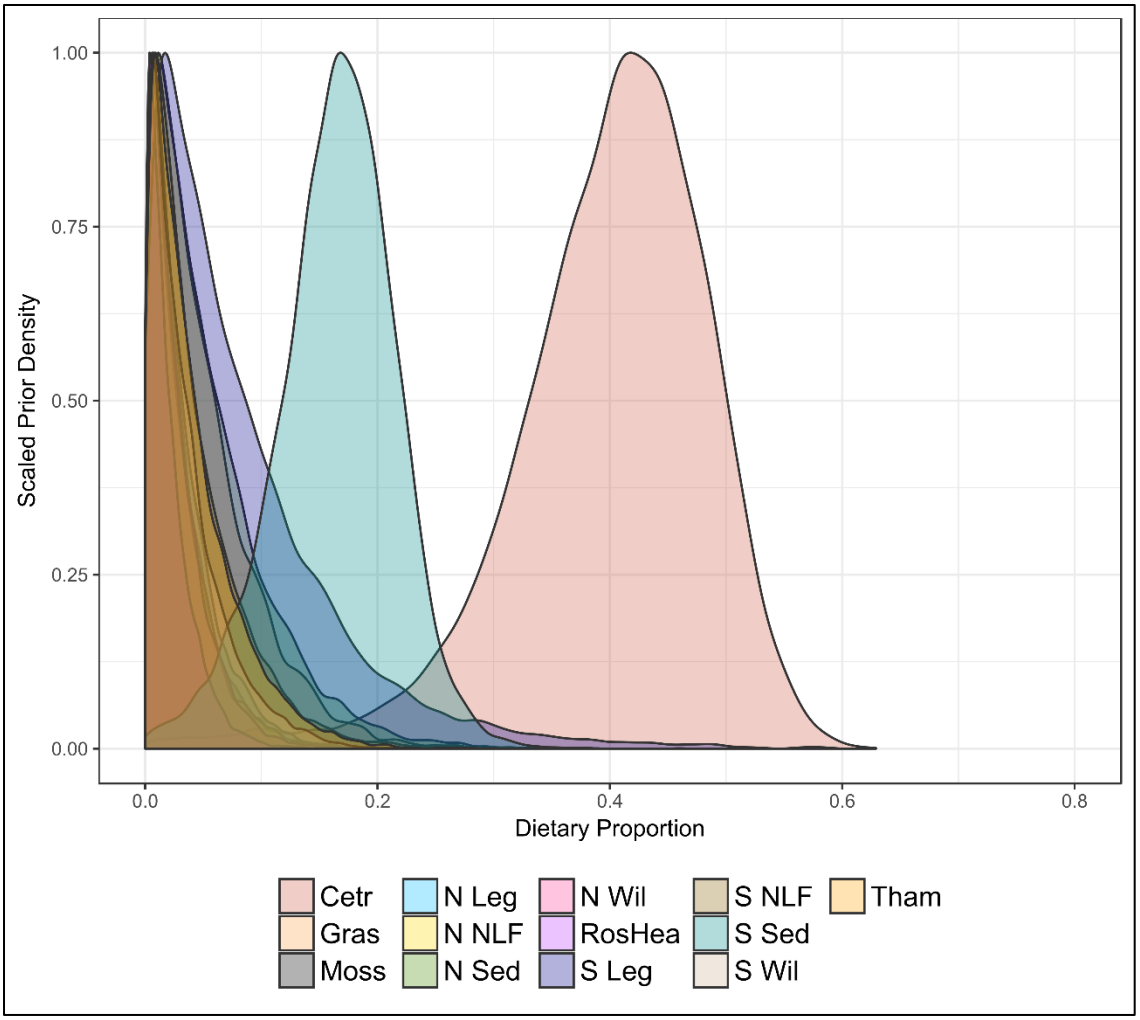


Figure A1. Posterior probability distributions of all forage sources to caribou bone collagen using carbon and nitrogen TDFs from Szpak et al. (2012). Forage items are: *Cetraria tilesii* (Cetr); grasses (Gras); moss (Moss); northern legumes (N Leg); northern non-leguminous forbs (N NLF); northern sedges (N Sed); northern willow (N Wil); rose/heath (RosHea); southern legumes (S Leg); southern non-leguminous forbs (S NLF); southern sedges (S Sed); southern willow (S Wil); and *Thamnolia vermicularis* (Tham). Posterior probability distributions change significantly compared to those in Figure 2.8 (Chapter 2), but only in the sense that *Cetraria* has a higher proportional contribution. That is, there is no significant change in the proportional contributions of other forage types, such as willow.

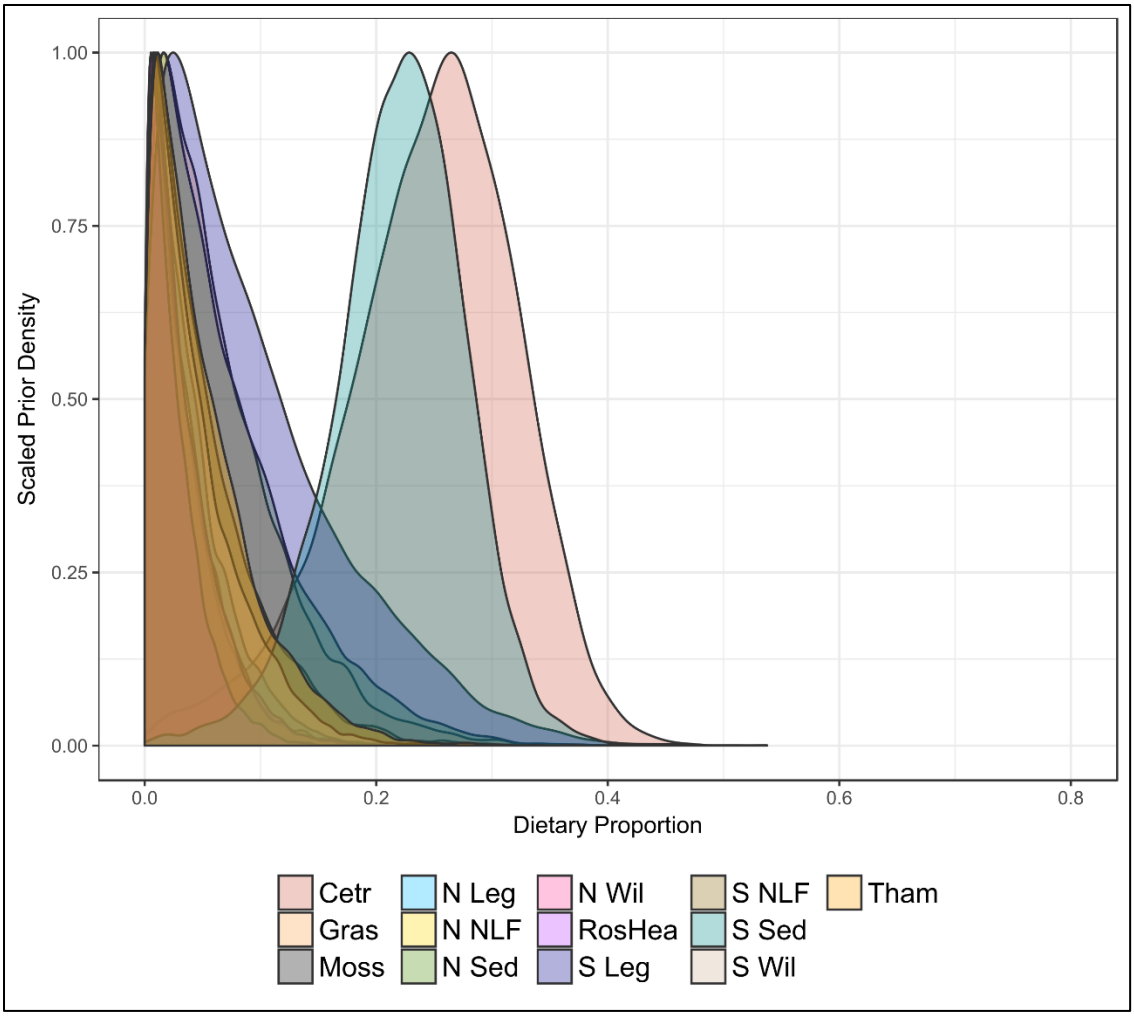


Figure A2. Posterior probability distributions of all forage sources to muskox bone collagen using carbon and nitrogen TDFs from Szpak et al. (2012). Forage items are: *Cetraria tilesii* (Cetr); grasses (Gras); moss (Moss); northern legumes (N Leg); northern non-leguminous forbs (N NLF); northern sedges (N Sed); northern willow (N Wil); rose/heath (RosHea); southern legumes (S Leg); southern non-leguminous forbs (S NLF); southern sedges (S Sed); southern willow (S Wil); and *Thamnolia vermicularis* (Tham). In comparison to Figure 2.13 (Chapter 2), posterior probability distributions do change when different TDFs are used: *Cetraria* and southern sedge make smaller proportional contributions to muskox bone collagen, and southern legumes make a slightly larger proportional contribution. Still, there's no significant increase in the proportional contributions of willow or forbs.

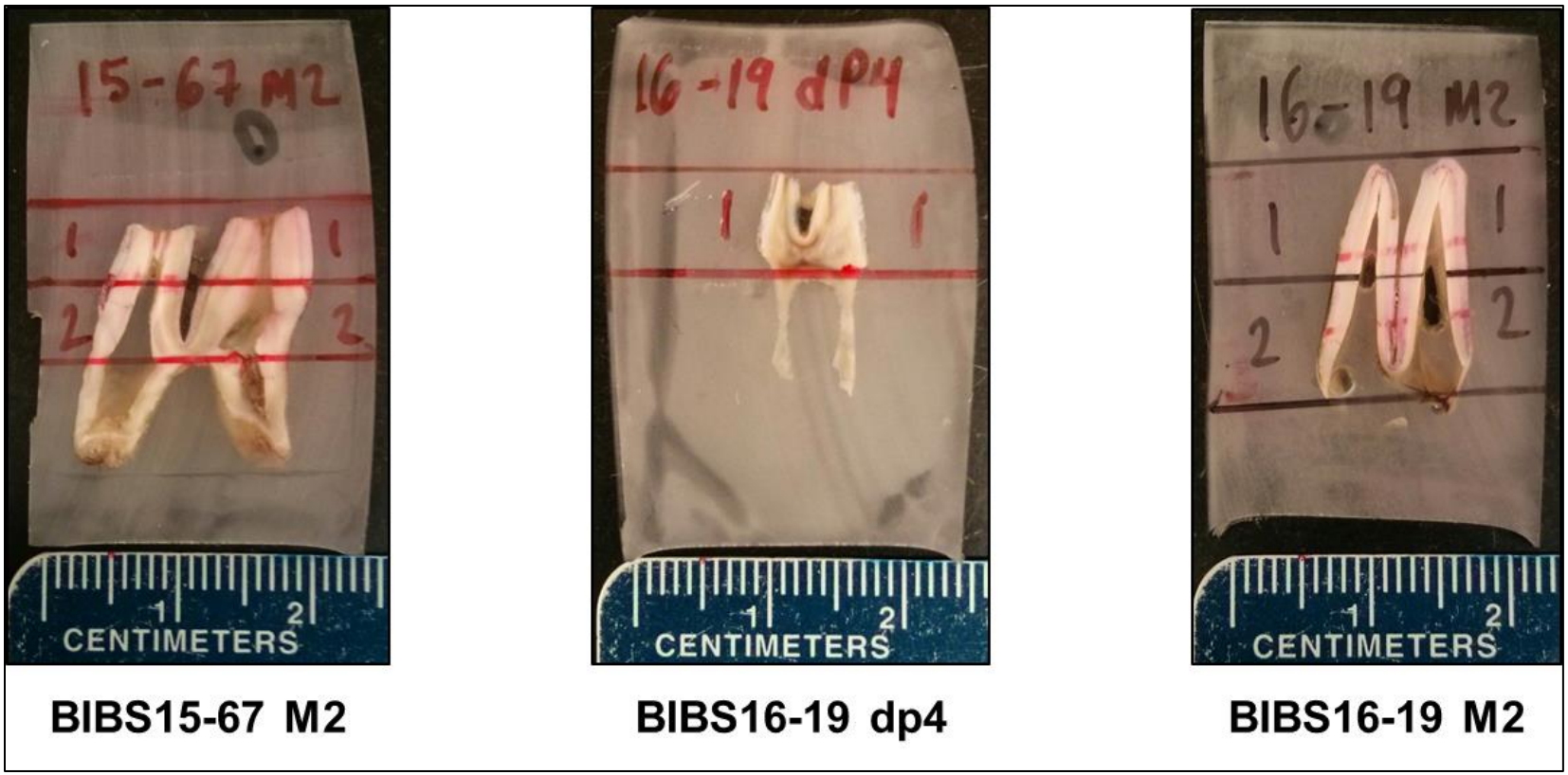


Figure A3. Buccolingual thick sections taken from modern caribou teeth, showing each ~ 5 mm tall microbulk sample ID (e.g. "1", "2"). The image for tooth sample BIBS16-19 M1 was inadvertently deleted. Micromilled spots on the enamel, used for enamel structural carbonate $\delta^{13}C$ and $\delta^{18}O$ analysis (Chapter 4), are visible on each thick section.

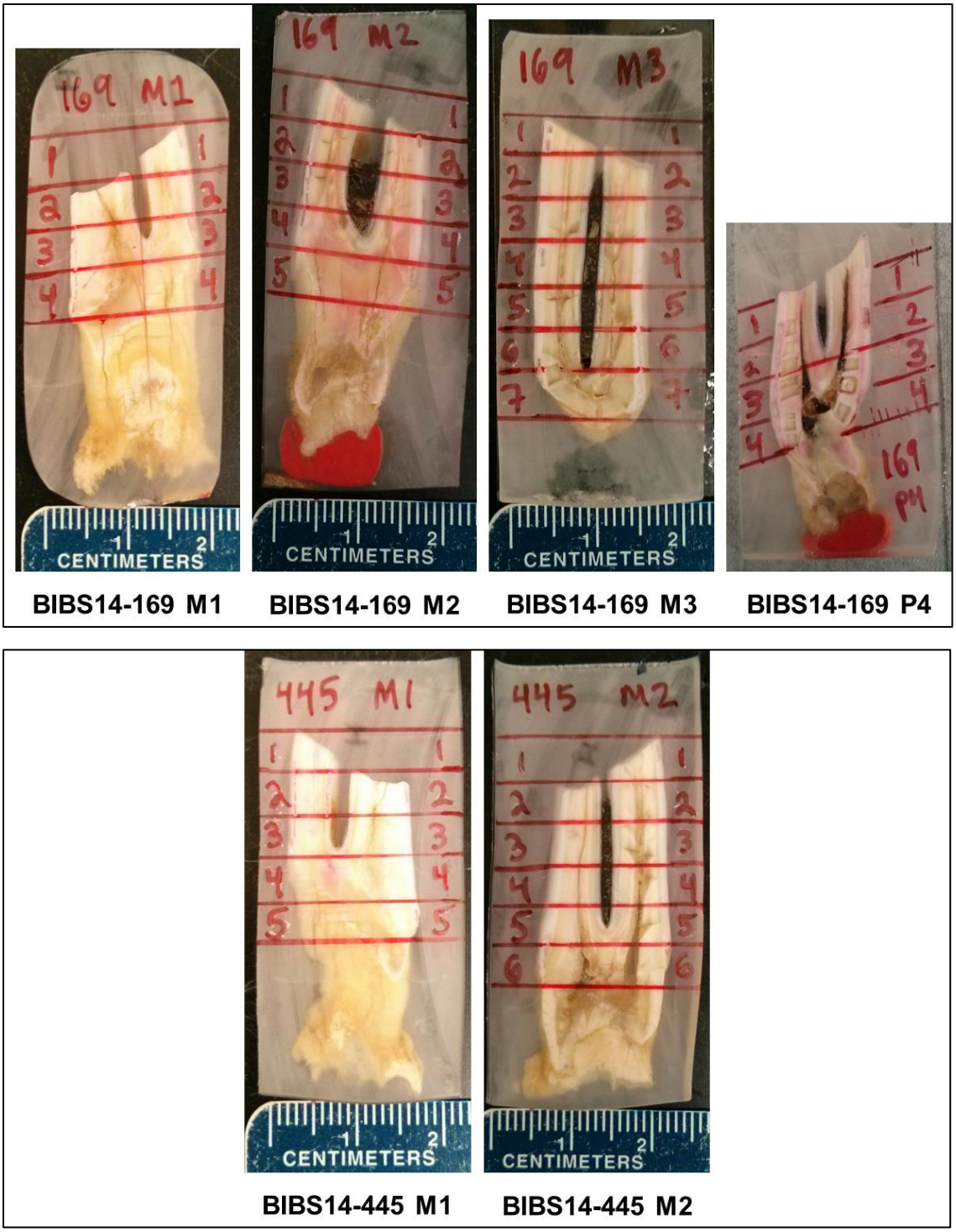


Figure A4. Buccolingual thick sections taken from modern muskox teeth, showing each ~ 5 mm tall microbulk sample ID (e.g. “1”, “2”, “3”, “4”).

Appendix B

Figure B1. Buccolingual thick sections taken from archaeological caribou teeth, showing each ~ 5 mm tall microbulk sample ID (e.g. "1", "2"). Micromilled spots on the enamel, used for enamel structural carbonate $\delta^{13}C$ and $\delta^{18}O$ analysis (Chapter 4), are visible on each thick section.

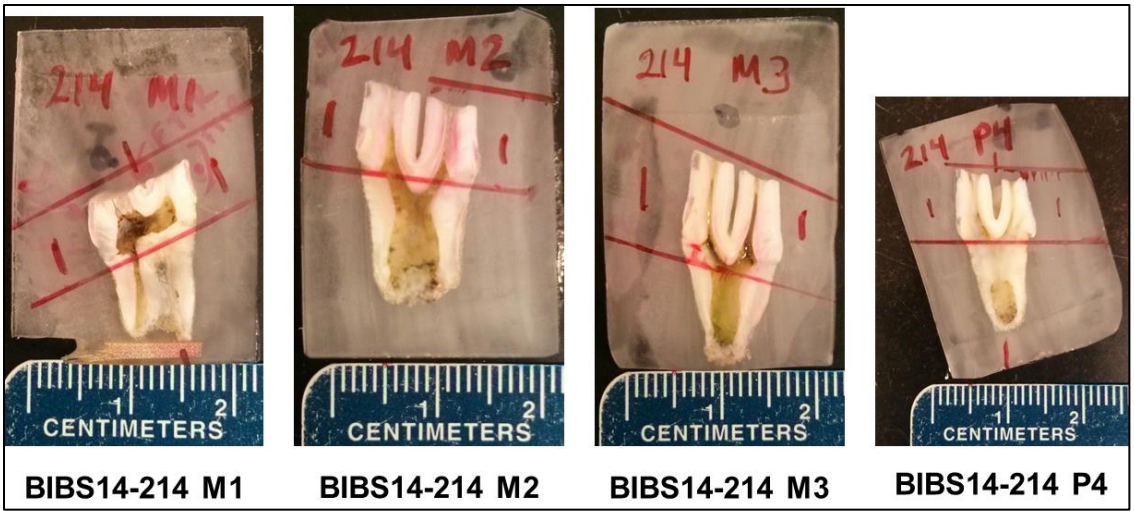
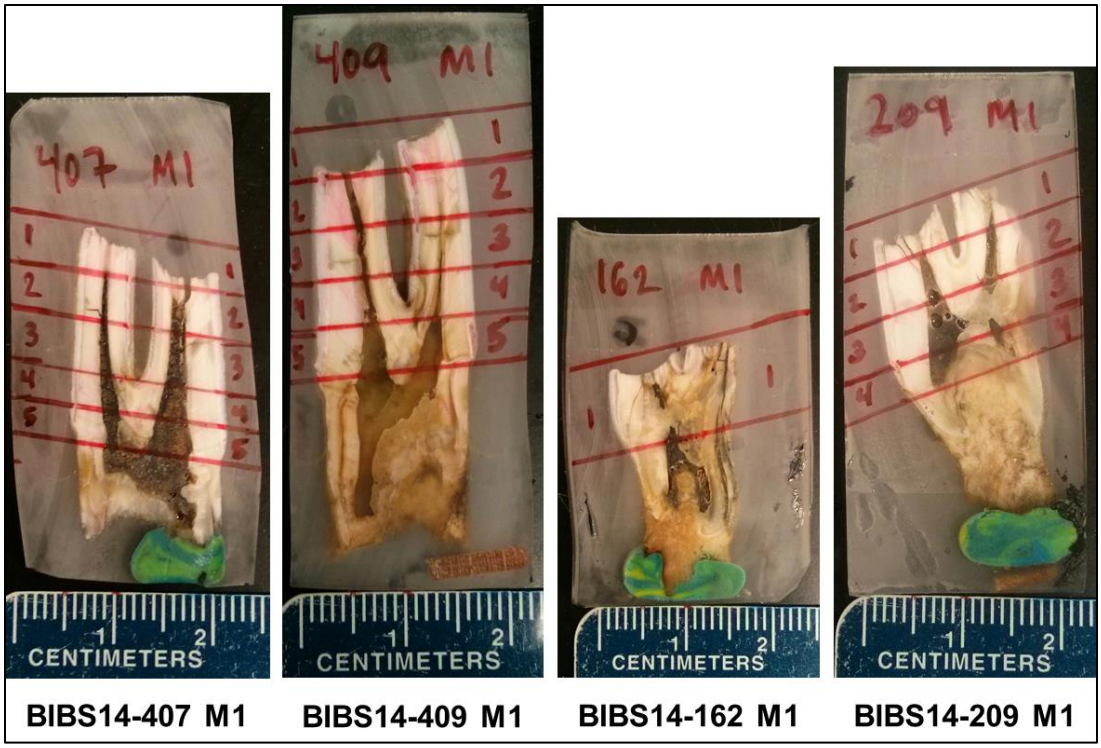


Figure B1 continued.



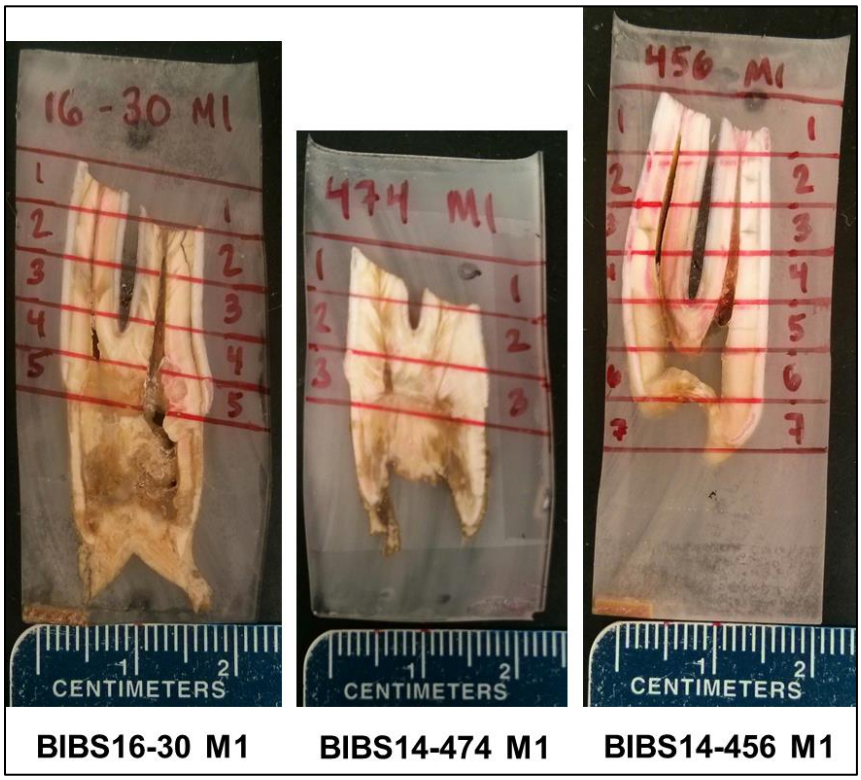
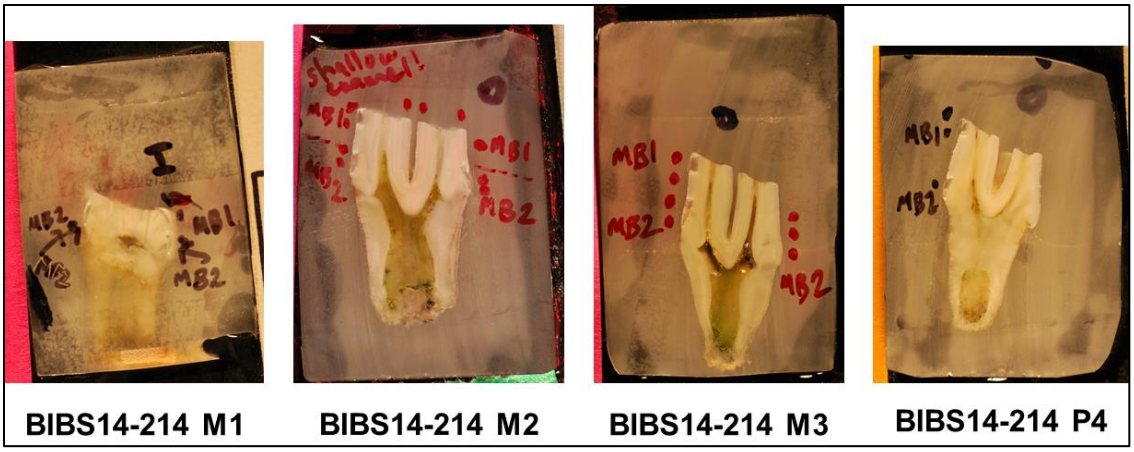


Figure B2. Buccolingual thick sections taken from archaeological muskox M1s, showing each ~ 5 mm tall microbulk sample ID (e.g. “1”, “2”, “3”, “4”).

Appendix C

Figure C1. Buccolingual thick sections taken from modern and archaeological caribou teeth, showing micromilled spots on the enamel used for FTIR and structural carbonate $\delta^{13}C$ and $\delta^{18}O$ analysis.



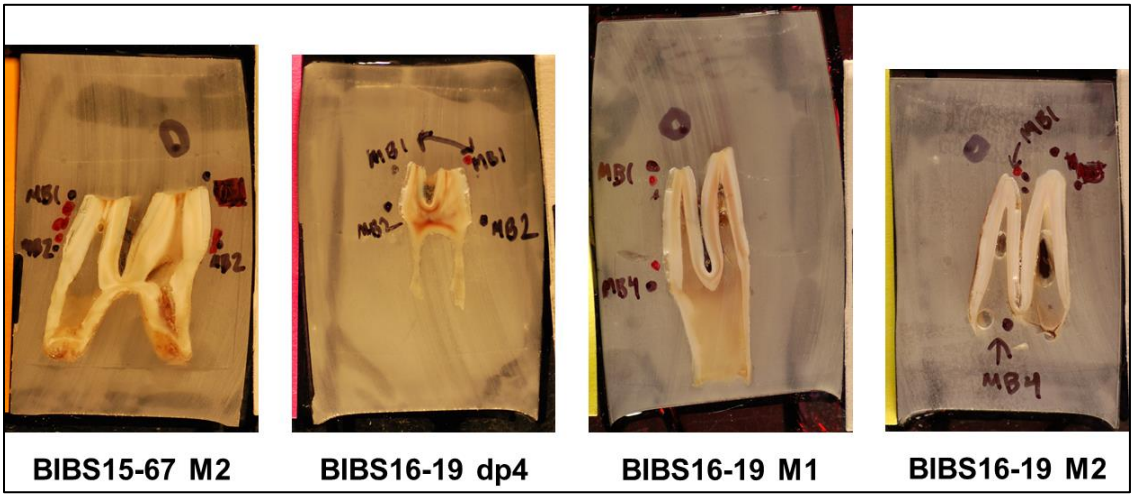
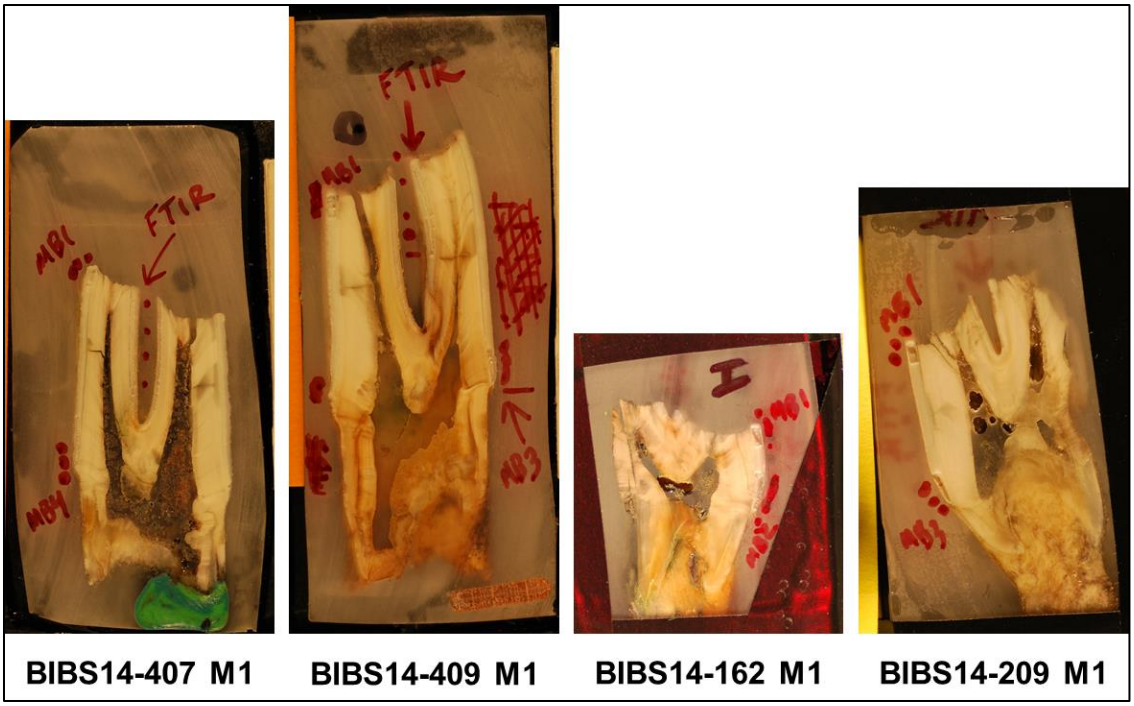


Figure C1 continued.



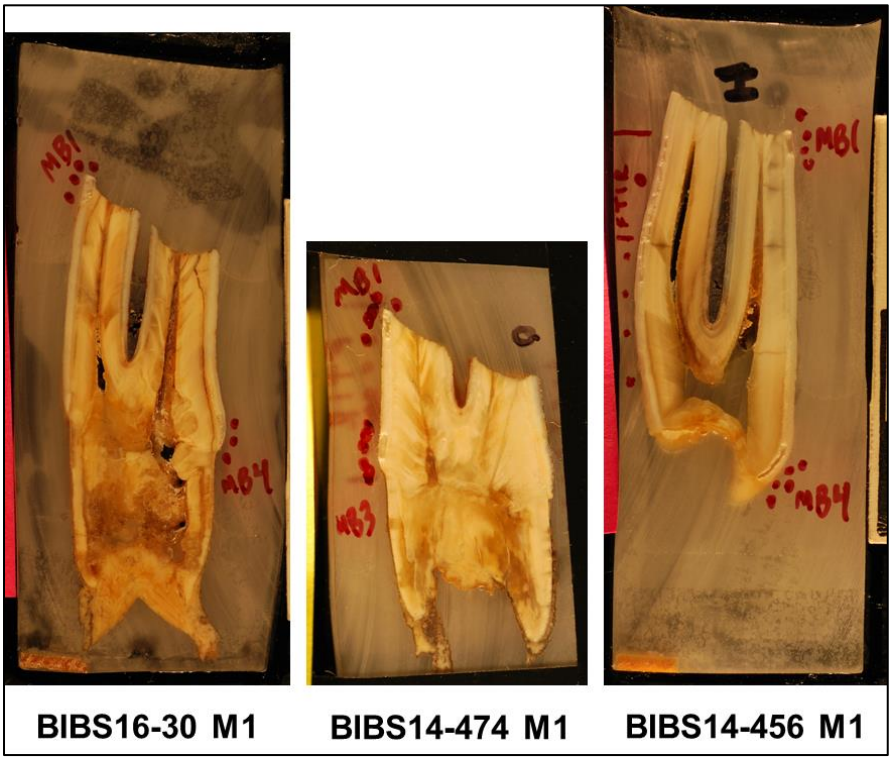


Figure C2. Buccolingual thick sections taken from modern and archaeological muskox M1s, showing micromilled spots on the enamel used for FTIR and structural carbonate $\delta^{13}C$ and $\delta^{18}O$ analysis.

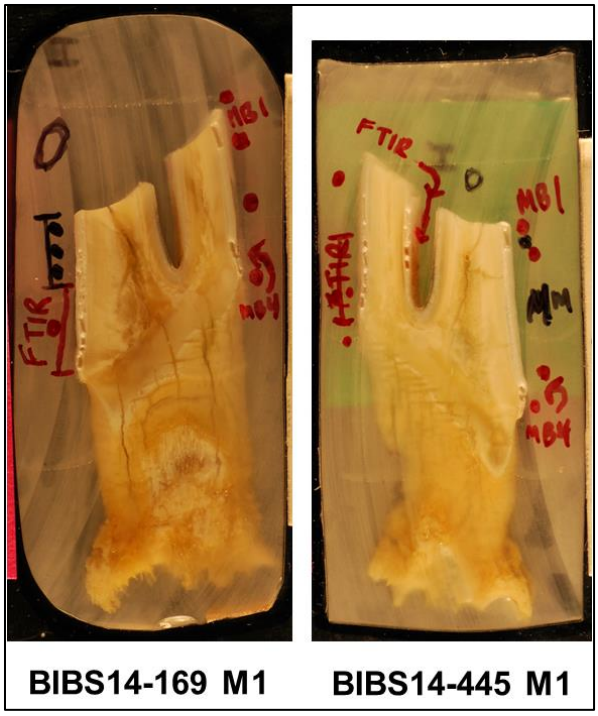


Figure C2 continued.

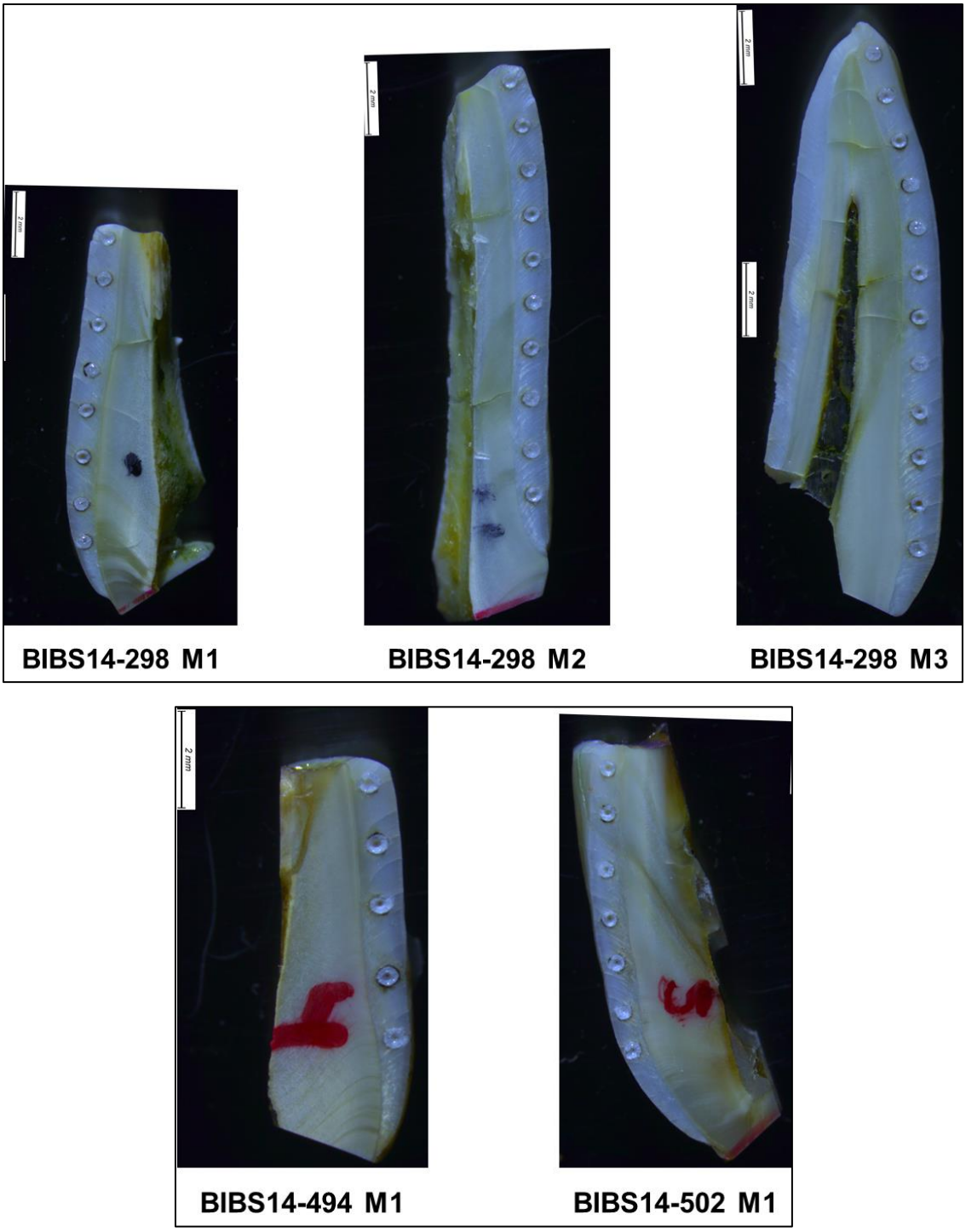


Figure C3. Enamel slices from modern and archaeological caribou buccolingual tooth thick sections, showing ablation spots. Spots were ablated starting at the apex/occlusal surface and moving towards the cervix/root-enamel junction (REJ).

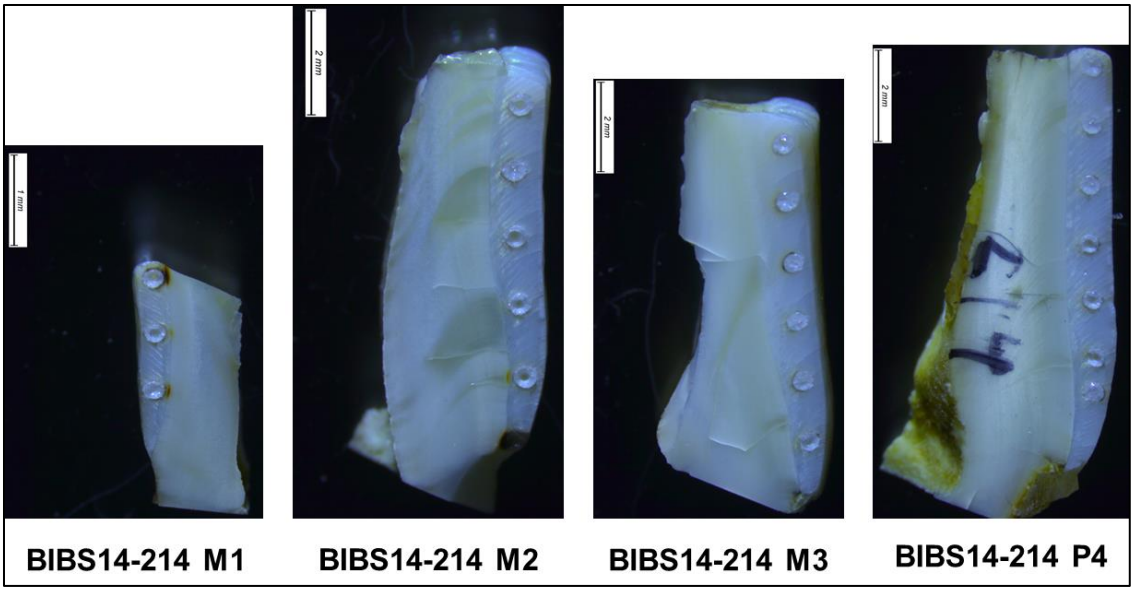


Figure C3 continued.

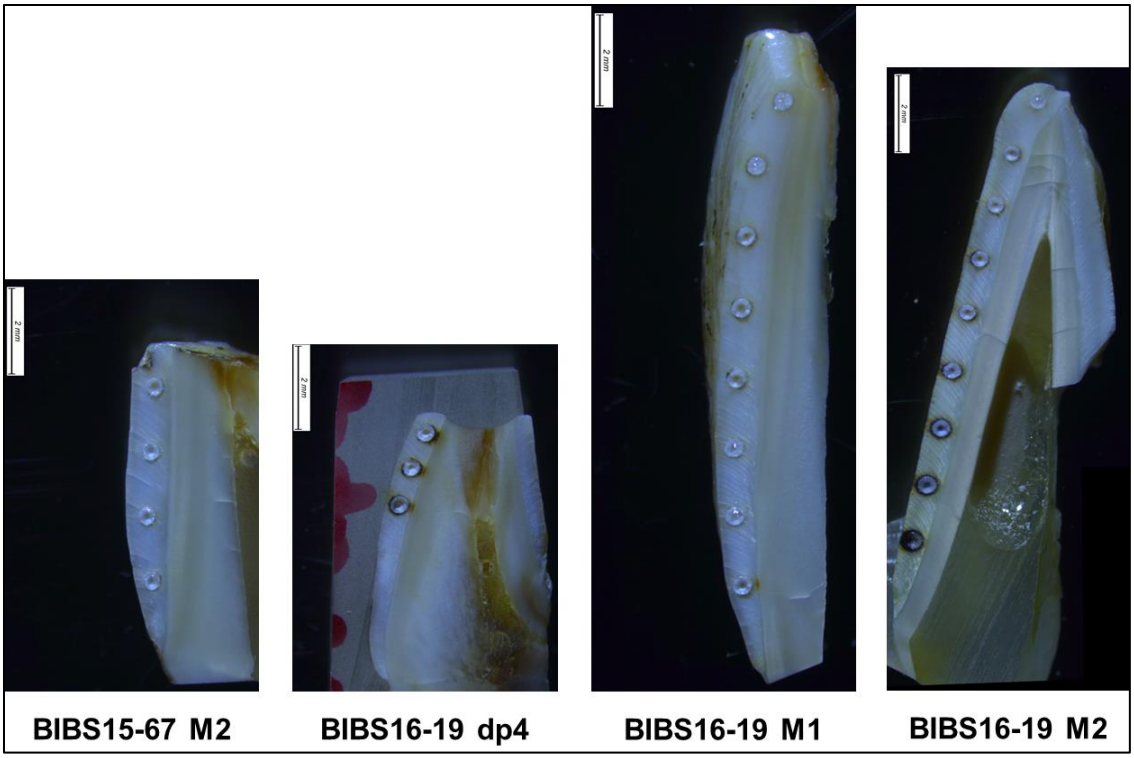


Figure C3 continued.

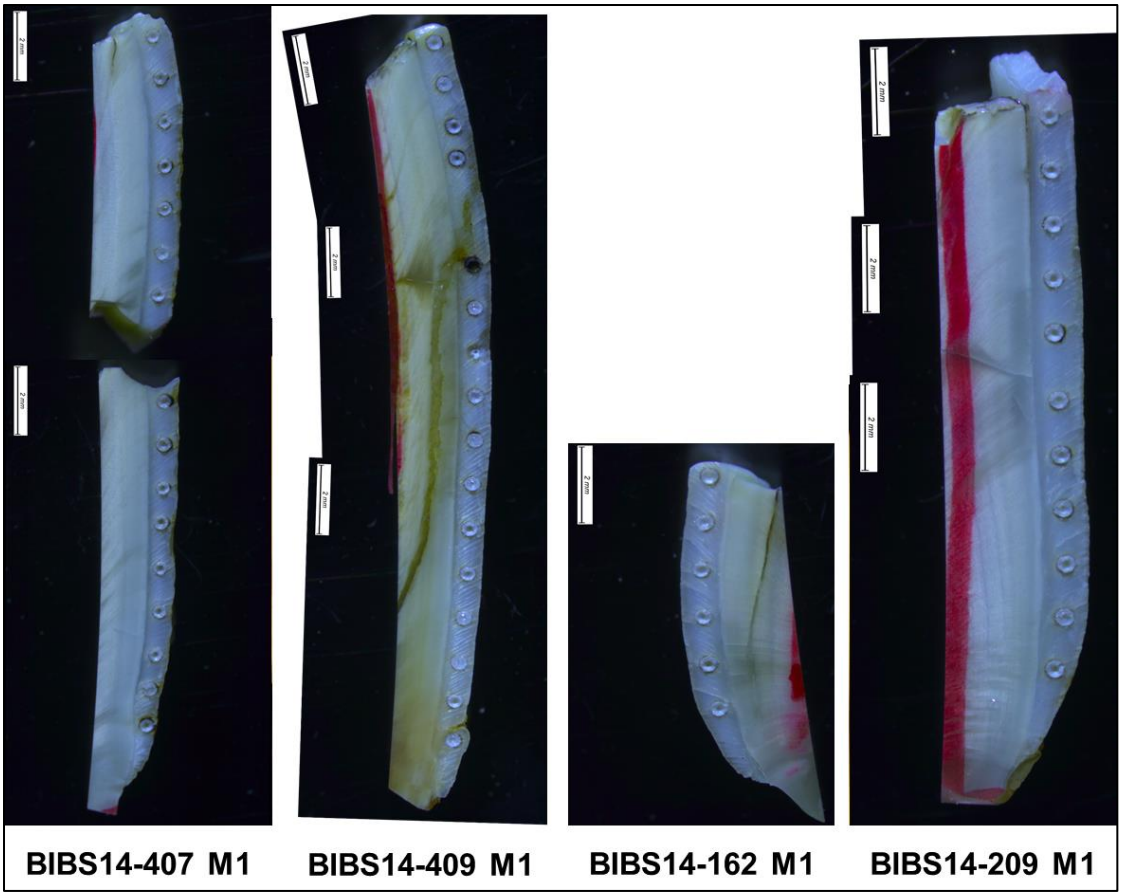


Figure C4. Enamel slices from modern and archaeological muskox buccolingual M1 thick sections, showing ablation spots. Spots were ablated starting at the apex/occlusal surface and moving towards the cervix/root-enamel junction (REJ).

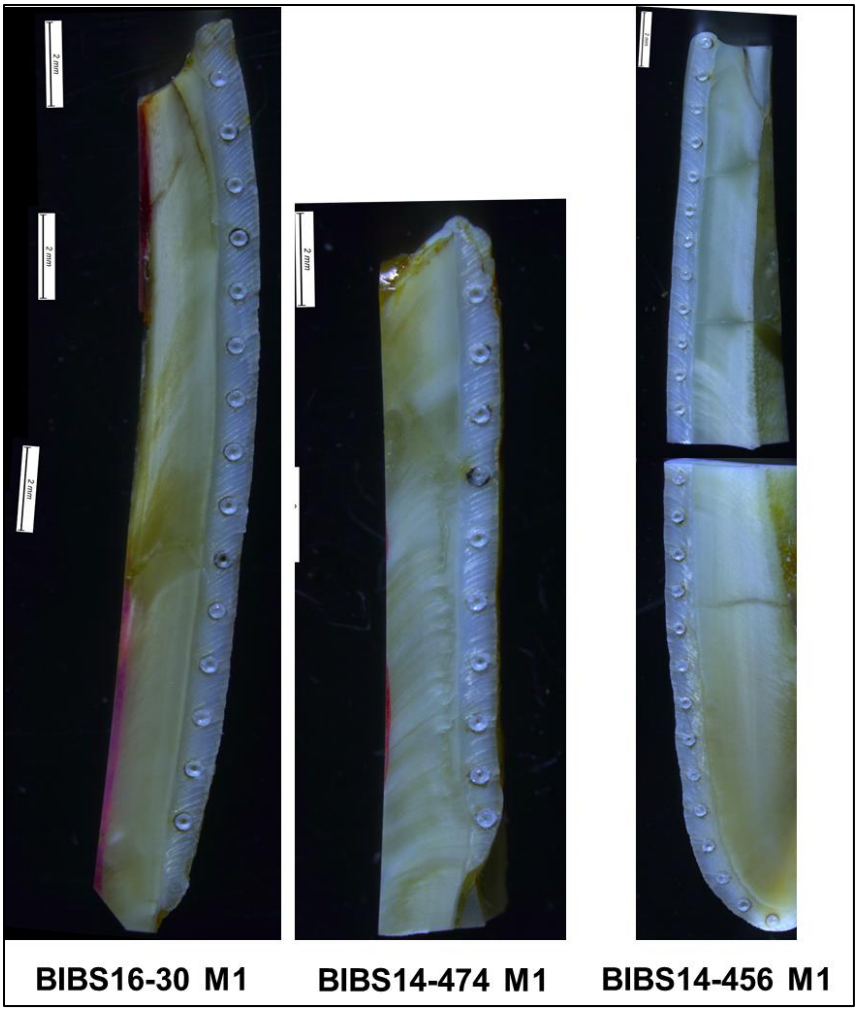


Figure C4 continued.

Figure C4 continued.

Curriculum Vitae

Name:	Jordon Simon Munizzi
Post-secondary Education and Degrees:	The University of Western Ontario London, Ontario, Canada 2013-2017 Ph.D. The University of Central Florida Orlando, Florida, USA 2011-2013 M.A. The University of Central Florida Orlando, Florida, USA 2006-2011 BA with Honors in the Major.
Honours and Awards:	University of Western Ontario Graduate Research Scholarship 2013-2017 Arctic Institute of North America Grant-In-Aid 2015 University of Western Ontario Graduate Research Award Fund 2015
Related Work Experience:	Contract Analytical Technician Laboratory for Stable Isotope Science The University of Western Ontario July to October 2017 Contract Laboratory Technician Laboratory for Stable Isotope Science The University of Western Ontario October to December 2017 Research Assistant Department of Anthropology The University of Western Ontario 2016-2017 Teaching Assistant

Department of Anthropology
The University of Western Ontario
2013-2017

Laboratory Research Associate
Laboratory for Bioarchaeological Sciences
University of Central Florida
2012-2013

Teaching Assistant
The University of Central Florida
2011-2013

Internal Technical Memoranda:
Munizzi J, Moreiras D, Huang L, Longstaffe FJ. 2016. Laser Ablation of Tooth Enamel Using LA-GC-IRMS. On File at Laboratory for Stable Isotope Science, The University of Western Ontario.

Moreiras K, Munizzi J. 2016. Embedding, Sectioning and Micromilling of Teeth For Isotopic Analysis. On File at Laboratory for Stable Isotope Science, The University of Western Ontario.

Munizzi J, Huang L, Law K. 2016. Operation of the EA-IRMS in Continuous Flow Mode. On File at Laboratory for Stable Isotope Science, The University of Western Ontario.

Munizzi J, Moreiras D, Webb E, Szpak P, Olsen K, Morris Z. 2015. Collagen Extraction Protocol for Isotopic Analysis. On File at Laboratory for Stable Isotope Science, The University of Western Ontario

Munizzi J. 2013. Freeze Drying Carbonate via Manifold for Stable Isotope Analysis. On file at Laboratory for Bioarchaeological Sciences, University of Central Florida.

Field Reports:
Hodgetts L, Munizzi J. 2015. The Ikaahuk Archaeology Project: 2014 Fieldwork in Aulavik National Park. On file at Parks Canada Western and Northern Service Centre, Winnipeg.

Hodgetts L, Eastaugh E, Munizzi J. 2015.The Ikaahuk Archaeology Project: Report of the 2014 Field Season. On file at Prince of Wales Northern Heritage Centre, Yellowknife.

Short Courses Taught:
Contemporary Approaches to Isotopic Data Analysis in R

The University of Western Ontario
May 10-11, 2017

Service to Profession:
Bioarchaeology Editor
The University of Western Ontario Journal of Anthropology Volume 24

Manuscript Reviewer
The University of Western Ontario Journal of Anthropology Volume 22 and 23

Grant Application Reviewer
The University of Western Ontario Northern Awards Committee