Palaeodiet and Infant Feeding in Coastal Arctic Settlements

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For my father, Don Harris

Abstract

This dissertation research employs biomolecular methods (stable isotope analysis, ancient DNA, amino acid analysis) to study the day-to-day activities that sustain human societies in the arctic and subarctic environments of North America and Siberia. Maintenance activities, such as food preparation, childcare, and the care of domestic animals, are commonly inflected by social identity and can provide insight into the experience of gender among archaeological populations. The dissertation is comprised of five manuscripts: a methodological paper presenting a best practice for the pre-treatment of arctic bone samples; a review of stable isotope studies of Arctic populations; and three bioarchaeological applications that variously employ stable isotope analysis, ancient DNA, and isotopic analysis of amino acids to examine dog provisioning and infant feeding practices in the North American and Siberian Arctic.

The isotopic evidence for dog diets largely corresponded to zooarchaeological and ethnographic evidence for local subsistence practices. Dog bones dating to between the 15th and 19th centuries, from coastal Labrador, Canada, carried a strong marine isotope signature as did dog furs collected during the early 20th century in Greenland, coastal Labrador, and Alaska. Dogs living among reindeer herders in early 20th century Siberia consumed terrestrial protein sources, while those on the Kamchatka Peninsula consumed terrestrial protein supplemented by limited quantities of salmon. Dog provisioning required considerable human labour and was an important structuring component of daily life in the Arctic.

The final manuscript presents the first study of infant feeding practices among prehistoric hunter-gatherers of the Bering Sea coast. This study used stable isotope analysis of bulk collagen from dentine increments to show that breastfeeding and weaning practices varied considerably across the sampled group. The novel isotopic analysis of amino acids from dentine indicated that amino acids, such as lysine, that are routed directly from collagen, show promise for distinguishing between the dual influences of dietary change and systemic stress on human nitrogen isotope values.

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Author's declaration

I declare that this thesis is original work and I am the sole author. This work has not been presented previously for an award at this, or any other university. All sources are acknowledged as references. The work carried out as part of this thesis has resulted in the following publications:

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Chapter 1: Introduction

This thesis is focused on the North American Arctic and Chukotka, Siberia during the late Holocene (~500–1900 CE). The Neo-Inuit tradition developed from cultural antecedents, the Old Bering Sea, Punuk and Birnik cultures, around the Chukotka and Alaskan coast of the Bering Sea, and during the second millennium (CE), spread eastward to the Canadian Arctic Archipelago, Greenland, and Labrador where it diversified into present-day Inuit, and in Alaska and Siberia, Yup'ik/Yupiget communities (Friesen, 2016; Friesen and Arnold, 2008). This early population expansion was characterized by the development and use of sled dog traction, boating technology, marine mammal hunting and fishing, hierarchical social organisation, varied mortuary traditions, and, likely, gendered division of labour (Braymer-Hayes et al., 2020; Friesen and Mason, 2016; Whitridge, 2016; Bodenhorn, 1990).

Human lives are measured out by the performance of day-to-day tasks that sustain life, also known as maintenance activities. Maintenance activities leave behind archaeological traces in the ways that physical space was used, the use of particular objects, and pathophysiological changes to the human skeleton (Sánchez Romero et al., 2008). Although mundane in nature, maintenance activities track social and technological change and are integrated within larger social systems, presenting an opportunity to study the development of subsistence and ontological systems. The present study takes human-canid dietary relationships and infant feeding practices as a point of departure to examine aspects of daily life in the North American and Siberian Arctic. The following sections present the research aims, objectives and questions that have informed this dissertation.

1 Research aims and objectives

In this PhD, I apply a stable isotope-based approach to the study of maintenance tasks in the North American and eastern Siberian Arctic during the late Holocene. The stable

isotope data are interpreted within a theoretical framework combining standpoint theory and the archaeology of maintenance activities. Using archaeological samples from the North American and Siberian Arctic and Subarctic (Figure 1.1), the research composing this thesis is designed to address three main research aims.

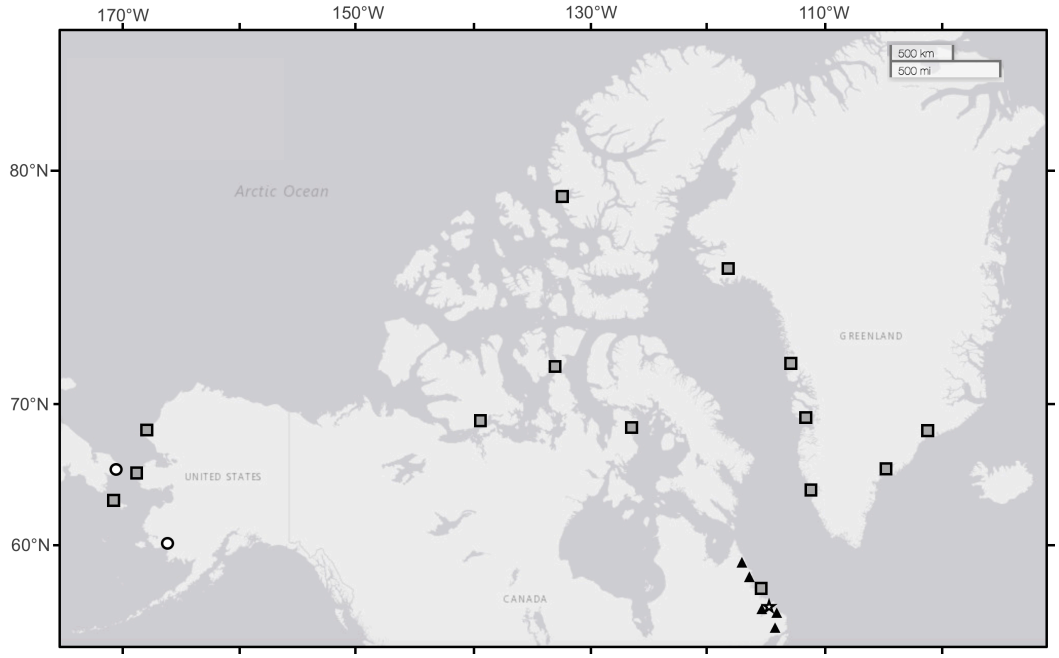

Figure 1.1 Sample locations for the archaeological case studies presented in the thesis. Stars represent the samples in Chapter 2; triangles represent samples in Chapter 4; squares represent the samples in Chapter 5; circles represent the samples in Chapter 6. The dog fur samples from the Polar Urals and Kamchatka Peninsula not shown. Map made using National Geographic Mapmaker Interactive.

1.1 Understand soil humics–bone interactions to improve extraction protocols

Before beginning my analyses, I sought to determine if the destructive analysis of arctic zooarchaeological and osteological assemblages could be minimized through better sampling and sample pretreatment protocols. This aim was achieved by comparing the effects of dilute sodium hydroxide versus ultrafiltration on preservation indicators, stable isotope, and amino acid data from archaeological bone collagen and providing initial chemical characterization of extracted humic substances. I sought to answer the research questions:

> RQ 1) Can a lower concentration of NaOH be used to extract humic acids from bone collagen while simultaneously preserving collagen yields?

RQ 2) Are ultrafilters more or less effective than NaOH at removing humic contaminants from bone collagen?

RQ 3) What are the amino acid and isotopic composition of humic substances extracted from bone?

1.2. Explore reciprocal social and dietary relationships among humans, dogs and other non-human persons in arctic and subarctic societies

As historically the only domestic species in much of the Arctic, dogs occupied a unique social position among Yup'ik and Inuit communities. Dogs played important roles in transportation and hunting and much more rarely were themselves a source of fur and food. Evidence of dog sled traction dating to approximately 8000 BP can be found in far eastern Siberia (Pitulko and Kasparov, 2017, 1996), but the full dog sled traction package did not arise until 1000 BP and facilitated the Neo-Inuit migration across the North American Arctic (Whitridge, 2018). The position of the dog among Arctic societies was not solely dependent on the economic role of the dog; dogs participated in social relationships with humans and with other non-human beings, they received names at birth, and participated in ritual activities (Hill, 2018; Whitridge, 2018; Laugrand and Oosten, 2002). Dog diets are of interest archaeologically because working dogs, particularly those in cold climates, require a high number of calories to sustain life and energy (Lupo, 2019) which makes the labour relationship between Arctic communities and dogs reciprocal. In order to reap the benefits of dog sled traction, dogs had to be regularly supplied with the flesh of other animals.

The first step to achieving this aim involved examining and reviewing the sources of isotopic and dietary variation among Arctic Inuit and Yup'ik populations, including environmental, physiological, cultural, and economic factors. A number of stable isotope studies of Arctic populations have been conducted over the first two decades of the 21st century, but these have not yet been united and considered with respect to current archaeological or zooarchaeological research and biocultural factors that may influence the interpretation of the data. My research questions were:

RQ 4) What is the full range of isotopic variation within and between Arctic populations?

RQ 5) What biological factors should be considered in the interpretation of human isotope data from Arctic groups?

RQ 6) How might food preparation and storage influence human stable isotope data?

Next, I characterised the diets of archaeological Inuit sled dogs between 1450 to 1840 CE in coastal Labrador. These results were further contextualized by comparing domestic dog provisioning practices across the Siberian and North American Arctic in the early 20th century using stable carbon and nitrogen isotope analysis of the furs of genetically identified dogs, wolves, and wild Arctic species. Together these analyses were designed to answer the question:

RQ 7) How do dog diets vary geographically across the Arctic and in relation to their social and economic roles in Arctic societies?

1.3 Examine the interactions between biocultural factors and infant feeding practices of coastal Arctic hunter-gatherers

Modern infant feeding practices in the Arctic are of social relevance due to the relationship that exists between infant nutrition and long term health, however, very little is known about historical infant feeding practices in this region. Oral tradition in the Canadian Arctic and Alaska, recorded during the mid-20th century, held that infants were breastfed until the second or third year of life (Heller et al., 1967; Rasmussen, 1931), but with colonisation came rapidly increasing rates of bottle- and formula-feeding (Maynard and Hammes, 1970). Adoption as a way of uniting kin groups also has a long history in the Arctic (Billson and Mancini, 2007; Bodenhorn, 1990; Rasmussen, 1931) and particular strategies were developed over time to feed newborn infants with non-milk sources of food (Rasmussen, 1931). I aimed to examine the interactions between biocultural factors and infant feeding practices of hunter gatherers affiliated with the Old Bering Sea Culture, in Chukotka. This aim was achieved by analysing dentine collagen and amino acids and contextualising the results against my review of dietary practices in the Arctic. I combined these data with evidence from the Arctic ethnographic record to answer the following questions:

RQ 8) How long were infants breastfed in prehistoric Arctic societies?

RQ 9) What was the duration of the weaning period?

RQ 10) Can the sources of nitrogen isotope variation in infant collagen be better characterised using nitrogen isotope analysis of dentine amino acids?

2 Background

2.1 Historical context

The Arctic was one of the last places on the planet to be occupied by humans. Successful habitation of these environments required cultural developments, such as dog sledding, warm fur clothing, and specialized technology for harvesting and storing marine resources. The Arctic does not represent a single, uniform environment, but includes a range of ecoregions and biological communities. The archaeological record reveals some shared characteristics among northern cultures, such as a reliance on marine species, dog domestication, and boating technology, but like the varied environment, Arctic cultures were, and are, diverse, with specific subsistence practices and social organization. The following section provides an introduction to the archaeological history and environment of the North American and eastern Siberian Arctic.

2.1.1 Chukotka, Siberia

The culture history of the Siberian coast of the Bering and Chukchi Seas is complex and the relationships between the archaeological cultures are difficult to disentangle with archaeological and chronometric evidence. This is due, in part, to poor chronometric hygiene, uncertainties in determining the local deviation in the marine radiocarbon reservoir in the region, sea level rise, and to the practice of subsistence digging and amateur archaeology that disturbed some critical archaeological contexts (Mason and Rasic, 2019; Mason, 2016a).

The maritime adaptations that were characteristic of North American Inuit and Yup'ik populations first arose among cultures of the Bering Sea coast. The earliest ancestral Asiatic Yup'ik sites were found along the eastern coast of Chukota (Bronshtein et al., 2016). The Yup'ik may have descended from the Palaeo-Inuit Denbigh Flint Complex (Flegontov et al., 2019), or Chukchi Archaic, but a clear cultural link is absent, and no human skeletal remains attributed to earlier Chukotka cultures exist to test this hypothesis (Mason and Rasic, 2019). The present study focuses on

the Old Bering Sea (OBS) culture, and in particular, on the mortuary site of Ekven (Fig. 1.2). The OBS represents the first fully marine adaptation in Northeastern Siberia and is known through archaeological and genetic evidence to be ancestral to present-day Asiatic Yup'ik, Alaskan Yup'ik, and Inuit populations in Canada and Greenland (Flegontov et al., 2019; Fitzhugh, 2016; Raghavan et al., 2014; Ackerman, 1998). Although single artefacts have been located in Alaska, to date all unequivocal OBS sites are situated on the northeastern coast of Chukotka, and on St. Lawrence Island. Early expressions of OBS, known as Okvik, date to ~500 CE and are found on St. Lawrence Island and at Uelen, Chukotka (Mason, 2016a). The majority of human mortuary activities at Ekven appear to date between 600–1000 CE (Dury et al., in prep). The OBS possessed a complete marine mammal hunting tool kit that featured umiaq and kayak, toggling harpoons, and floats. It is a matter of some debate as to whether the intended prey was walrus (*Odobenus rosmarus*) or bowhead whale (*Balaena mysticetus*) (Mason and Rasic, 2019). The skeletal remains of ringed seal (*Pusa hispida*), geese, and reindeer (*Rangifer tarandus*) do occur on OBS sites, but the large size of many walrus ivory harpoon heads recovered from Ekven makes it clear that this culture was capable of targeting larger and more dangerous prey (Arutiunov and Sergeev, 1975). Drawing on the extensive use of walrus ivory, the types of hunting implements, and the presence of walrus skeletal remains at OBS sites, Mason and Rasic (2019) and Hill (2011) argue that walrus played a central role in both OBS subsistence and cosmology. Bowhead whale hunting may also have occurred as whale bones feature prominently in dwelling and grave construction, and baleen vessels and nets have also been recovered from Ekven (Gusev and Zagoroulko, 1999; Arutiunov and Sergeev, 1975). Subsistence practices of the OBS people may have varied with site location; on St. Lawrence Island, OBS settlements were situated near walrus haul outs, while bowhead whales may have featured heavily in the subsistence of communities located on the Bering Sea coast of the Siberian mainland (Mason and Rasic, 2019; Whitridge, 1999; Mason, 1998).

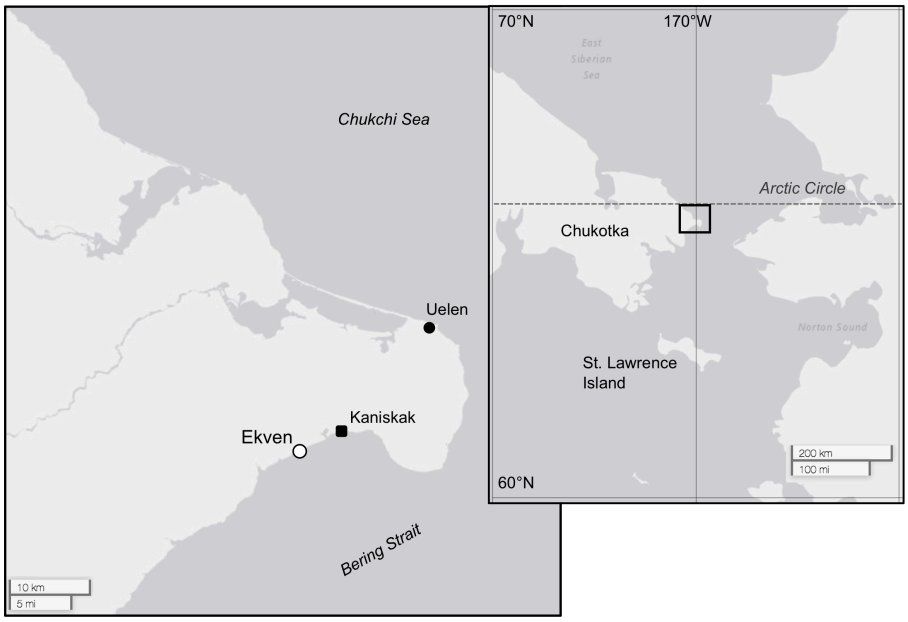

Figure 1.2. Map of Chukotka with Ekven and two other sites mentioned in the text. Map made using National Geographic Mapmaker Interactive.

The OBS was contemporaneous with and overlapped geographically with the Birnik and Punuk archaeological cultures. The relationship between these three is uncertain. For example, at Ekven, Birnik and OBS artefacts co-occur in graves (Arutiunov and Sergeev, 1975). While Birnik sites tend to be smaller and are found on both the Siberian and Alaskan coasts, what appears certain is that these archaeological cultures do not represent separate populations. Whitridge (1999) suggests that the Birnik developed out of the OBS. As the OBS population grew and became increasingly specialized whale or walrus hunters, some families travelled into uninhabited coastal lands where they relied upon a more general subsistence base (Whitridge, 1999). The harvest of large marine mammals, such as bowhead whales, is facilitated by cooperation between families and communities, and the smaller Birnik settlements, often composed of single-family dwellings, make it unlikely that whaling was a regular activity (Mason, 2016b; Whitridge, 1999). Punuk sites were broadly contemporaneous with both OBS and Birnik, but late dates also occur in the 14th century (Whitridge, 1999). Punuk sites occur along the southern Chukotka coastline and on St. Lawrence Island (Mason 2016b). The Punuk may have been engaged in warfare or conflict to a greater extent than other groups as slat armour and bow and arrow technology, derived from Siberian populations further south, occur in archaeological assemblages (Mason, 2016b; Whitridge, 1999).

2.1.2 Labrador, Canada

Approximately 800 years ago, the ancestors of present-day Inuit and Yup'ik peoples rapidly expanded from the Bering Sea across the North American Arctic (Friesen and Arnold, 2008). Using skin-covered boats, dog sled traction, and relying on the marine mammals for food and raw materials, they settled in a variety of environments in Greenland and Arctic Canada, reaching as far south as the Quebec Lower North Shore, in Subarctic Canada. In some regions, they encountered other Indigenous populations, and may have even supplanted local Pre- or Palaeo-Inuit groups (Raghavan et al. 2014). These early explorers and settlers of the North American Arctic developed sophisticated material culture for harvesting and storing a variety of food types; they maintained extensive trade and social networks, and had complex relationships with the dead that were expressed through varied mortuary ceremonialism; some communities engaged in regular seasonal mobility, while others were more sedentary (Friesen, 2016; Savelle, 2002; Whitridge, 1999).

Beginning at least 6000 years prior to the arrival of the Inuit, in the 15th century CE, the Labrador coast was inhabited by several other Indigenous populations, represented by the Labrador Archaic, Pre-Dorset and Dorset archaeological cultures. The Archaic Period is dated from 5500–1550 BCE but may actually extend further into the past (Fitzhugh, 2006; Tuck and Mcghee, 1975). The onset of the Archaic occupation may coincide with a period of climate amelioration, while the disappearance of the Labrador Archaic culture is associated with a period of cooling temperatures (Rosenberg et al., 2005; MacPherson, 1981) and the arrival of the people of the Palaeo-Inuit tradition (Fitzhugh, 1977). The Palaeo-Inuit were mobile hunter gatherers with cultural and genetic roots in eastern Siberia who migrated across the eastern Arctic approximately 4000 years ago (Flegontov et al., 2019; Sikora et al., 2019; Raghavan et al., 2014; Renouf, 1993). They were a marine-adapted group, very distantly related to Inuit (Raghavan et al., 2014). The Palaeo-Inuit occupation of coastal Labrador may have disappeared between 800 and 700 years ago (Appelt et al., 2016).

The ancestors of the Labrador Inuit reached northern Labrador by the mid-15th century (Whitridge, 2016, 2012; Kaplan, 1983). By the 17th century, Inuit had at least established seasonal occupations in southern Labrador and the Quebec Lower North Shore (Fitzhugh, 2016, 2015; Rankin, 2015; Stopp, 2002). Archaeological traces of

these early Inuit settlements are found in the outer coastal areas of Labrador, and also on the shores of Nachvak Fiord (Fig. 1.3). Inuit constructed small, sometimes multi-lobed, semi-subterranean houses, and from these settlements, hunted large whales, multiple species of seal and fish, and some terrestrial species, such as caribou and furbearers (Kaplan and Woollett, 2016).

Figure 1.3. Labrador, Canada, and locations mentioned in the text. Map made using National Geographic Mapmaker Interactive.

From the 16th century to the present day, Labrador Inuit participated in an increasingly dynamic social environment. They shared the landscape with local Innu populations, and in the 16th century, came into indirect contact with Basque whalers and French fishers. In their pursuit of Atlantic cod (*Gadus morhua*) and bowhead whales, European fisherfolk established shore stations along the southern coast of Labrador (Pope, 2015; McLeod et al., 2008; Rastogi et al., 2008; Stopp, 2002; Barkham-Huxley, 1984). In the mid-18th century, the Moravian Church was granted 100 000 acres of land in Northern Labrador, and established mission stations at Nain (1771), Okak (1776) and Hopedale (1782) to Christianize the Inuit and regulate Inuit-European interactions.

The presence of Europeans in place like Hamilton Inlet may have prompted a number of changes to Inuit culture. Inuit were able to diversify their toolkits with European-manufactured materials, such as iron nails and hardwood, either through trade or by collecting these items from European fishing stages following their seasonal abandonment (Rankin and Crompton, 2016a; Jordan, 1978). Powerful Inuit traders moved French and English goods north and Inuit-harvested raw materials, such as baleen, whale and seal oils, south along the coast (Taylor, 1976). The increasing hunting pressure by Europeans on local marine mammal stocks may have prompted changes to Inuit social organization, housing, and target species (Crompton and Rankin, 2017; Fitzhugh, 2016; Woollett, 2003), discussed further in Chapter 4.

2.2 Theoretical context

The research in this thesis is inspired by standpoint theory and uses the archaeology of maintenance activities as a way to operationalize the principles of feminist archaeology. Wylie (1997) documents two types of feminist critique in archaeology:

- Content critiques argue that women were erased from earlier narratives of the archaeological and historical past and attempt to make history more inclusive. These can be extended to include other underrepresented groups
- Equity critiques examine the ways in which researchers, students and other stakeholders are actively marginalised in the research process today and the implications for knowledge production

In archaeological discussions of social organisation, gender is often defined in opposition to sex; gender is social construction and performed through activities, personal adornment, dress, economic and reproductive roles, whereas sex is defined categorically by biological characteristics, usually from skeletal remains and, more rarely, using ancient DNA or proteomics (Gilchrist, 2012). Gender is intersectional and tightly integrated within other existing social structures, such as those based on economic status, race, age, ethnicity, ability, health, education, and more (Whitridge, 2002; Hill Collins, 1989). Gender analyses were not regularly conducted in Arctic archaeology prior to the 21st century and there remains considerable scope for research of this topic. Gender analyses of the past are important as they can better

represent the diversity of human experience in the past. As Tarlow (2006, p.214) writes, '...archaeologists should try to ensure that the experiences of a particular and limited set of people are not allowed to represent the whole of their society."

Standpoint theory takes the lives of women and other marginalized individuals as the starting point to academic inquiry. This approach, as championed by Nancy Hartsock, finds its roots in Marxism but has undergone modifications to overcome the androcentric concepts of labour and production (Haraway, 1988). Hartsock (1983, p. 285) argued that reality was structured within a gendered framework that positioned men in the dominant position and women in the subordinate position. The male perspective was partial, but not false as it dictated the structure of everyday life while the female perspective encompassed the reality created by the dominant gender, but conserved an awareness of its oppression (Hartsock, 1983, p. 285) and was thus better positioned to identify patterns in social relations (Wylie, 2013). Since the development of standpoint theory, a number of valid criticisms have been made, most importantly, the original definition of standpoint theory essentialized the experiences of women and did not acknowledge the role that other aspects of personal identity, such as ethnicity, race, economic status, and sexuality, could have in shaping reality (Hill Collins, 1989; hooks, 1989).

Standpoint theory is well suited to the practice of bioarchaeology in the Arctic as it presents an opportunity to create narratives of Arctic history that decenter the, often European, male perspective. Standpoint theory, as a guiding framework, can be used to reject normative views or unspoken assumptions that exist in many disciplines and bias the knowledge production process. Androcentric and western Eurocentric biases are widely apparent in many studies of the archaeology and ethnography of Indigenous cultures. Bodenhorn (1990) contrasted mid-20th century Euroamerican representations of gender dynamics in Yup'ik societies with how these relationships were interpreted by Yup'ik elders. She suggested that western conceptions of gender and sex differences acted as a set of metaphorical blinders for ethnographic and anthropological research from the early 20th century (Bodenhorn, 1990). While labour in Arctic societies was divided along gender lines, the tasks performed by males and females were interdependent and given equal value (Bodenhorn, 1990).

This thesis attempts to make Arctic archaeology more inclusive by focusing on bioarchaeological evidence of women's activities among Inuit and Yup'ik societies. Both my position as an outsider and the context of knowledge production

call for efforts to increase the social relevance of the research. As a feminist archaeologist, it is incumbent upon me to ground my research in gender issues and to address research questions that may be of concern to underrepresented groups (Wylie, 2007). Through representation of a greater diversity of experiences of the past, it may be possible to create more robust knowledge claims in our discipline (Longino, 1987).

This thesis research applies the tenets of standpoint theory using the archaeology of maintenance activities to address several gaps in the archaeological literature of the Arctic. Throughout the life course, we engage in specific activities that reflect our social position, and the archaeological traces of these activities can reveal aspects of identity, such as gender (Whitridge, 2002). Everyday usage of materials and the performance of daily tasks provide one avenue for examining diachronic change in social organisation. In the present study, human-canid dietary relationships (Chapters 4-5), clothing production (Chapter 5), and infant feeding practices (Chapter 6) form the topics of analysis. The care and feeding of human infants and sled dogs are tasks that must be performed daily (and multiple times a day) and these tasks were integrated within larger social systems.

Human lives are measured out by the performance of day-to-day tasks that sustain life, also known as maintenance activities. These include, but are not limited to, caregiving, food preparation, clothing and textile production, dwelling maintenance, care of domestic animals, and hygiene (Sánchez Romero et al., 2008). The context in which these activities occur is usually the domestic sphere, or household. The household is not synonymous with a single-family dwelling but includes built and maintained physical and social environments with their associated material culture and behaviours, or as Meyers (2003, p. 426) puts it, the household is a strategy for human survival. Many of household tasks were (and continue to be) performed by women in the past and the archaeology of maintenance activities has emerged as a useful framework for conducting feminist archaeological research (Rubio, 2011).

Drawing from ethnographic and archaeological data, Table 1.1 breaks down the expression of different household elements among Inuit and Yup'ik societies to show how gender and other aspects of social identity could interact with the archaeological record. The major social unit among Arctic societies varies across space and time. In Alaska, in the early 20th century, a married couple formed the centre of the household network, and children, elders, sled dogs, and other more distant relatives connected

to this central node (Bodenhorn, 1990). In the Canadian Arctic Archipelago during the Classic Thule archaeological phase (1200–1400 CE), umiaq boat crews could be said to be the central social unit as participation in the whale hunt, and ownership of an umiaq were major structuring components of Thule society organization, and were also strongly intertwined with gender (Savelle, 2002; Whitridge, 2002). The material components of Arctic life, such as qariyit and hunting tools have long been associated with gender, but other components, such as storage vessels and processing tools used during the performance of maintenance activities are also imbued with the manufacturer and user. For example, Michelle Davies (2014) analysed the frequency of metal use among traditionally men's and women's tools in Labrador and found that women's tools, such as ulus, tended to conserve traditional materials whereas men's tools were more likely to feature materials obtained from Europeans.

Table 1.1 The expression of household elements (after Meyers, 2003) in Arctic and Subarctic contexts, drawing from ethnographic and archaeological lines of evidence (discussed in the text).

Household element	Arctic/Subarctic expression
Social/demographic unit	Married couple, children, elders, siblings, sled dogs. May include multiple families, e.g. Communal House Phase of Labrador
Material components	Seasonal dwelling (snow house, tent, semi-subterranean sod house); Ritual structures (qariyit), caches, hunting technology, storage vessels, toys, tools, amulets, graves, transportation, etc.
Behavioural components	Food sharing, food preparation activities, manufacturing activities, ritual activities, caregiving, mortuary activities

The present study is concerned more with the behavioural components of maintenance activities, such as food preparation and consumption, and the chemical traces that these leave in human and faunal biological remains. Figure 1.4 summarizes the activities traditionally performed by males and females in Inuit and Yup'ik communities according to ethnographic records from the 20th century.

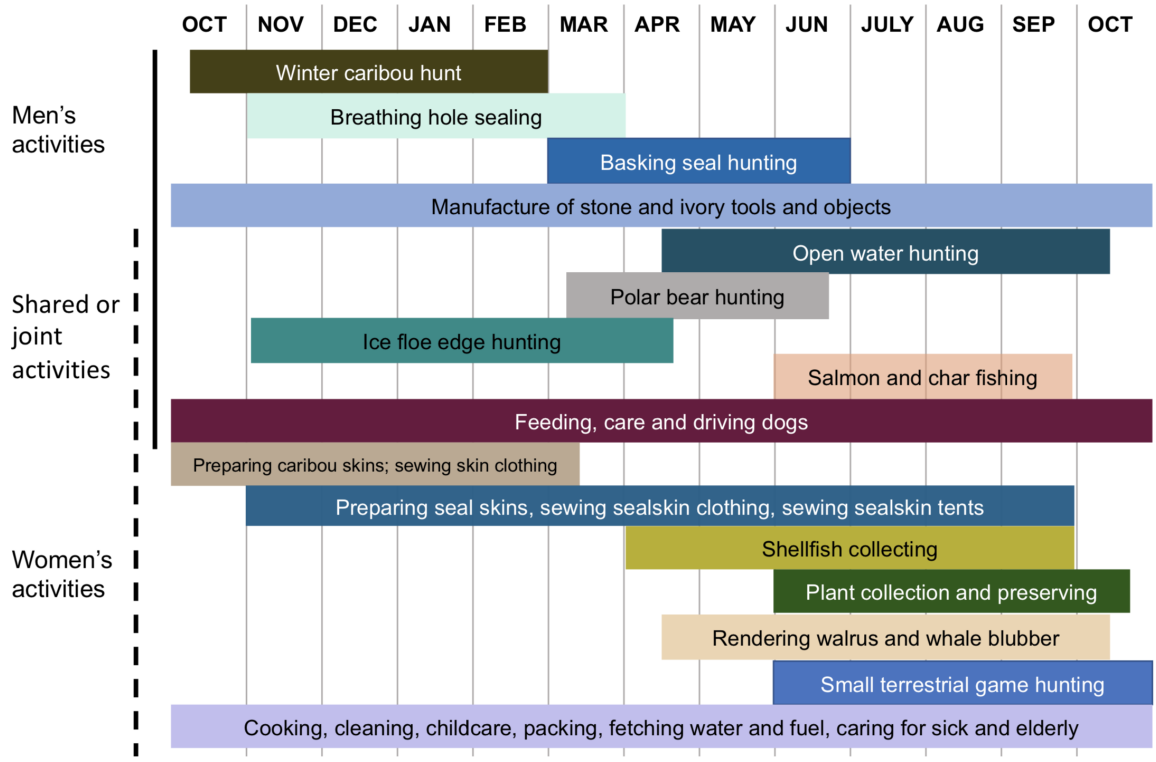

Figure 1.4. A general summary of some of the seasonal productive tasks typically conducted by men and women in traditional Inuit and Yup'ik societies. Image modified from Braymer-Hayes et al. (2020) and Billson and Mancini (2007).

Women's activities were focused around the processing of raw materials for dwelling, clothing, food and food storage, but also included the care of children and elders; traditional male activities were focused on harvesting food resources and other raw materials (Braymer-Hayes et al., 2020; Billson and Mancini, 2007; Bodenhorn, 1990). Males and females shared the care of dog teams, and both genders may have participated in open water and floe-edge hunting, although female participation in these activities likely varied with location (Braymer-Hayes et al., 2020; Zdor, 2010). Figure 1.4 does not include the types of supportive activities, beyond processing skins for umiat and clothing, that were performed by women to ensure a successful hunt. These rituals included observance of food taboos, and other prescribed behaviours and activities (Hill, 2011; Bodenhorn, 1990).

2.3 Methodological context

The following section presents a short summary of the primary methods used in this thesis research. Further details are presented in each chapter and in the supporting

materials provided in the appendices. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope analysis is a commonly used method for estimating the average sources of dietary protein consumed by archaeological human and animal populations. Type I collagen, the dominant protein in bones and teeth, preserves well over archaeological timescales and is an excellent analyte for palaeodietary studies. As shown in Figure 1.5, $\delta^{15}N$ and $\delta^{13}C$ measurements of collagen, presented as delta values using per mil (‰) units, can distinguish marine and terrestrial consumers, and different trophic levels (Schoeninger and DeNiro, 1984). Marine consumers typically have very high $\delta^{13}C$ and $\delta^{15}N$ values relative to terrestrial consumers, but in some marine environments, there can be further separation in the $\delta^{13}C$ values between pelagic (open water) and benthic zones (Szpak et al., 2019; Sherwood and Rose, 2005). Inuit and Yup'ik communities have a long tradition of marine mammal hunting and fishing (Whitridge, 1999), making stable isotope analysis an ideal method for the investigation of past dietary practices.

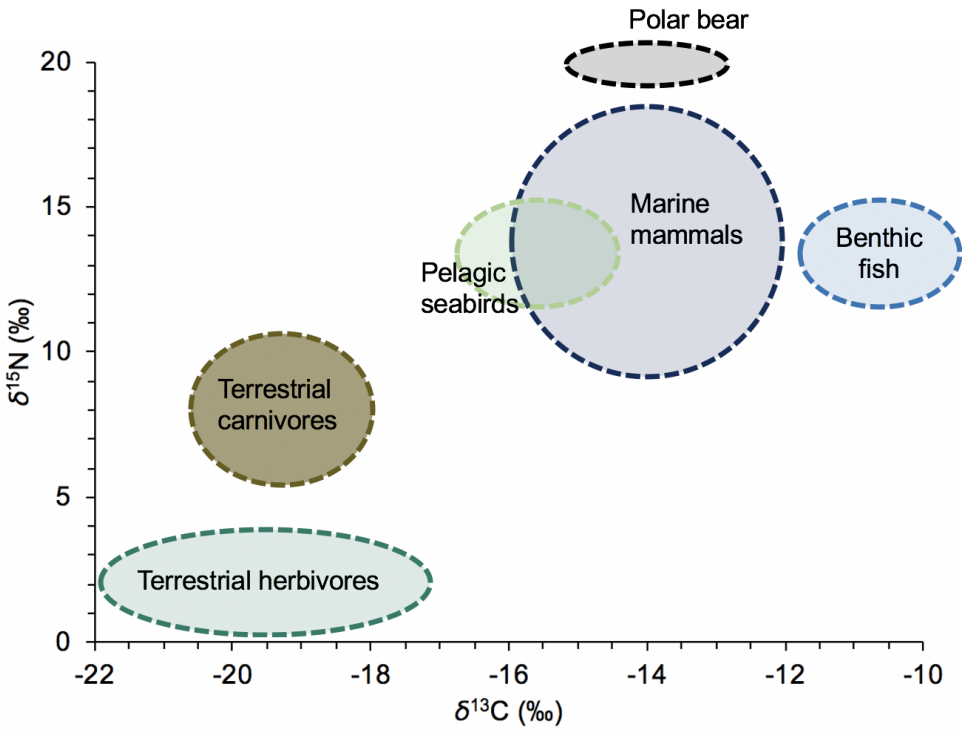

Figure 1.5 Approximate isotopic values for an Arctic food web. Adapted from Britton et al., (2013), Harris et al. (2019), and McManus-Fry et al., (2018)

Humic acid contamination of archaeological bone is a persistent issue in Arctic and Subarctic archaeology. Humic acids, present in the soil, form strong bonds with bone collagen (van Klinken and Hedges, 1995) and cause discolouration (Fig. 1.6), and, as humic acids typically have very low $\delta^{13}C$ values, contamination with these

substances can alter the $\delta^{13}C$ values and radiocarbon ages of archaeological skeletal remains (Stafford et al., 1988). If stable isotope analyses of human and faunal palaeodiet are to be successful, it is imperative that humic acids are removed from collagen prior to its analysis. The published literature is divided on how humic acid-contaminated bone should be pre-treated. Humic acids are low-molecular-weight substances, therefore, ultrafiltration should serve to isolate larger collagen peptides from humic substances (Brown et al., 1988). A recent study by Szpak et al. (2017) suggests that this is not the case, that ultrafilters do not effectively remove humics acids and leaching with sodium hydroxide is the best practice. Sodium hydroxide, usually at a concentration of 0.1 M, is known to cause collagen hydrolysis, leading to reduced collagen yields and concerns that certain amino acids could be more affected than others, which would also lead to an alteration of the biogenic stable isotope values (Lidén et al., 1995). This issue forms the focus of the research in Chapter 2.

Figure 1.6 Archaeological bone from the site of Rattler's Bight, Labrador, Canada, showing extreme contamination with humic substances.

Stable isotope analysis can also be used to investigate infant feeding practices.

Studies of infant feeding practices are of critical importance to archaeology and anthropology as they can shed light on human health, hominid evolution, and the intersection of culture and biology (Jay, 2009). This method relies on the trophic relationship between nursing infants and their mothers (or wet nurses). At birth, the mother and baby have similar $\delta^{15}N$ and $\delta^{13}C$ values, but the ingestion of breastmilk causes infant collagen $\delta^{15}N$ values to increase by +2-3‰ and $\delta^{13}C$ values to increase by ~+1‰ relative to maternal tissue values (Fuller et al., 2006). Following the introduction of weaning foods, infant $\delta^{15}N$ values will decline until they are again similar to maternal values, providing mother and baby have similar diets (Jay, 2009; Fuller et al., 2006; Fogel et al., 1989). This relationship was first determined in modern studies of mother-infant pairs and has also been demonstrated in other primates, and in a range of mammalian species (Reitsema et al., 2016; Fahy et al., 2014, Dalerum et al., 2007; Newsome et al., 2006, Polischuk et al., 2001) The increase in isotopic values with exclusive nursing and the decrease following the introduction of weaning foods has been observed in enough modern contexts (although it remains to be fully understood) that the trophic relationship between mother-infant pairs is now used to interpret isotopic data from archaeological human skeletons.

Archaeological breastfeeding studies began by comparing the $\delta^{15}N$ values of different osteological age cohorts in skeletal assemblages (Jay, 2009). These studies identified the onset of weaning as the point at which the majority of individuals showed a decline in $\delta^{15}N$ values and the conclusion of weaning as the point at which most individuals had isotopic values that were similar to the adults in the same population (Jay, 2009). This approach contained several sources of uncertainty. For example, were those who died during infancy or early childhood representative of all individuals at that age, or could ill health or different feeding practices bias the isotopic data?; did the relatively slow turnover rate of collagen affect estimations of weaning age?; how did the changing rate of infant growth affect the isotopic composition of bone collagen at death? were the average bone collagen isotope values of adults representative of the diets of pregnant and lactating women? (Reynard and Tuross, 2015; Millard, 2000;).

One means of dealing with some of these sources of uncertainty emerged in the first decade of the 21st century. The primary dentine of human teeth grows in conical layers (Hillson, 2005), and once fully formed, does not undergo subsequent collagen turnover as is common in other hard tissues of the human body (Nanci, 2003). This

means that the isotopic signature of infant diet is retained in the teeth of all adults, and that the childhood diets of those who survived infancy and childhood could be determined from the skeletal remains of adults. Sampling protocols that follow the growth lines in dentine, or take horizontal samples from tooth roots, can track dietary inputs at particular moments in time during an individual's childhood (Czermak et al., 2018; Beaumont and Montgomery, 2015).

Incremental sampling of human teeth can also reveal aspects of maternal diet, something that, in the past, was inferred simply by taking the mean isotopic values of adult biological females in a skeletal assemblage. Deciduous molars begin to form in utero and finish growing during the fourth year of life (Al Qatahni et al., 2010). While in utero, these teeth incorporate isotopic signals from maternal diet and thus can be used to analyse dietary and physiological inputs during the third trimester (Beaumont et al., 2015). Figure 1.7 shows the carbon and nitrogen isotopic profiles of Burial 279 from the Old Bering Sea site of Ekven in Chukotka. The data were obtained by slicing a deciduous first molar into 1 mm horizontal sections (after Beaumont et al., 2013). Over the last trimester, infant δ^{15}N values were consistent at +22.9‰. This value is +2.5‰ higher than the mean female bone collagen δ^{15}N value of +20.4‰. This suggests that either the female mean does not reveal possible seasonal fluctuations in diet, or that this pregnant individual may have experienced physiological stress that temporarily shifted her nitrogen balance (Beaumont et al., 2015; D'Ortenzio et al., 2015; Neuberger et al., 2013; Mekota et al., 2006; Fuller et al., 2005). Shortly after birth, the tooth δ^{15}N values began to rise, hitting a peak of +23.8‰ at approximately 1.5 years of age. Following this peak, the tooth δ^{15}N values declined to +22.9‰, potentially indicating the onset of the weaning process. The tooth δ^{15}N values stabilised shortly after the age of two years, and within several months of weaning, the individual died. Additional information can be obtained by examining the δ^{13}C values. Between the samples that formed during the last trimester and birth, the δ^{13}C values of the infant increased by +0.6‰, this may indicate a change in maternal diet over this period. Infant δ^{13}C values then remained static until the completion of weaning (indicated by the δ^{15}N values), when they fall by –0.4‰.

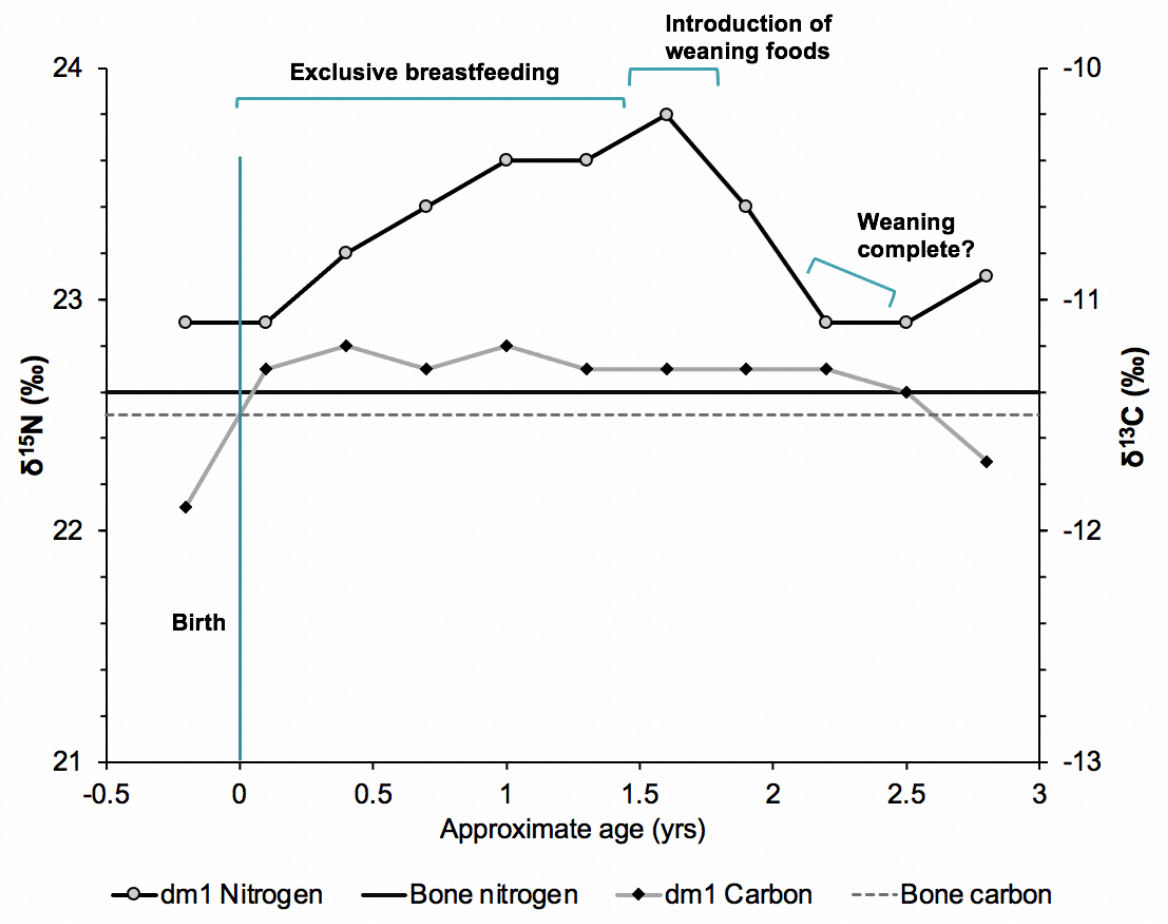

Figure 1.7 A plot of tooth δ^{15}N values vs age from a sequentially sampled deciduous first molar from Burial 279, Ekven, Chukotka. Each point represents the median age of sample formation. This individual died around the age of three years, but likely after the weaning process was complete. Bone collagen isotope values do not correspond to the x-axis.

Illness or malnutrition can also cause the δ^{15}N values of infants or their mothers to increase, mimicking the effect of breastfeeding or dietary In these cases, increasing δ^{15}N values are often observed to occur with decreasing δ^{13}C values due to the catabolism of body proteins and lipids change (Beaumont et al., 2015; Mekota et al., 2006; Fuller et al., 2005). This effect may be seen in the last dentine increment from Burial 279 (Fig. 1.7), but the effect on the δ^{15}N value is within analytical error.

In addition to the analysis of bulk proteins, such as collagen or hair keratin, individual amino acids, found within those proteins, also possess unique isotopic compositions that can be measured to provide information about diet and health. Every amino acid is formed through a unique biosynthetic pathway, and records different elements of diet, as well as the influence of physiology and health (Reitsema and

Holder, 2018; Jim et al., 2006; Howland et al., 2003; McClelland and Montoya, 2002). For the purpose of $\delta^{15}N$ analysis, amino acids can be categorized as either trophic: those that undergo considerable isotopic change between trophic levels; or source: those that do not change between trophic levels and reflect the isotopic composition of primary producers within a specific food chain (O'Connell, 2017; McClelland and Montoya, 2002).

3 Reflexivity and community outreach

Feminist research requires the research subject to have an acute awareness of their particular situatedness and how this may influence the shape that the research may take (Wylie, 2013; Harding, 2004; Haraway, 1988). The results of this thesis research should be considered with respect to the research context (academic, science, PhD-level), the researcher (white, educated female of European-Canadian descent), the funding agency (the EU and the Canadian government), and by my own interests and experiences (Alcoff, 1993; Code, 1993). While the results of this research may be of interest to Indigenous stakeholders, Indigenous research concerns were not incorporated consistently into the initial research design. The studies comprised Chapters 2, 4, and 5 were conducted in collaboration with the Rigolet Community Archaeology Project (Chapters 2 and 4) and the Qimmik Project (Chapter 5) with the support of local Labrador and Greenland Inuit communities. The research comprising Chapter 6 occurred in a different context. While federal and provincial state legislation exists in Canada, the EU and United States to protect Indigenous archaeological human remains and cultural heritage, no such laws exist in Russia. To the detriment of Indigenous sovereignty and of archaeology, bioarchaeologists are not required to collaborate or consult with Indigenous populations in Siberia (Buzhilova, 2011). This places limitations on the quality and social relevance of archaeological interpretations in this region. One of the planned outcomes of this thesis research was to travel to Chukotka in the summer of 2020 to present a summary of the results to local descendent populations of the Old Bering Sea culture. It was hoped that the ArchSci2020 project would be the initial step in a multi-year research programme that would integrate archaeological science and Indigenous research concerns into a holistic approach. These plans were indefinitely disrupted by the global COVID-19 pandemic. However, through continued collaboration with colleagues at the Russian

Academy of Sciences and at Stockholm University, I am developing a way to disseminate the results of the research online for Russian Indigenous communities in advance of publication of the human stable isotope study that forms the basis for Chapter 6.

4 Structure of the thesis

The thesis is composed of eight chapters. Chapter 2 considers the problem of humic acid contamination in more detail through a comparison of the effects of different pre-treatment methods on marine mammal bone collagen stable isotope values, amino acid composition, and amino acid racemization. The same analyses are conducted on humic substances extracted from bone collagen in order to contextualise the results and better understand the relationship between soil humics and archaeological bone. Chapter 3 reviews the stable isotope studies conducted to date in the North American Arctic and identifies future challenge areas that need to be addressed. Chapter 4 presents the results of stable carbon and nitrogen isotope analysis of sled dog bone from six sites in coastal Labrador dating between 1500–1840 CE. The data are interpreted in relation to Inuit trading activities, the geographic distribution of prey species, and the reciprocal relationship between dogs and humans. This theme is revisited in Chapter 5 which presents the results of an interdisciplinary study, combining stable isotope analysis, ancient DNA and ethnography, of fur garments that were collected from arctic cultures in the late 19th and early 20th century. Chapter 6 presents the results of the first isotopic study of arctic infant feeding practices. This study combines incremental sampling of tooth dentine with novel compound specific nitrogen isotope analysis of dentine amino acids to examine breastfeeding duration and weaning at the Old Bering Sea culture site of Ekven (~600–1000 CE) in eastern Chukotka, Siberia. Chapter 7 discusses the major findings in light of the research aims and objectives laid out in Chapter 1 and Chapter 8 concludes the thesis with a summary of the research.

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Chapter 2

An improved extraction protocol for humic-contaminated bone collagen: Experimental evidence and insights from humic acid chemistry

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Abstract

Diagenetic contamination of archaeological bone collagen with humic substances can alter stable carbon isotope values and produce inaccurate radiocarbon ages. Current collagen extraction protocols may employ ultrafiltration or sodium hydroxide at a pH of 13 or higher to isolate bone collagen from humic contaminants. Both methods are known to reduce collagen yields and the former may concentrate humic acids in the sample. Humic acids are soluble above a pH of 10, so the objective of this study is to determine if humic substances can be reliably leached from archaeological mammal

bone using basic reagents at a lower pH. Cold, dilute (0.025 M) sodium hydroxide is used to solubilise collagen bound humic acids, and the effects of this pretreatment are compared with three other collagen extraction procedures, including ultrafiltration, on elemental carbon and nitrogen content, atomic C/N values, stable carbon and nitrogen isotope ratios, amino acid composition and racemization. We collect the humic substances isolated from six NaOH treated samples to better understand the isotopic, elemental and amino acid composition of this material. We find that humic acids can be solubilised and isolated from bone collagen extracts in weaker NaOH solutions than those used in current protocols. When compared with NaOH treated samples, ultrafiltered samples have less consistent atomic C/N and lower $\delta^{13}C$ values. We provide further evidence that ultrafiltration may not effectively remove humic acids from archaeological bone collagen.

1 Introduction

Post-depositional contamination of archaeological bone with humic substances (humic and fulvic acids) is a persistent problem in archaeology and palaeontology. The presence of humic substances in bone collagen can alter stable carbon ($\delta^{13}C$) isotope values and produce inaccurate radiocarbon ages. Bone samples that are suspected to be contaminated with humic substances, usually identified by brown staining, are commonly leached with an alkaline solution followed by gelatinization. Alternatively, samples may be demineralised, gelatinised and filtered with ultrafilters to remove low-molecular weight contaminants (Brown et al., 1988) which include young or low complexity humic acids (Tomati et al., 2000). The extraction of humic acids has been problematised in a number of archaeological studies. Most recently, Szpak and colleagues (2017) compared of the effects of two common collagen extraction procedures, leaching with 0.1 M sodium hydroxide (NaOH) and filtration with 30 kDa ultrafilters, on the removal of humic acids from archaeological bone. By examining the effects of each procedure on collagen yield, atomic C/N, and $\delta^{13}C$ and $\delta^{15}N$ values, they demonstrated that while the application of 0.1 M NaOH hydrolysed the collagen protein and reduced yields, the ultrafilters might have actually concentrated humic substances in solubilised collagen (Szpak et al., 2017).

In this study, we build upon the previous study by Szpak et al., (2017) and compare dilute (0.025 M) sodium hydroxide with three other collagen extraction

procedures to determine which effectively removes humic contamination while preserving the bone collagen yield. The procedures are evaluated using the carbon and nitrogen content, atomic C/N values, $\delta^{13}C$ and $\delta^{15}N$ values, amino acid concentration, composition and D/L values of archaeological faunal bone. The results are contextualized through comparison with humic solids extracted from faunal bone.

2 Background

2.1 Humic acids and archaeological bone

Humic substances (Fig. 2.1) occur naturally in soils through oxidative alteration of organic matter (Hatcher et al., 2019). Humic substances are complex macromolecules that can contain differing fractions of lipids, sugars, proteins, carbohydrates and their degradation products (DiDonato et al., 2016). Through the use of different spectroscopic methods humic substances are now thought to be composed of diverse low-molecular-weight molecules (<1000 Da) that aggregate through hydrogen bonds and hydrophobic interactions (Hatcher et al., 2019; Sutton and Sposito, 2005). Humic acids, of concern in archaeological chemistry, are operationally defined as compounds that can be leached from soils or other matrices with an alkaline solution (pH > 8) and precipitated in acidic (pH 1-3) solution (Kipton et al., 1992; Rashid and King, 1969). Fulvic acids can be distinguished from humic acids as they are soluble in acidic and basic solutions, but humic acids and fulvic acids should not be considered as separate and distinct molecular types (Sutton and Sposito, 2005; Kipton et al., 1992). Humic acids can form cross-linkages with the collagen of buried archaeological bone (Collins et al., 1995; van Klinken and Hedges, 1995) making them a potential source of contaminating exogenous carbon in radiocarbon dating and stable isotope analysis.

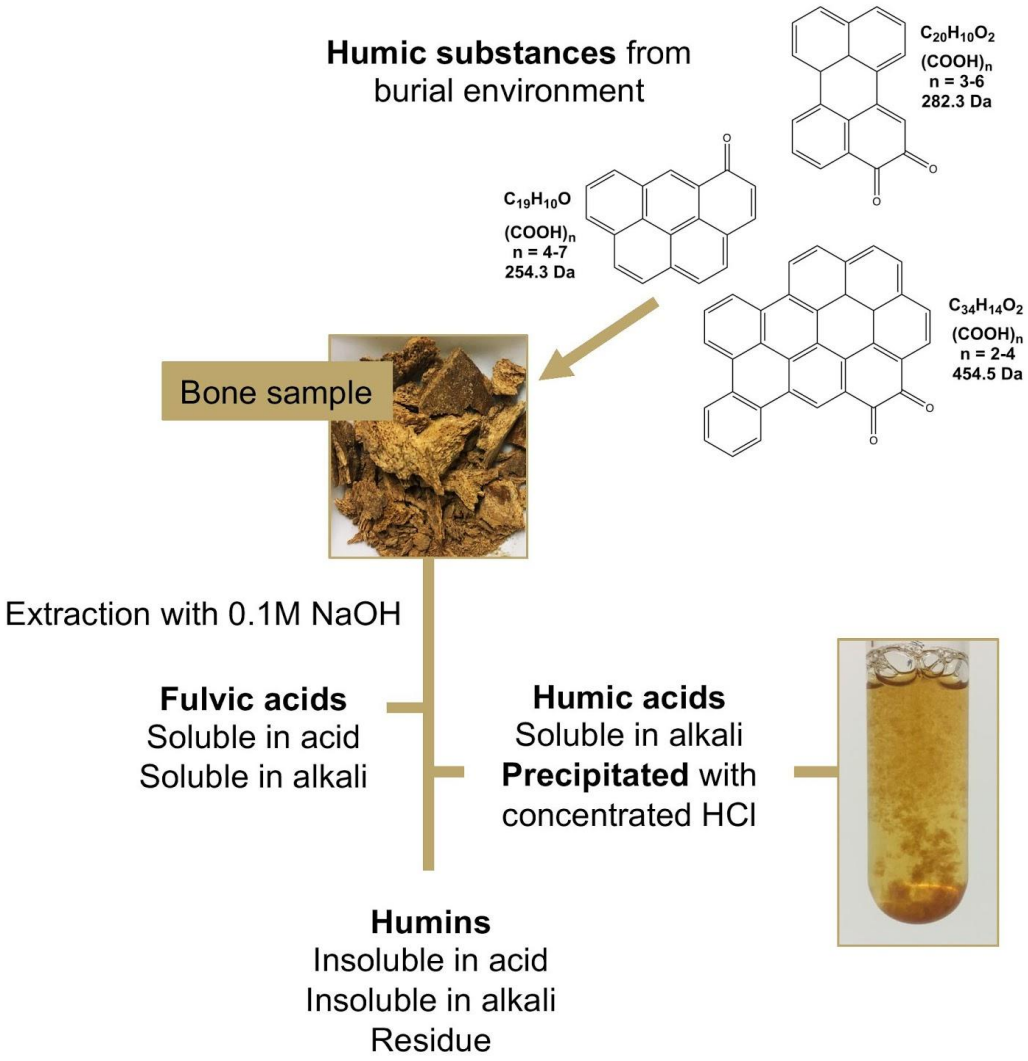

Figure 2.1 Schematic of relevant properties of the humic substances that may contaminate archaeological bone. Molecular data adapted from Waggoner et al. (2015).

In living organisms, intermolecular cross-linkages are critical to the formation, maturation and strengthening of Type I collagen. The slow turnover rate of mature collagen exposes the molecule to reactive metabolites, such as glucose and aldehydes, which form additional cross-linkages with amino groups found on the surface of, or between, collagen fibrils (Gautieri et al., 2017). These cross-linkages are the foundation of the leather tanning process as they decrease the solubility of collagen and increase resistance to protein denaturation (Harlan and Feairheller, 1977). After the death of an organism, these processes continue to link collagen to humic compounds in the post-depositional environment. Van Klinken and Hedges (1995) demonstrated that even though the products of Maillard reactions are present

in collagen, exogenous chromophores – humic acids and metabolites – produced through the decomposition of plant matter are the likely source of dark colouration in archaeological bone. Unmineralized, modern collagen rapidly bonds to humic acids *in vitro*, and similar processes may occur in post-depositional environments, mediated by the presence of bone bioapatite (van Klinken and Hedges, 1995). Humic acids are rich in carbon and if these contaminants are not removed prior to analysis, subsequent $\delta^{13}C$ measurements may be inaccurate (van Klinken, 1999; Stafford et al., 1988). A simple mixing model (Fig. 2.2), using theoretical $\delta^{13}C$ values as endpoints for humic acids (–26‰) (Prentice and Webb, 2010), marine (–13‰), and terrestrial C_3 (–21‰) consumers (Schoeninger and DeNiro, 1984), shows the effect of increasing humic acid content on the $\delta^{13}C$ value of a collagen sample. The effect on a sample from a C_3 environment, recorded as an offset from the true collagen $\delta^{13}C$ value, has a shallower gradient than that observed for a marine sample, as humic acids and consumers of C_3 plants would share a similar carbon source.

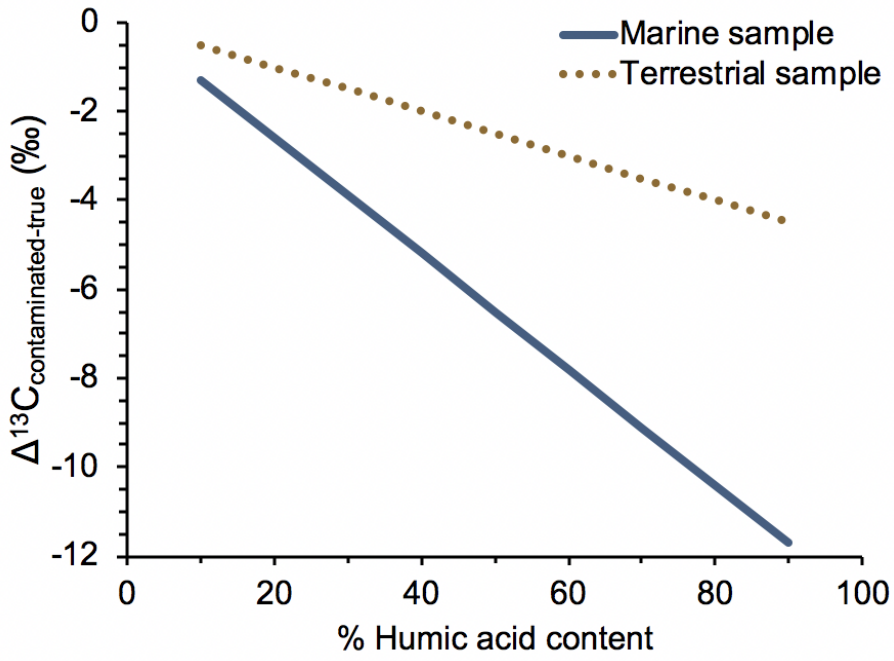

Figure 2.2 Mixing model showing the $\Delta^{13}C$ offset between true and contaminated samples with increasing humic acid content.

2.2 Detecting humics in archaeological collagen

Type 1 collagen is the dominant protein in bone but the residue extracted from archaeological bones is rarely representative of the *in vivo* protein as it will have

undergone some degree of diagenetic alteration and is likely to include non-collagenous proteins (Wadsworth and Buckley, 2017; Brock et al., 2013). In this paper, we use the term collagen to refer to the proteinaceous residue resulting from archaeological collagen extraction methods, but acknowledge that other non-collagenous bone proteins, such as osteocalcin, and some exogenous contaminants, are likely to occur within this residue.

Collagen preservation and the degree of diagenetic contamination are commonly assessed using four indicators: collagen yield, calculated as a percentage of the initial mass of the bone sample; the carbon and nitrogen content of collagen, expressed as weight percentages (wt. % C, wt.% N); and the atomic, or molar, ratio of carbon to nitrogen (C/N). The collagen yield depends on bone preservation and on the collagen extraction method. The conditions of the burial environment may promote collagen preservation (e.g. permafrost) or result in rapid degradation (e.g. tropical, desert, or acidic conditions) (Buckley et al., 2008; Hedges, 2002). Bone pretreatment procedures may extract all protein components of bone (collagen and non-collagenous proteins) (Wadsworth and Buckley, 2017; Sealy, 1986), or may attempt to isolate only those peptides above a certain MW, usually 30 kDa (Brown et al., 1988).

The wt.% C and N are a function of the amino acid (AA) composition of the protein and the number of C and N atoms within each AA, but in archaeological collagen, some carbon may also be contributed by non-collagenous proteins and contaminants. The concentration of carbon in archaeological collagen varies between 25 and 48%, while the nitrogen content can range from 11 to 17% (e.g. van Klinken, 1999; Ambrose, 1990). Because glycine represents a third of the AA residues in collagen, Type I collagen has a lower atomic C/N value than other bone proteins (Schwarcz and Schoeninger, 1991) (Fig. 2.3), therefore C/N values that are significantly higher or lower signify the addition of exogenous carbon from other proteins or diagenetic contaminants, or alternatively, the loss of N (Table 3.1). Humic substances are depleted in ^{13}C and have high atomic C/N values (Tatzber et al., 2007; Francioso et al., 2005). If atomic C/N value greater than 3.5–3.6 are measured in archaeological collagen, it can suggest the addition of ^{13}C-depleted carbon from decomposing plant matter (van Klinken, 1999; Stafford et al., 1988; DeNiro, 1985 [but see Guiry and Szpak, 2020]). The presence of contaminating humic substances in collagen may be further identifiable by a wt.% C greater than ~47% with negatively covarying wt.%N (van Klinken, 1999), and anomalously low $\delta^{13}C$ values.

Table 2.1. Atomic C/N ratios of glycine, Type I collagen and other bone proteins, and humic substances.

Protein	C atoms	N atoms	C/N
Glycine	2	1	2.0
Human Type I Collagen	12141	3908	3.1
Keratin, Type II cytoskeletal	2792	858	3.3
Bone Matrix-Gla protein	537	162	3.3
Keratin, Type I cuticular	1981	576	3.4
Osteocalcin	457	125	3.7
Biglycan	1846	498	3.7
Hemoglobin	685	187	3.7
HSA (albumin)	2936	786	3.7
Pepsin A-4	1541	374	4.1
Fulvic acid	135	5	27
Humic acid*			10 - 35

*Humic acids contain various chemical compounds but tend to contain 50-60% carbon and 1-2% nitrogen

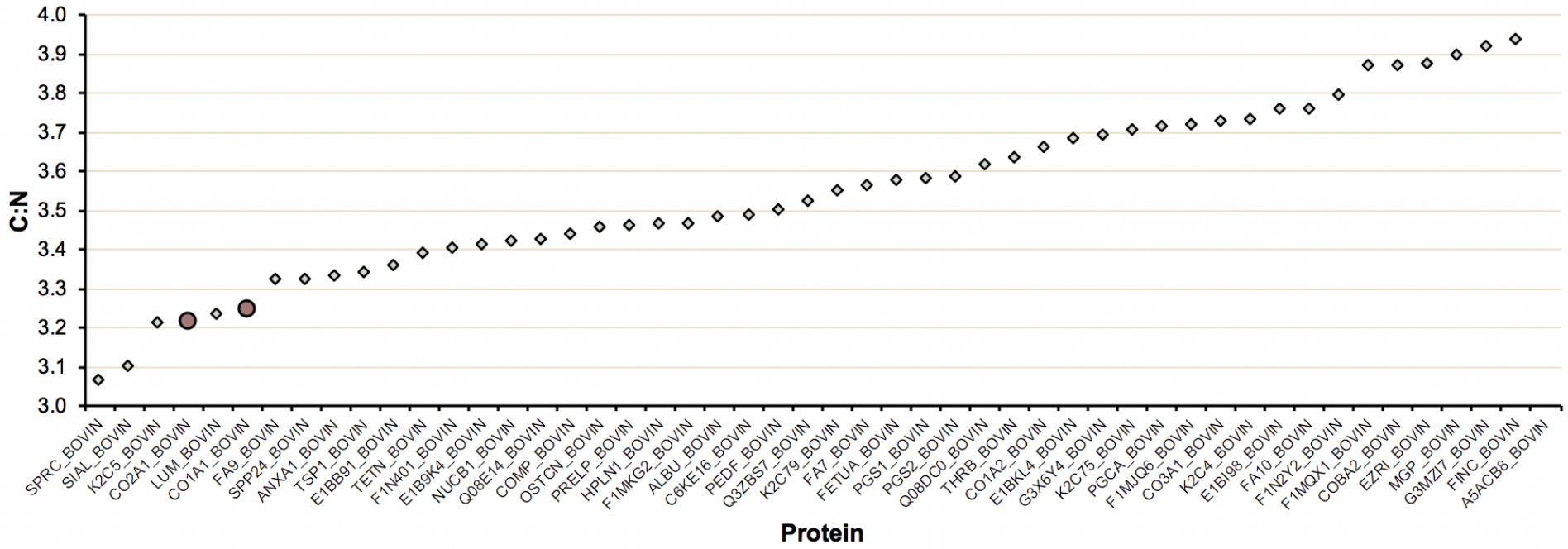

Figure 2.3 Proteins recovered from a bone sample of an ancient bison (*Bison latifrons*) (Hill *et al.* 2015) ordered by C/N ratio; Type I collagens are presented as circles

2.3 Removal of humic acids

As humic acids form cross-linkages with collagen and may bond to calcium (Stevenson, 1994), humic acid removal protocols are designed to hydrolyse the bonds between collagen and humic acids and/or separate humic acids from solubilised collagen through filtration or precipitation. In this study we hypothesize that dilute (0.025 M) NaOH will effectively remove humic substances from archaeological bone collagen while preserving collagen yield to a greater extent than protocols that use 0.1–0.2 M NaOH (e.g. Szpak et al., 2017; Sealy et al., 2014; Jørkov et al., 2007; Ambrose, 1990; Berglund et al., 1976). Figure 2.4 shows the estimated change in the charge of the collagen molecule with ascending pH (Putnam, 2013). At pH 9 and above, collagen will hydrolyse into solution as the molecule becomes increasingly negatively charged (Uquillas and Akkus, 2012). Humic acids follow a similar trajectory, but at a lower amplitude. Humic carboxylic compounds have a range of pKa values and corresponding differences in solubility in acidic and neutral solutions (Prado et al., 2011; Abate and Masini, 2001). Humic phenolic compounds are weak acids and require a higher pH to dissociate, however, no further change in electric charge occurs above a pH of 10. This means that increasing the pH of the NaOH solution above this point will not result in greater humic acid solubility but will result in greater collagen hydrolysis.

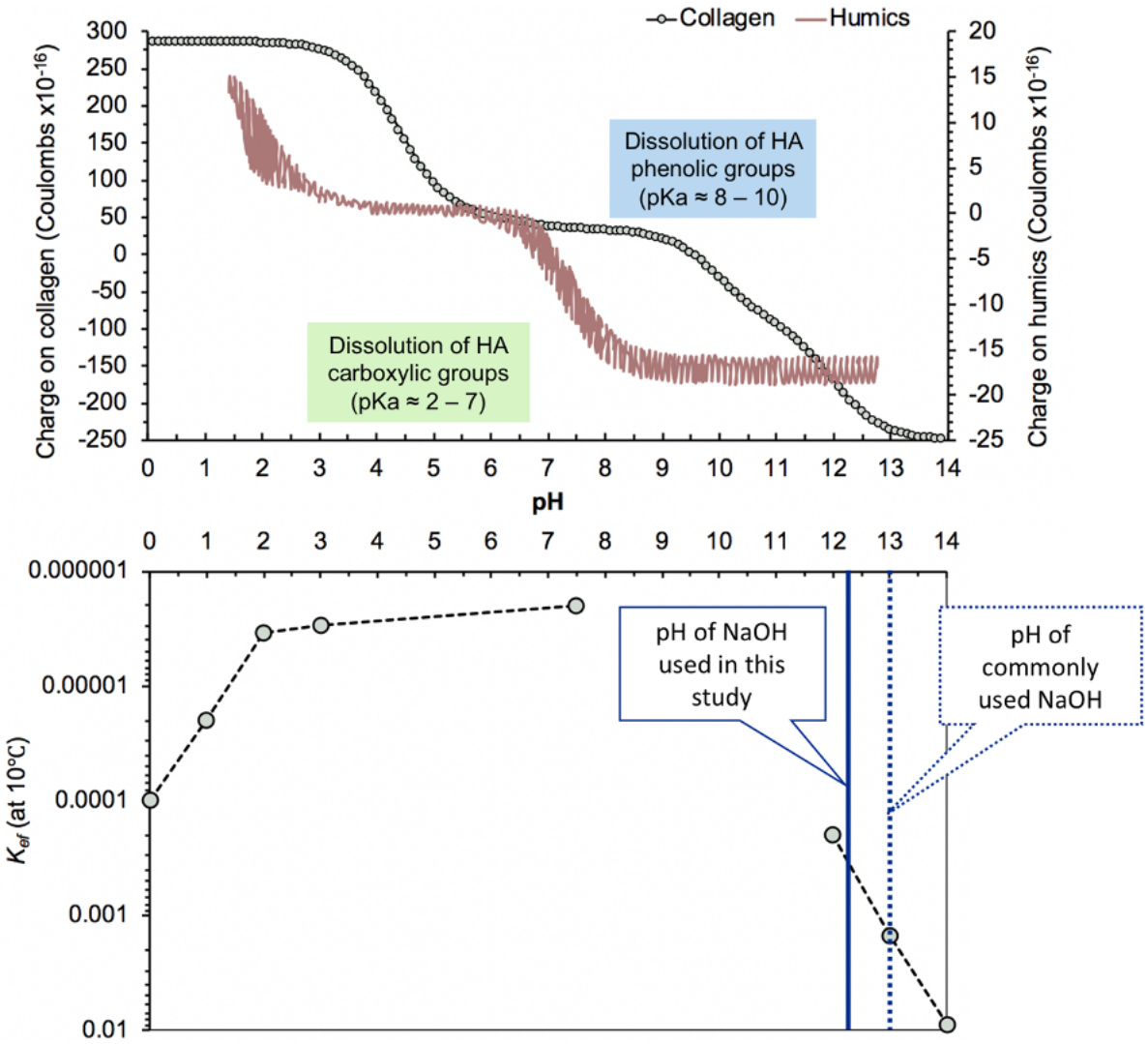

Fig. 2.4 Relationship between pH, the electrical charge of Type I collagen and humic acids (HA), and the rate of collagen hydrolysis (Collins *et al.* 1995). The collagen charge was estimated using published data (Hill *et al.* 2015) and the protcalc v3.4 calculator (Putnam 2013). Humic acid data from Abate and Masini (2001) and Prado et al. (2011).

Ultrafilters are frequently employed to remove low MW (<30 kDa) humic acids and peptide fragments from solubilised collagen (e.g. Brown et al., 1988). A number of recent analyses showed ultrafilters to have slight to statistically significant unfavourable effects on $\delta^{13}C$ values and collagen preservation indicators (Szpak et al., 2017; Sealy et al., 2014; Jørkov et al., 2007). Therefore, we compare the effects of 0.025 M NaOH with ultrafiltration and two other collagen extraction methods (described in section 3.2) on collagen preservation, elemental and AA composition. These results are further contextualized through comparison with humic solids extracted from the collagen samples.

3 Materials and methods

3.1 Samples

We obtained samples of terrestrial and marine mammal bone from an Inuit site, Double Mer Point, in Labrador, Canada. The site was occupied between AD 1750 and 1840 and the samples came from two contiguous semi-subterranean houses (Bohms, 2018; Rankin, 2014). The bone samples were recovered from poorly drained dark brown organic soil with small, patchy areas of permafrost. We predominantly selected the bones of animals (seals and domestic sled dogs) with marine-based diets to maximise the difference between the $\delta^{13}C$ values of collagen and humic acids derived from terrestrial plant matter. The collagen of marine mammals is generally characterised by high $\delta^{13}C$ values (–16‰ to –10‰) while subarctic terrestrial species have lower collagen $\delta^{13}C$ values (–22‰ to –18‰) (Szpak et al., 2019; McManus-Fry et al., 2018; Britton et al., 2013; Nelson et al., 2012; Coltrain et al., 2004) that are more similar to the range of $\delta^{13}C$ values measured in humic acids (e.g. Prentice and Webb, 2010).

3.2 Bone pretreatment and analytical methods

Complete details of the methods and analytical parameters are presented in Appendix 1, SI File 1. In brief, chunks of bone (~500 mg) were cut from skeletal elements using a handheld Dremel tool and the surfaces were mechanically abraded using a stainless-steel burr attachment. The bone samples were manually crushed into smaller pieces, divided into four subsamples and demineralised in ~10 mL of 0.5 M hydrochloric acid at 4°C These were submitted to one of four pre-treatment procedures (Fig. 2.5). Less than 2 mg of the crushed, untreated bone was retained, powdered, and submitted for elemental nitrogen analysis at the Stable Isotope Lab, Department of Geological Sciences, Stockholm University (SIL). Humic solids were precipitated from the waste NaOH solutions through acidification. The $\delta^{13}C$ and $\delta^{15}N$ values of both bulk collagen and collagen amino acids were measured at the BioArCh facility, University of York; the humic solids were analysed at SIL. Amino acid racemization and composition of control, NaOH, ultrafiltered (UF) collagens and humic solids were measured at the NEaar facility, University of York.

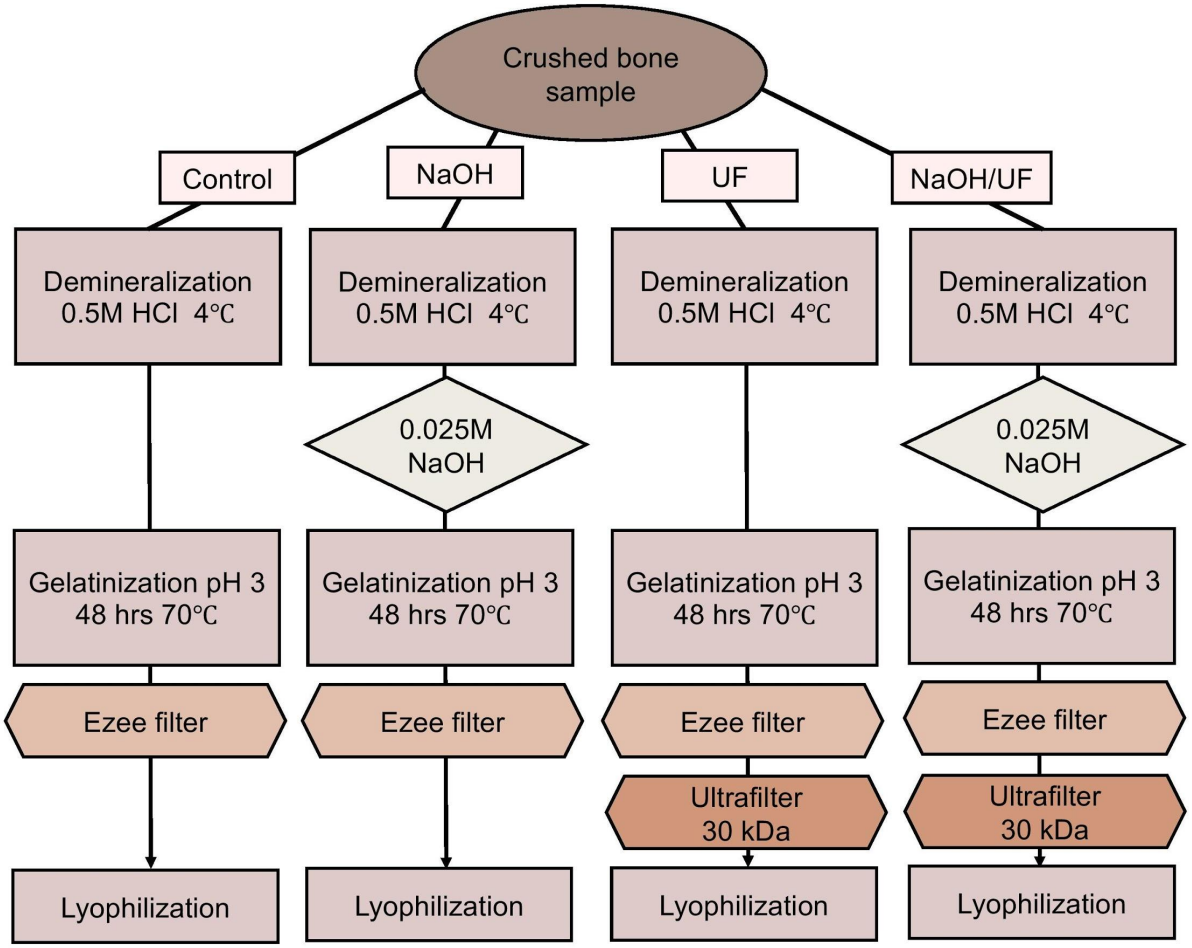

Figure 2.5 Schematic of experimental procedure.

4 Results

The results of stable isotope and elemental analyses are summarized in Table 2.2. The complete data set, including the stable isotope data and collagen quality indicators (SI Table 1), amino acid concentrations (SI Table 2), composition (SI Table 3), and D/L ratios (SI Table 4), and amino acid $\delta^{13}C$ values (SI Table 5) is presented in Appendix 1.

4.1 Collagen quality indicators

The nitrogen content of the untreated bone samples ranged between 2 and 4%, consistent with well- to moderately preserved bones (Stafford et al., 1988). The mean collagen yields were greatest for the control samples, followed closely by the NaOH-treated samples, while the ultrafiltered (UF) and NaOH/UF treatments produced the lowest yields. One of the NaOH/UF samples did not produce sufficient collagen for analysis. Ultrafilters appeared to reduce collagen yields more than the dilute NaOH

(Table 2.2) which, in turn, appeared to have little effect on collagen yields relative to the control samples.

Table 2.2. Summary statistics for different collagen extraction procedures and extracted humics. Standard deviation (1s) in brackets.

Procedure	N	Collagen yield (%)	Wt. %C	Wt. %N	C/N	δ^{13}C (‰)	δ^{15}N (‰)
Control	12	6.7 (4.0)	41.02 (2.50)	14.65 (1.08)	3.27 (0.09)	–15.19 (1.90)	+13.03 (6.35)
NaOH	12	6.1 (2.8)	40.18 (2.75)	14.98 (1.04)	3.13 (0.07)	–14.94 (2.09)	+13.05 (6.30)
UF	12	2.9 (2.8)	43.28 (1.37)	14.85 (1.19)	3.42 (0.24)	–15.52 (1.67)	+13.12 (6.33)
NaOH/UF	10	2.2 (1.5)	42.15 (1.75)	15.32 (0.88)	3.22 (0.07)	–15.05 (1.98)	+12.50 (6.30)
Humics	6	N/A	41.63 (2.12)	6.76 (0.74)	7.26 (0.89)	–21.07 (1.40)	+16.80 (5.42)

Carbon concentrations varied significantly among procedures, as did atomic C/N values, but no statistically significant differences were observed among nitrogen concentrations (Table 2.3). The wt.% C measurements were highest in the UF samples, followed by the NaOH/UF, control, and NaOH treated samples. The highest wt.% N was found in the NaOH/UF samples, while the control and other pretreatments produced nearly identical results. A strong positive correlation was observed between the wt.% C and N for the control (R=0.949), NaOH (R=0.891), and NaOH/UF (R=0.961) samples (Fig. 2.6). The wt.% C and N of the UF samples (R=0.509) were not as strongly correlated as five of the 12 samples with high wt.% C did not have accompanying high wt.% N. This suggests the addition of low-nitrogen content material, such as humic acids. This assumption is supported by the wt.% C of the humic extracts which was approximately seven times that of the N content, and by the atomic C/N values.

Table 2.3: Results of Wilcoxon signed rank tests comparing each procedure to the control. Significant results are presented in bold type.

Variable	Treatment			
Carbon (%)		NaOH	UF	NaOH/UF
	Control	0.388	**0.002**	0.328
Nitrogen (%)		NaOH	UF	NaOH/UF
	Control	0.456	0.135	0.169
Atomic C/N		NaOH	UF	NaOH/UF
	Control	**0.004**	**0.009**	**0.016**
$\delta^{13}C$		NaOH	UF	NaOH/UF
	Control	0.166	0.085	**0.017**
$\delta^{15}N$		NaOH	UF	NaOH/UF
	Control	0.306	0.090	0.429

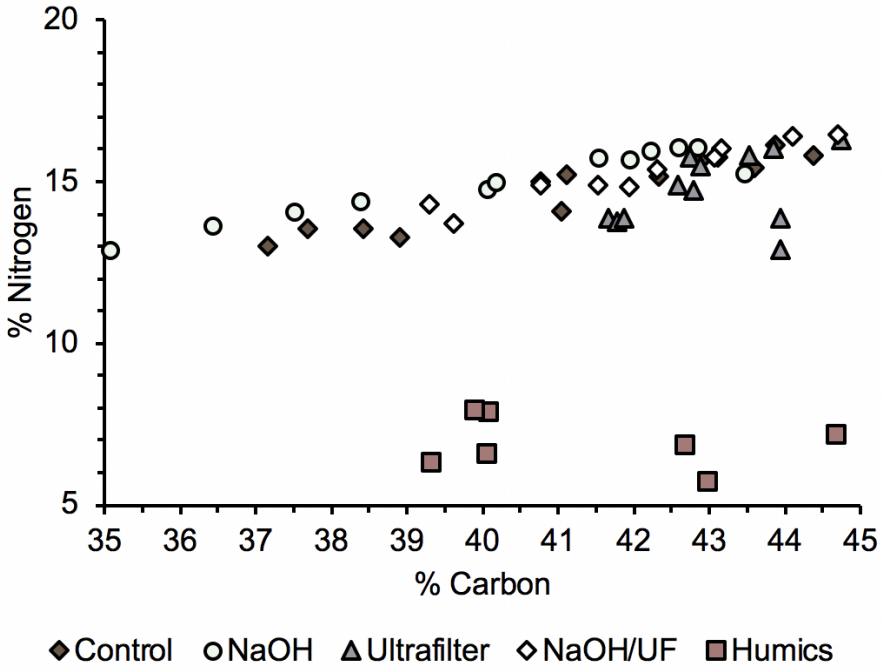

Figure 2.6 Comparison of %C and %N concentrations among pre-treatment procedures and humic substances.

The lowest and highest atomic C/N values were measured in the NaOH and UF samples, respectively. The atomic C/N values of four of the 12 UF samples exceeded

the theoretical cut-off of 3.5 for uncontaminated collagen (van Klinken, 1999). The humic solids had atomic C/N values ranging from 5.9 to 8.7, much higher than modern bone collagen, but considerably less than commercially available humic acids (e.g. van Klinken and Hedges, 1995), or those extracted from peat, which can be greater than 25 (Francioso et al., 2005). This suggests that the higher atomic C/N values of the UF samples may have resulted from the retention of carbon from a non-collagenous source.

4.2 Amino acids: Composition and racemisation

Figure 2.7 compares the AA % composition of a sample of archaeological dog collagen, pretreated three ways, and extracted humic solids with published data from five other proteins, including Type I collagen, that were extracted from an ancient bison bone sample (Hill et al., 2015). After undergoing one of three pretreatments, the dog collagen samples have similar AA % compositions to each other and to published collagen data. The extracted humics contained less glycine and slightly more aspartic acid/asparagine, valine, and leucine than collagen, but were also dissimilar from other bone proteins.

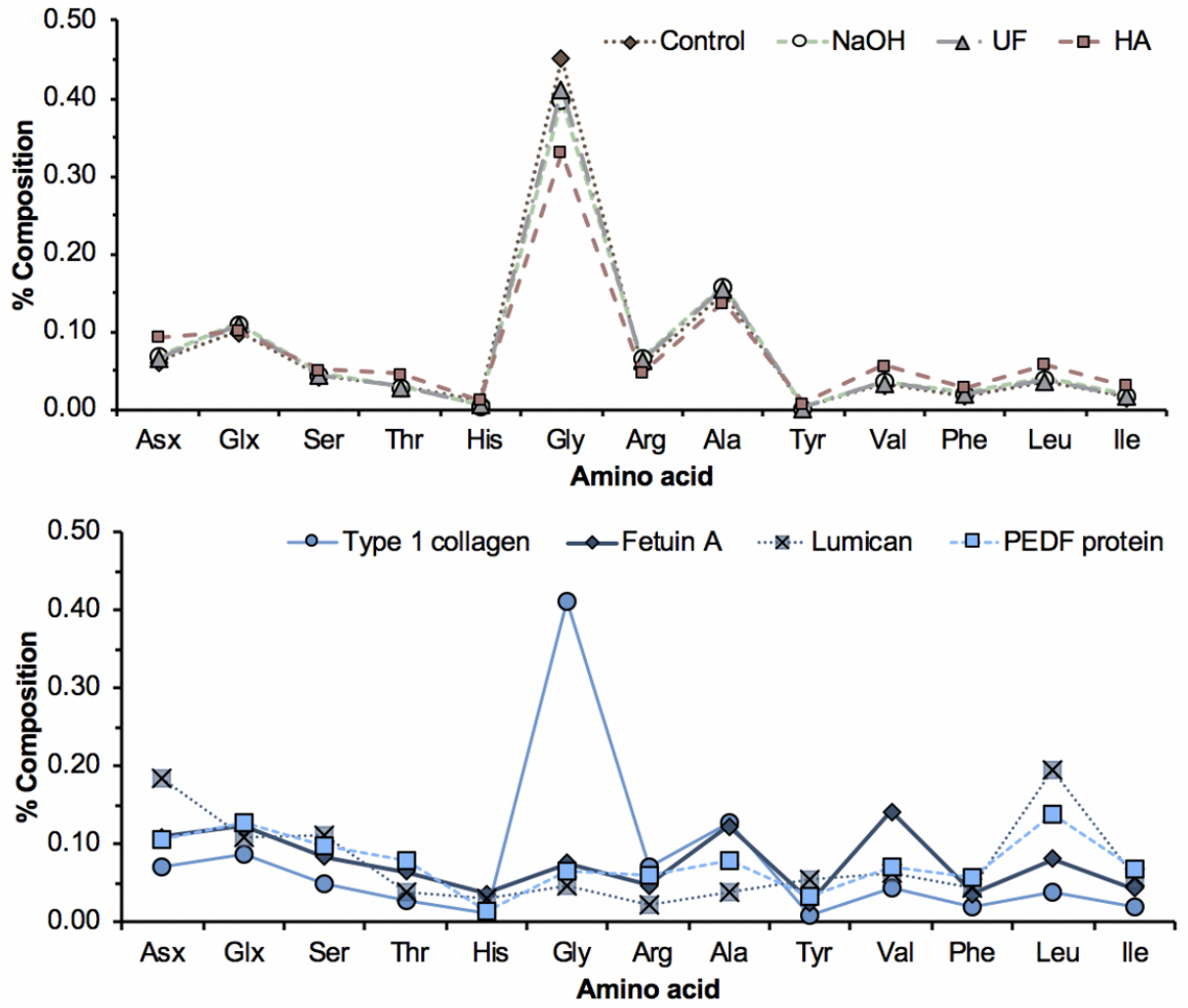

Figure 2.7 Amino acid % composition of collagen and humic extracts contrasted with that of other common bone proteins (Hill *et al.* 2015).

Amino acid concentrations were slightly higher in the NaOH treated samples than in the UF and control samples (Fig. 2.8A). Aspartic acid/asparagine, threonine, histidine, valine, phenylalanine, leucine, and isoleucine were present in the humic solids at 45 to 57% of the concentration of those found in collagen. Serine, glutamic acid/glutamine, alanine and arginine were present at 25 to 30% of the concentration of those found in collagen, while the concentration of glycine in the humic solids was only 20% of that found in collagen. D/L values from the control and UF collagen extracts were below 0.1 for all amino acids (Fig. 2.8B), a common pattern in bone (High et al., 2016; Collins et al., 2009). D-Asx, D-Ser, D-Leu, and D-Val were elevated in the NaOH-treated collagen relative to the control and UF collagen. Aspartic acid and serine can undergo in-chain racemization (Demarchi et al., 2013) implying a

greater degree of backbone flexibility, while leucine racemises while terminal and free, potentially implying greater peptide bond hydrolysis in the NaOH treatment (Collins and Riley, 2000). Each pretreatment had relatively similar D/L values of Glx, Ala, and Phe. D-Asx, D-Glu and D-Ala are also found in peptidoglycan (Schleifer and Kandler, 1972), but as only one of these had elevated racemization in these samples, there was little or no bacterial cell wall contamination. The humic solids had lower D- Asx than the collagen samples, but the D/L values of all other AAs measured were higher, particularly for tyrosine.

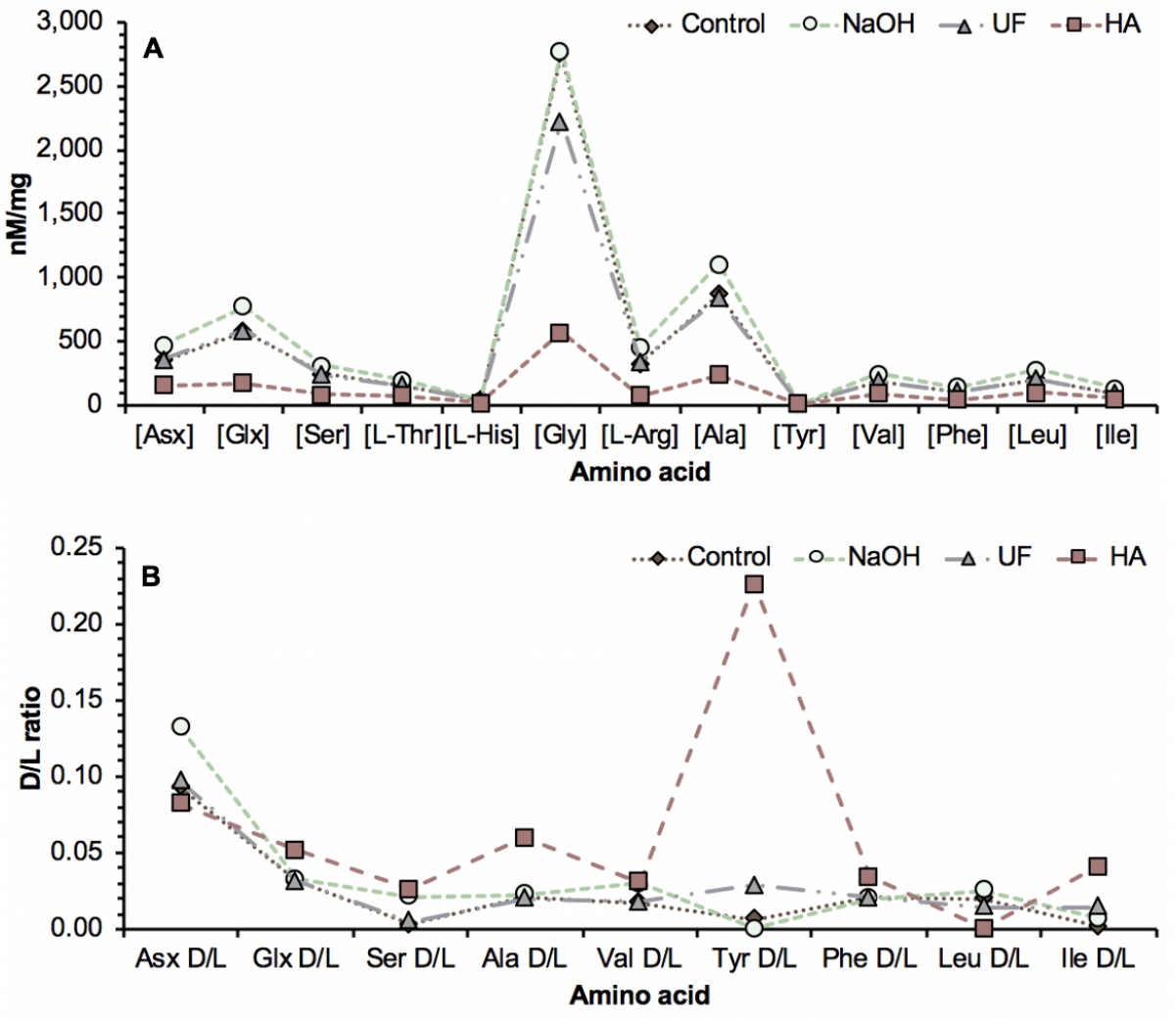

Figure 2.8 A) Concentration of amino acids in collagen and humic extracts; B) Racemisation of amino acids in collagen and humic extracts.

The collagens produced by each pretreatment appear to be consistent with the AA composition of type I collagen. The higher D/L values of amino acids in the NaOH

treated collagen suggest that more peptide hydrolysis occurred during this pretreatment, but the higher concentration of amino acids in the NaOH treated collagen relative to other pretreatments, and the AA composition of the NaOH treated collagen shows that the remaining residue is still consistent with type I collagen.

4.3 Stable isotope data

4.3.1 Carbon isotope data

The results can be further understood by comparing the atomic C/N and $\delta^{13}C$ values of the collagen samples (Fig. 2.9A-B). Only the $\delta^{13}C$ values of the NaOH/UF samples differed significantly from the control. Of greater concern was the offset between the NaOH and UF samples. The $\Delta^{13}C_{NaOH-UF}$ ranged from –0.3‰ to +2.3‰ (mean +0.6‰). The $\delta^{13}C$ values of NaOH and UF collagen from *R. tarandus* bones were generally within analytical error, while the greatest differences in $\delta^{13}C$ values were observed in marine mammal and dog bones, as was expected based on the difference in ^{13}C enrichment between plant-derived humics and the collagen of marine consumers (see Fig. 2.2). The $\delta^{13}C$ values of the extracted humic materials were approximately 4 to 8‰ lower than those in collagen (Fig. 2.9C-D).

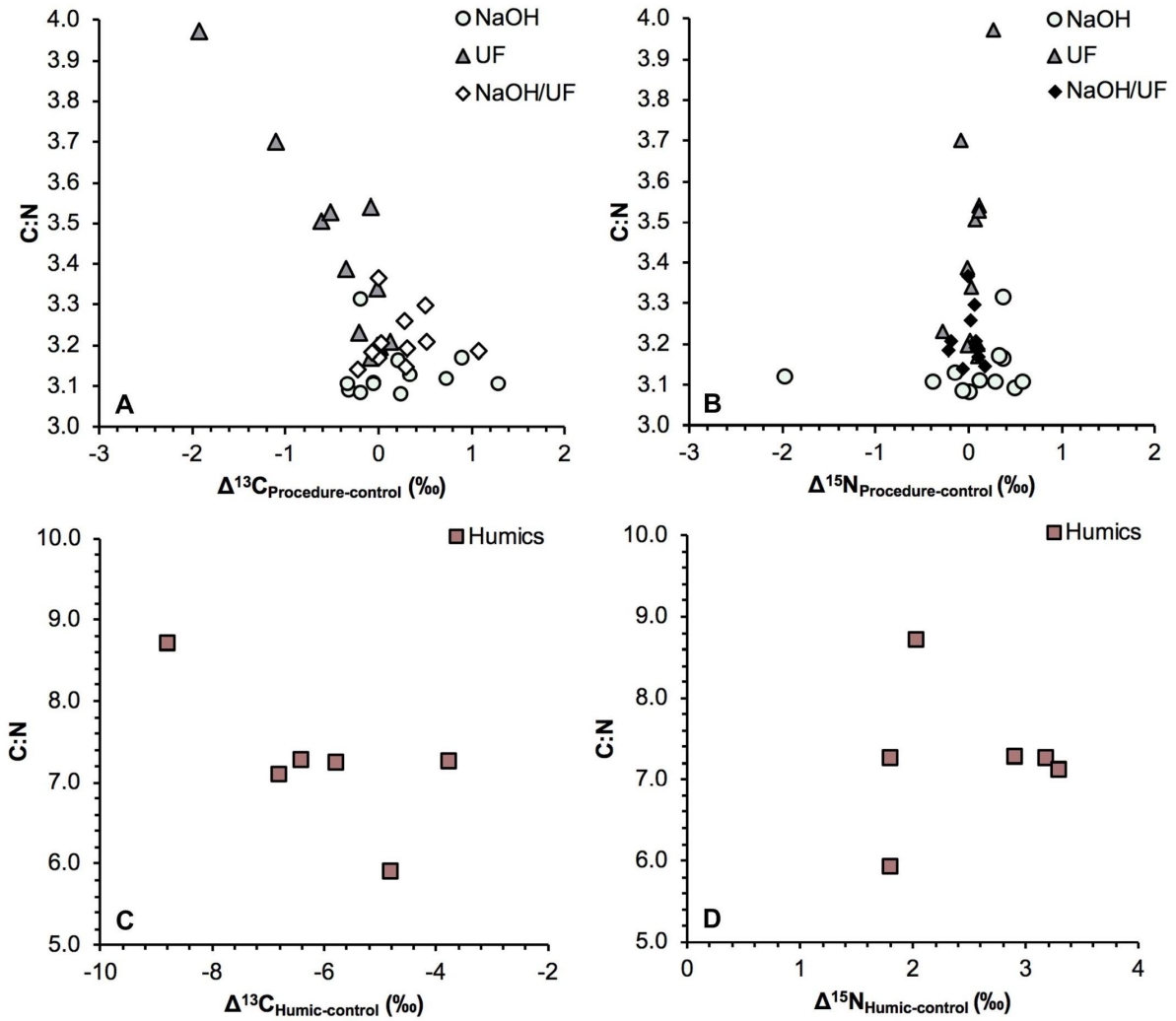

Fig. 2.9 a-b) The difference in isotope values between samples treated with the control procedure and those treated with sodium hydroxide (NaOH), ultrafilters (UF), or a combination of the two (NaOH/UF); c-d) the difference in isotopic values between the control samples and extracted humic solids. Analytical error on the isotopic measurements was better than 0.2‰.

Next, we compared the measured bulk collagen $\delta^{13}C$ values from each pretreatment with a theoretical $\delta^{13}C$ value calculated from the mass balance of the $\delta^{13}C$ values of amino acids extracted from NaOH-treated bearded seal collagen (Appendix 1, SI Table 5). The $\Delta^{13}C_{estimated-measured}$ ranged from +2.5‰ for the NaOH-treated collagen to +4.8‰ for the UF-treated collagen. Part of the discrepancy between measured and estimated values may be attributed to missing $\delta^{13}C$ values for methionine, arginine, and histidine. Arginine and histidine, representing 5.1% and 0.6% of the C atoms in collagen, respectively, are not derivatized by the N-acetyl-i-propyl derivatization method (Corr et al., 2007), and baseline resolution could not be

achieved for methionine which contributes 0.6% of the C atoms in Type I collagen. Methionine and histidine $\delta^{13}C$ values are not regularly reported in bone collagen studies due to difficulties in achieving baseline resolution, but do tend to be lower than bulk collagen values (Webb et al., 2015), while arginine $\delta^{13}C$ values are on average 3.6 ± 1.2‰ lower than bulk collagen $\delta^{13}C$ values (Webb et al., 2016; Honch et al., 2012; Choy et al., 2010; Raghavan et al., 2010;), which may account for some of this offset.

The $\delta^{13}C$ values of the UF-treated collagen and extracted humic solids were 5‰ and ~10‰ lower than the estimated bulk collagen $\delta^{13}C$ value, respectively. The lower $\delta^{13}C$ value of UF-treated collagen could be due to the retention of exogenous contaminants, such as humic acids. If the NaOH-treated collagen represents the biogenic $\delta^{13}C$ value of the sample, and the extracted humic $\delta^{13}C$ value approximates that of soil-derived humic acids, then the UF-treated collagen may contain ~30% humic-derived carbon. This assumption is supported by the difference in atomic C/N values between the NaOH (3.13), control (3.29), UF (3.97) and extracted humic solids (7.28). The high atomic C/N value of the UF collagen indicates the inclusion of an exogenous source of carbon that was not present at the same concentration in the control or in the NaOH-extracted collagen.

4.3.2. Nitrogen isotope values

The $\delta^{15}N$ values of all pretreated samples were largely consistent with the control, similar to previously published findings (Szpak et al., 2017). Unexpectedly, we found that the extracted humic materials had $\delta^{15}N$ values that were approximately +2‰ to +3.5‰ higher than the collagen values, which may indicate selective removal of particular amino acids. Humic materials contain little nitrogen and are unlikely to account for the high $\delta^{15}N$ values reported here. Based on the AA composition of the extracted humic solids, we suggest that the $\delta^{15}N$ values may be attributed to the presence of collagen-derived aspartic acid/asparagine (Asx), alanine, glutamic acid/glutamate (Glx), and valine in the humics. Alanine, Glx, and valine are enriched in ^{15}N over bulk proteins in the collagen of marine consumers (Matthews and Ferguson, 2014; Naito et al., 2010; McClelland and Montoya, 2002).

5 Discussion

The results of our comparison of four different pretreatments suggest that dilute (0.025 M) NaOH can remove some humic acids from archaeological bone more effectively than the use of 30 kDA ultrafilters alone. Collagen yields were somewhat inconsistent across all pretreatments: the NaOH collagen yields were higher than ultrafiltered samples and were generally consistent with the control (untreated, gelatinized) samples, however, the control samples did not produce consistent yields. This may be due to the presence of humic-collagen cross-links which could reduce the solubility of collagen in mildly acidic conditions (Schropfer and Meyer, 2016). Although we did not compare the effects of 0.025 M NaOH and 0.1 M NaOH on collagen yields, previous studies have shown that stronger NaOH solutions do reduce collagen yields relative to control procedures (Szpak et al. 2017; Jørkov et al. 2007). It is probable that the NaOH caused the loss of some bone protein. The higher rates of racemization in the NaOH-treated collagen may be due to alkali-induced degradation of the collagen protein. An experimental study in the field of nutrition and food science showed that alkali leaching of casein in heated (80°C) 0.1 M NaOH for 60 minutes resulted in the complete racemization of Asx, Tyr, and Ser, and extensive racemization of other AAs (Liardon and Hurrell, 1983). We could not verify if a higher rate of racemization also occurred in the NaOH/UF samples, as insufficient collagen remained for AA analysis. Despite the difference in the racemization data, the effects of the different pretreatments on the amino acid composition and on the $\delta^{15}N$ values of the collagen were minimal. The most striking differences between the pretreatments were found in the $\delta^{13}C$ values and collagen quality indicators. The NaOH-treated collagen had the highest $\delta^{13}C$ values across all pretreatments, and consistently produced atomic C/N values that were most similar to 3.1, the theoretical C/N value of collagen. The ultrafiltered collagen samples had the highest C/N ratios and wt. % C values which strongly suggested that some contaminating carbon was retained in the ultrafiltered residue. The $\delta^{13}C$ values of the ultrafiltered collagen were also low relative to the NaOH and control collagen which suggests that the contaminating carbon came from an allochthonous, possibly terrestrial source.

Our analyses of the extracted humic solids further helped to characterize the source of contaminating carbon and allowed us to better evaluate the effects of NaOH on collagen preservation. The six humic solids had very low $\delta^{13}C$ values but $\delta^{15}N$

values that were considerably higher than the collagen. The amino acid composition of the humics was similar to collagen, but the amino acids were present at different concentrations than in collagen. The atomic C/N values were much higher than collagen, and higher indeed than most other bone proteins (Fig. 3.3), therefore it seems probable that both bone- and lignin-derived proteins were present in the humic solids. We found higher D-Tyr in the humic solids. Racemisation would be expected if the amino acids in the humic solids were highly degraded, but it is unclear why tyrosine would be the most affected. It is possible that another compound was co-eluting with tyrosine.

The poor performance of the ultrafilters relative to the other pretreatments was not unexpected, based on previously published results (2007 Szpak et al., 2017; Sealy et al., 2014; Jørkov et al., 2007), however the reason for this has not been thoroughly explored in archaeological research. Here we suggest that the behaviour of humic acids in acidic solution, such as that found in gelatinised collagen, may be the culprit. Published collagen extraction protocols solubilise collagen between a pH of 2 and 4 (Richards and Hedges, 1999; Ambrose, 1990; Brown et al., 1988; Longin, 1971). Below a pH of 7, humic acids will aggregate into higher MW species (Kipton et al., 1992) and if not separated from the collagen solution, they may adsorb onto the filter, as observed in waste water filtration studies (Yuan and Zydney, 2000), or may be concentrated in the collagen solution (Brock et al., 2013) and will be observable as a brown gradient in the ultrafiltered collagen.

Based on the results of our study, and on the chemistry of collagen and humic acids, we suggest that the following recommendations be taken into consideration when dealing with humic-contaminated archaeological bone (Fig. 2.10). If using sodium hydroxide or another alkaline reagent, such as potassium hydroxide, consider the relative solubility of collagen and humic acids. Humic acids can be extracted with fewer negative effects on collagen yield if a chilled, low pH (i.e. <12) solution is used. Rather than leaching the collagen for hours, following from Szpak et al. (2017), we also advise monitoring the reaction closely and removing the bone sample from the NaOH solution as soon as the reaction ceases, as indicated by the absence of brown chromophores. If using ultrafilters, we suggest that the solubilised collagen be neutralised prior to filtration to disaggregate the humic acids back into low molecular weight units or to centrifuge the collagen for 20–30 minutes to pellet the humic acids,

as is done is soil chemistry (Tatzber et al., 2007; Francioso et al., 2005; Ikeya and Watanabe, 2003), and then only filter the supernatant.

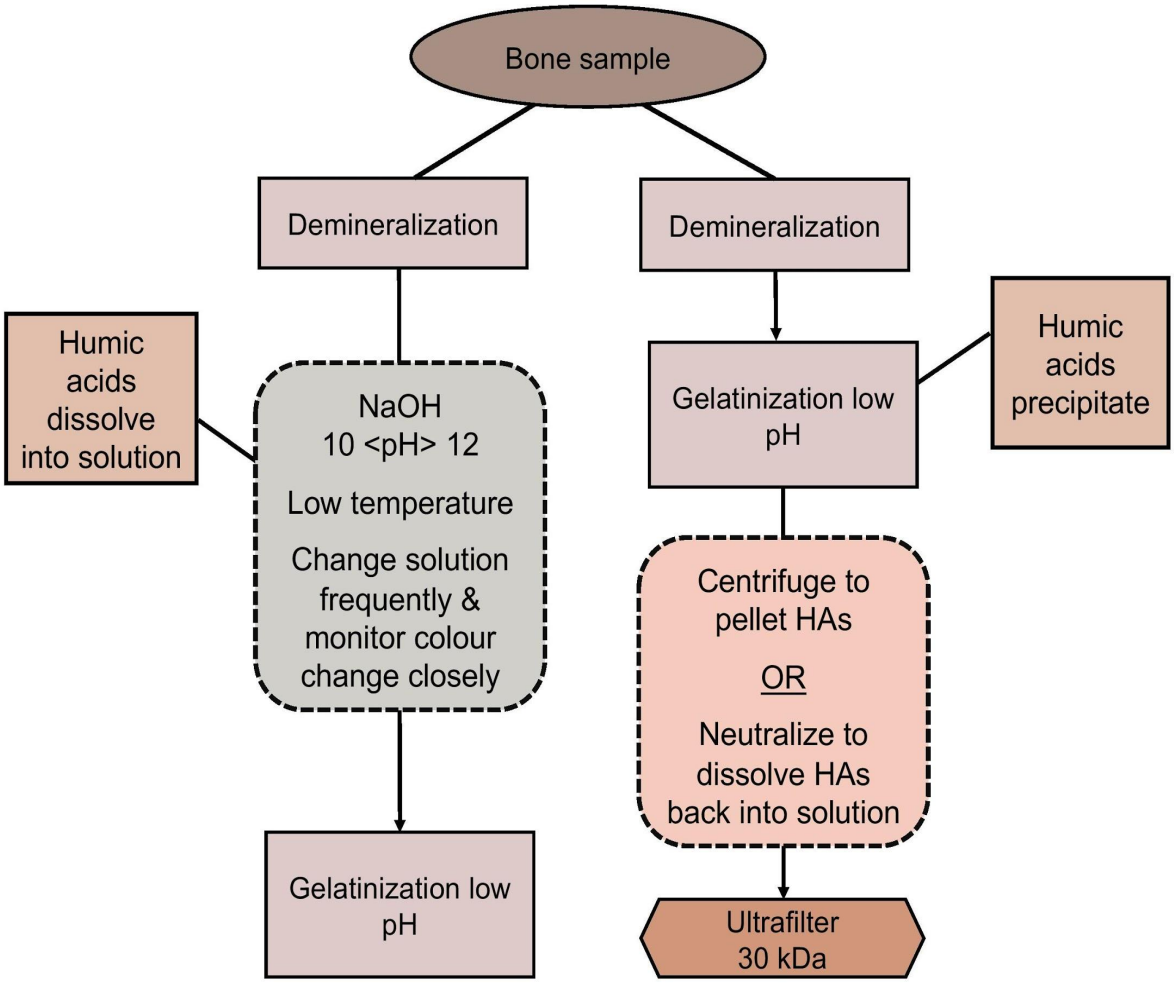

Fig. 2.10 Schematic of suggested modifications to collagen extraction protocols using either NaOH or ultrafilters to remove humic contaminants

6 Conclusion

In accordance with previously published research (Szpak et al., 2017), we found that the treatment of collagen with NaOH removes humic acid contamination more effectively than the use of 30 kDa ultrafilters alone (Szpak et al., 2017; Jørkov et al., 2007). However, we were able to extend these results by demonstrating that humic acids could be leached from collagen using weaker (0.025 M) NaOH solutions which may allow for greater collagen yields. We found that atomic C/N ratios and wt.% carbon were consistently lower, and $\delta^{13}C$ values on average higher in NaOH treated collagen samples than in ultrafiltered or control samples. Higher D/L values in the

NaOH-treated samples evidenced that some amino acid degradation did occur, but this effect on amino acid composition was minimal. Humic solids extracted from the collagen of marine mammals appeared to be mostly derived from terrestrial plant matter, as suggested by low $\delta^{13}C$ values and high atomic C/N ratios relative to the collagen samples. From these results, we can recommend the use of 0.025 M NaOH over more basic solutions to remove humic acids and reduce collagen loss.

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Supporting information: Appendix 1

SI File 1: Methods

SI Table 1: Sigma Aldrich amino acid mixture used as in-house standard for the calculation of $\delta^{13}C$ values of amino acid derivatives

SI Table 2: Stable isotope values and collagen quality indicators of experimental collagen samples and humic extracts

SI Table 3: Amino acid concentrations in three samples of collagen and a humic solid extracted from dog bone.

SI Table 4: Amino acid composition of three samples of and humic solids extracted from dog bone

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Chapter 3

Stable Isotope Studies of North American Arctic Populations: A Review

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Abstract

We review the major stable carbon and nitrogen isotope studies conducted on human remains in the North American Arctic (NAA) and discuss the findings with respect to two major research themes: diachronic subsistence, and the development of food cultures across the NAA. The interpretation of stable isotope data from human bone collagen and hair keratin is complicated by issues of equifinality in addition to uncertainty arising from the high fat/high protein diets of Arctic hunter gatherers. We suggest future lines of inquiry which may help to alleviate some of these challenges. Our review of Arctic stable isotope studies shows the ongoing potential of stable isotope analysis of Arctic hunter-gatherers and faunal populations, but we include the caveat that regardless of how cutting-edge or refined the analytical method, future stable isotope studies must be contextualized with other lines of evidence from well-excavated sites, and would profoundly benefit from the incorporation of Indigenous perspectives and research priorities.

1 Introduction

Human populations settled the North American Arctic (NAA) relatively late in human history as the resource-limited terrestrial landscape prompted the development of specialized technological and cultural adaptations to extract resources from marine and riverine environments. The focus of this paper is on the Late Holocene (1000 – 100 BP) human occupation of Greenland, and the Canadian and Alaskan Arctic coasts. Circa 800 years BP ancestors of modern Inuit and Yup'ik groups, known collectively as the Thule culture, spread from northwestern Alaska eastward across the Canadian Arctic to Greenland and south to Labrador and the Quebec Lower North Shore, in some cases supplanting local Pre-Inuit groups (Raghavan et al., 2014; Friesen and Arnold, 2008; Friesen, 2000). In most of these regions, there is a direct line of genetic descent from the Thule culture to modern Inuit and Yupik populations (Tackney et al., 2019; Raff et al., 2015; Raghavan et al. 2014; Tackney et al.), however population movement within regions is known to have occurred (Friesen et al., 2019). Whitridge (2016) has pointed out the negative historical implications of the term *Thule*, and following from this work, we have chosen not to refer to ancestral Inuit and Yupik populations as Thule. Instead we will refer to groups occupying the NAA during the Late Holocene, but before European contact as precontact Arctic peoples, while those of the post-European contact period will be referred to by their modern names. The cultures of precontact Arctic peoples, including the Old Bering Sea, Birnik, and Punuk cultures, in addition to those known as the Thule, were characterized by the use of sled dogs and large open skin boats (*umiat*, sing. *umiak*) for transportation, sophisticated technology for harvesting and storing a variety of land and sea resources, and social systems featuring settled communities, extended trade and social networks, mortuary ceremonialism, and hierarchical interpersonal relationships (Friesen, 2016; Savelle, 2002a, Whitridge, 1999; Arutiunov and Sergeev, 1990).

In this paper we review the major stable isotope studies conducted to date on archaeological populations dating to the Late Holocene in the NAA. We consider the data with respect to research themes held in common among these works and identify the challenges most frequently cited. We describe how applications of new isotopic methods and analyses may help to refine existing interpretations and emphasize the importance of robust supporting lines of evidence, and the incorporation of Indigenous perspectives and community-led research, for the interpretation and success of future

stable isotope research.

2 Environmental and archaeological context

Despite wide geographic separation and a diversity of marine and terrestrial environments (spanning three oceans and myriad currents, freshwater deltas, tundra and boreal forest), arctic subsistence is generally characterised by reliance on only a few primary taxa common to all regions, with variable input from other secondary taxa where they are locally common. Marine taxa include seabirds and eggs, fish found at least seasonally in near-shore environments, as well as virtually all arctic marine mammals. Most of these taxa have patchy distributions that vary seasonally. Harp seals, some narwhal and beluga, bowhead whales, some walrus populations, salmonids, and most birds practice long-distance seasonal migrations (Turner, 2014; Lavigne, 2009; Schell et al., 1989; Brice-Bennett, 1977), while most other pinnipeds have preferred habitats in terms of sea ice. Thus, harbour (common) seals tend to occupy only open-water environments with access to beaches on which to haul out (including near-shore polynyas in the winter) (Woollett, 2007), and walrus, ringed seals, bearded seals, and hooded seals seek out ice-edge or pack ice environments, bringing them nearer to or farther from human settlements at different times of the year, depending on climate and currents (Stewart and Lockhart, 2004). Of these migratory taxa, those that tend toward gregariousness have generally been more heavily relied upon where they are present (harp seals, beluga, walrus), as they can be hunted *en masse* and the surplus stored for later consumption (Turner, 2014; Brice-Bennett, 1977). Marine mammals were valued as well for their secondary products, such as blubber for lamps or whale bone and baleen for tool manufacture and house construction, and pinnipeds in particular were valued for their skins, which were used in clothing, footwear, boats, house construction, and for lines (Taylor, 1974). Marine and anadromous fish species played significant roles in annual subsistence rounds in the Western Arctic, including the Aleutian Islands, coastal Western Alaska, and the Mackenzie River Delta (Masson-McLean et al., 2019; Britton et al., 2018a; Coltrain, 2010). The presence of fish on archaeological sites in the Eastern Arctic is more sporadic due in part to taphonomic bias against delicate fish remains (Whitridge, 2001), but also due to the timing of fish runs conflicting with the availability of higher-ranked resources (Norman and Friesen, 2010). There are fewer indications that fish

played an important role in human subsistence on the Labrador coast (Woollett, 2007), but anadromous fish are important to modern Inuit and Métis communities in this region (Ames, 1977).

Far fewer terrestrial taxa have been of significant economic importance, particularly prior to European contact and the adoption of trapping economies by some northern peoples. Minor taxa include freshwater fish, which vary in importance by region (Betts and Friesen, 2004; Morrison, 2000), foxes (used mainly for fur), and ground birds, but these are generally eclipsed in importance by caribou (and/or muskox in certain areas) (Betts, 2005). Caribou migrate seasonally to varying degrees and are at peak condition in the late summer/fall. Caribou were important in virtually every arctic society for their furs, which were the best (and only) choice for warm winter clothing (Betts, 2005; Stefansson, 1914).

3 Stable carbon and nitrogen isotopes in arctic environments

Stable carbon isotope ($\delta^{13}C$) values are routinely used to distinguish between consumers of marine and terrestrial food, or between consumers of different photosynthetic groups of plants in archaeological studies (Chisholm et al.,1983; van der Merwe, 1982; Tauber, 1983). In the context of the North American Arctic and Subarctic, only C_3 plants and marine sources of carbon are present. Comprehensive reviews of carbon isotope dynamics in terrestrial and marine environments in the Arctic can be found in Szpak et al., (2019), or Coltrain et al., (2016). A range of just under 10‰ (–30‰ to –22‰), has been observed in the $\delta^{13}C$ values of Arctic and Subarctic plants (Kristensen et al., 2011; Hobbie et al., 2009; Blake, 1991; Ramsay & Hobson, 1991). These differences in baseline values are passed on to upper trophic level consumers: for example, caribou are greater consumers of lichens than other herbivorous species and as a result, tend to have higher $\delta^{13}C$ values than other local taxa (Harris et al., 2019; Guiry et al., 2012; Britton, 2010; Drucker et al., 2010). Marine organisms have considerably higher bone collagen $\delta^{13}C$ values ranging from –17‰ for some seabirds to between –12‰ and –15‰ for marine mammals (Clark et al., 2019; Harris et al., 2019; Szpak et al., 2019; McManus-Fry et al., 2018; Szpak et al.,

2017; Britton et al., 2013; Guiry et al., 2012; Nelson et al., 2012a; Coltrain, Hayes, & O'Rourke, 2004). Additional variation in $\delta^{13}C$ values is also observed between nearshore/benthic areas and the pelagic zone (Sherwood and Rose, 2005), but the degree of benthic-pelagic coupling varies across the Arctic Ocean and neighbouring seas (Feder et al., 2011; Grebmeier et al., 2006).

Stable nitrogen isotope values ($\delta^{15}N$) are used to track trophic relationships in ancient and extant ecosystems as animal tissues undergo stepwise enrichment in the isotope ^{15}N with increasing trophic level (Minagawa and Wada, 1984). Nitrogen occurs in every amino acid and undergoes considerable isotopic fractionation as amino acids sourced from diet or recycled during protein turnover and catabolism are incorporated into the body during growth or tissue maintenance (O'Connell, 2017; Macko et al., 1987). Terrestrial plants in the Arctic have very low $\delta^{15}N$ values, ranging from –8‰ for some evergreen trees to +1‰ for berries (Kristensen et al., 2011; Craine et al., 2009; Hobbie et al., 2009) which in turn produce low $\delta^{15}N$ values (+1‰ to +5‰) in terrestrial herbivores, like caribou or arctic hare (Drucker et al., 2010; Coltrain et al., 2004). Marine food webs contain more trophic levels, and carnivorous marine organisms, such as seal or polar bear, have high $\delta^{15}N$ values (+14‰ to +19‰) (Szpak et al., 2019; Szpak et al., 2017; Cherry et al., 2011).

4 Isotope analyses of preserved human proteins

There are occurrences of natural mummification of deceased individuals in the Arctic in which soft tissues are preserved (e.g. Lynnerup, 2015), but these occurrences are rare, and generally, bone collagen and hair keratin are the most commonly preserved human biological tissues. These tissues can act as proxies for human diet as the isotopic composition of each is derived from consumed dietary protein, and to a lesser extent, from dietary carbohydrates and lipids (Fernandes et al., 2012; Ambrose and Norr, 1993). The value of bulk collagen or keratin represents a weighted average of the $\delta^{13}C$ values of constituent amino acids. Isotopic offsets between collagen and diet average +5‰ but vary with the isotopic composition of different macronutrients (Ambrose and Norr, 1993). If dietary protein has a higher $\delta^{13}C$ value than whole dietary carbon, a greater diet-tissue isotopic offset will ensue than if dietary protein has a lower $\delta^{13}C$ value, or a value similar to that of whole dietary carbon (Ambrose and Norr, 1993). Arctic hunter-gatherers accessed different types of marine and terrestrial foods

sources, depending on local environmental conditions, therefore it is difficult to apply a blanket diet-tissue offset to all palaeodietary analyses conducted in the region. One way of circumventing this source of uncertainty is to compare human collagen $\delta^{13}C$ values directly to faunal collagen $\delta^{13}C$ values as experimental datasets show that the $\delta^{13}C$ value of consumer bone collagen tends to be offset by approximately +1‰ from that of prey collagen (Bocherens and Drucker, 2003). The offset between hair keratin and collagen $\delta^{13}C$ values is variable, but keratin tends to have a lower $\delta^{13}C$ value as it contains fewer glycine residues than collagen; experimental studies of modern and archaeological humans show an average offset of +1.4‰ between collagen and keratin (O'Connell et al., 2001; O'Connell and Hedges, 1999).

Nitrogen is present in amino acids as NH_2^+ molecule bonded to a carbon skeleton. As with carbon, the $\delta^{15}N$ value of collagen or keratin depends upon the biosynthetic pathway of amino acids, and more specifically, on the number of metabolic branches in the pathway (O'Connell, 2017; Petzke et al., 2005; Macko et al., 1987). Isotopic fractionation resulting in a positive increase in $\delta^{15}N$ values is associated with transfer (transamination) of the nitrogen-bearing amino group from one amino acid to another in the body's amino acid pool (O'Connell, 2017; Macko et al., 1987). Newly synthesized proteins are enriched in ^{15}N relative to whole dietary protein, resulting in a positive shift in $\delta^{15}N$ values between diet and consumer. The $\delta^{15}N$ value of proteins can be offset from that of consumed dietary protein by +2 to +6‰ (O'Connell et al., 2012; Bocherens and Drucker, 2003; Minagawa and Wada, 1984; DeNiro and Epstein, 1981), and an average offset of +3 to +4‰ is applied in many palaeodietary analyses, including those studies conducted on the collagen and hair of humans and fauna in the Arctic (e.g. Britton et al., 2018a; McManus-Fry et al., 2018; Coltrain et al., 2016; Coltrain, 2009; Coltrain et al., 2004).

The isotopic composition of bone collagen and hair keratin reflect different periods of time in an individual's life. Human bones begin to develop in utero and once fully matured (in early adolescence to young adulthood) undergo regular cellular maintenance through slow turnover of collagen, bioapatite, and bone cells. Stable isotope analysis of collagen produces a long-term average (often greater than 20 years) of consumed and assimilated dietary protein (Hedges et al., 2007). In contrast, hair keratin grows approximately one cm per month and once formed is metabolically inert (LeBeau et al., 2011), effectively sealing in the isotope values incorporated during growth.

5 Stable isotope analyses of North American Arctic populations

Many subsistence-focused research questions in the NAA can be answered through the analysis of well-preserved zooarchaeological assemblages in tandem with other lines of archaeological and ethnographic evidence, however, there are some cases that seem especially tailored for the addition of stable isotope analysis of human tissues. Butchery practices may bias zooarchaeological assemblages (Betts and Friesen, 2013), while the contribution of taxa such as whales or shellfish to arctic diets can be difficult to estimate due to use and reuse of whale skeletal elements in dwellings and tool manufacture, and incomplete collection and quantification of shellfish remains, respectively (Giovas, 2009; Claassen, 2000; Savelle, 1997; McCartney and Savelle, 1993; McCartney, 1980). A number of stable isotope studies have been conducted on human biological tissues to address the importance of whaling to arctic peoples (Coltrain et al., 2016 ;Coltrain, 2009; Coltrain et al., 2004), to assess the impacts of past episodes of climate change on arctic subsistence practices (Britton et al., 2013), and to provide further information regarding the diets of individuals (Britton et al., 2018a). Britton et al. (2018a) and Tackney et al. (2016) reviewed a number of these studies and noted significant geographic patterning in the types of foods consumed by pre- and post-contact Arctic hunter gatherers. Betts and Friesen (2004) emphasize the critical role that culture plays in fostering the diversity of dietary practices across the NAA. Inuit and Yup'ik populations are composed of discrete peoples with distinct food cultures that developed *in situ* in response to local resource availability and stressors (Britton et al., 2018a; Betts and Friesen, 2013; Betts, 2005; Friesen, 1999; Friesen and Arnold, 1995). In the following section, we provide a brief review of the isotope research completed to date with a focus on how these data were integrated with other lines of archaeological evidence to address two broad, related themes in Arctic research.

5.1 Diachronic perspectives on human subsistence in the Arctic

Stable isotope analysis of human and faunal remains can provide long-term ecological observations that are complementary to traditional ecological knowledge and historical observations, especially if they are used in tandem with palaeoenvironmental proxies

(Jones and Britton, 2019). If human isotope data are contextualized against a faunal isotope baseline (Casey and Post, 2011; van Klinken et al., 2002), then stable isotope analysis can be used to identify shifts in the trophic level of prey, or variation in the relative contributions of marine versus terrestrial sources of protein through time. Stable isotope analysis can also act as a blunt, but independent source of verification of observations from the historical period (Jensen, 2019), for example, by identifying deviations in animal behaviour between modern and archaeological time periods (e.g. Gigleux et al., 2019). Diachronic studies of diet are of particular interest in Arctic and Subarctic archaeology as they can often be linked to fluctuating prey numbers, technological change, cross-cultural interactions, or environmental/climate change (Friesen et al., 2019; Duggan et al., 2017; Betts and Friesen, 2006; Hodgetts et al., 2003; Arneborg et al., 1999). Migration to new physical environments with different suites of resources may have prompted cultural and/or technological adjustments to existing subsistence practices in terms of the types of animals hunted, seasonal harvesting schedules, or technology required to access available prey in sufficient quantities.

The first large-scale stable isotope study to apply a diachronic perspective to an Arctic context was conducted by Coltrain et al. (2004), later followed up by Coltrain (2009). These works estimated the importance of whaling to pre- and post-contact Inuit communities in NW Hudson Bay through $\delta^{13}C$ and $\delta^{15}N$ analysis of adult skeletons and contemporaneous faunal material. Radiocarbon dating of the skeletons revealed that most individuals post-dated the earliest Inuit occupations of the region and likely lived during the period of Neo-Boreal cooling known as the Little Ice Age which stretched from the 15th to 19th centuries (Friesen et al., 2019; Coltrain, 2009). Statistical modelling of the isotope data produced several findings of note. Coltrain et al. (2004) and Coltrain (2009) argued that intra-individual variation in trophic level (as indicated by $\delta^{15}N$ values) but not in the intake of marine protein (as indicated by $\delta^{13}C$ values) suggested differential consumption of low-trophic level marine sources of protein, such as bowhead whale or walrus. Coltrain (2009) posited an increase in consumption of bowhead whales through time at the Silumiut and Kamarvik sites. The suggestion that bowhead whale consumption increased over the Little Ice Age is contradictory to relatively long-held beliefs in Arctic archaeology that increased ice cover during the Little Ice Age would have restricted bowhead whale movements to ice free areas, forcing an increased reliance on animals that thrive in conditions of

increased sea ice cover, such as ringed seal (Schledermann, 1976, 1971). Over the same period of time, ringed seal appear to have played a consistent and prominent role in the diets of the Sadlermiut from Southampton Island, also in northwest Hudson Bay (Coltrain, 2009; Coltrain et al., 2004), but these results conflicted with ethnohistoric accounts of Sadlermiut whaling activities, and archaeological site descriptions from the 1950s (Ryan, 2011). The discrepancy between the ethnohistoric and archaeological sources and the isotopic data is difficult to reconcile here. It is possible that the site descriptions and ethnohistoric accounts may not have accurately quantified the foods actually consumed by the Sadlermiut. It is also important to note that stable isotope analysis of bone collagen largely measures consumed protein; animals that contributed mainly lipids to human diet (such as walrus and bowhead whales) may be underrepresented in bone collagen (Fernandes et al., 2012; Cherry et al., 2011). As will be discussed further below, there is still considerable uncertainty regarding how diets high in protein and fat, and low in carbohydrates will be metabolised by the human body (Wolf et al., 2015; Newsome et al. 2014). Further zooarchaeological and material culture analysis of Southampton Island assemblages are required, and this case serves to highlight how critical other lines of evidence are to the interpretation of stable isotope data.

The effects of past episodes of climate change, such as the Medieval Climate Anomaly (AD 950–1250), and the Little Ice Age (AD 1450–1850) on local climates and weather and by extension on lived human experience can be difficult to estimate using environmental proxies which can have variable temporal and spatial resolution, and may not line up with zones of human occupation in the Arctic (Friesen et al., 2019). Recent diachronic comparisons of human hair isotope values from the Norton Pre-Inuit site of Nash Harbour and the precontact Yupik site of Nunalleq in southwest Alaska may evidence human responses to climate change at the scale of the individual. Britton et al. (2013) demonstrated striking differences in the amount of marine protein typically consumed throughout the year between these temporally separated cultures. Norton diets at Nash Harbour were composed of a greater proportion of high trophic level marine foods while the diets of Nunalleq villagers featured mixed contributions of salmonids, marine mammals, and terrestrial protein (Britton et al., 2018a; Britton et al., 2013). The hair samples from Nash Harbour and Nunalleq were recovered from house-floor contexts and hair fragments were of approximately the same length. The isotopic differences in bulk hair samples between

each site could be attributed to seasonal differences in diet relating to the period of time over which the hair grew, but the isotopic differences persisted even in sequentially sampled locks of Nash Harbour and Nunalleq hair representing approximately one year of dietary inputs, suggesting that these differences must be due to either cultural or environmental factors (Britton et al., 2013). Britton et al. (2013) attribute these differences to geographic variation in the types of resources that could be accessed between the sites, and also suggest that past periods of climate change may have further influenced prey distributions. This hypothesis received additional support from Masson-MacLean et al. (2019) as they argued that a reliance on marine, anadromous and terrestrial species would have provided the Nunalleq community with a buffer against the direct (resource stress) and indirect (social stress) influences of climate change.

5.2 Food culture and social life in North American Arctic societies

The study of diet has long been linked to the efforts of past Arctic populations to regulate inter-personal relationships and control the stressors associated with increasing population density (Friesen, 1999). The analysis of archaeological and ethnographic data reveals diverse strategies for coping with social and resource stressors across the NAA that correspond to the type of resources available within the particular regions of study (Savelle, 2002a; Whitridge, 2000; Friesen, 1999). Over the course of the 21st century stable isotope analyses of human remains from a wide range of archaeological contexts are increasingly used to study the relationship between social organization and diet (e.g. Toso et al., 2019; Alexander et al., 2015; Linderholm et al., 2008). Stable isotope studies of pre-contact Arctic peoples have demonstrated regional variability in diet (reviewed in Britton et al., 2018a, Coltrain et al., 2016, and Tackney et al., 2016), providing additional support to zooarchaeological studies linking diet to ethnic identity (Betts, 2005; Betts, 2009). As the works discussed below will demonstrate, stable isotope-based approaches are particularly well-suited to characterizing intra-individual variation in diet and estimating the breadth of the social catchment area of a particular mortuary site. When used with additional lines of evidence from the archaeological record, stable isotope studies can speak to aspects of food culture, such as storage, or seasonality.

Britton et al. (2018a) measured $\delta^{13}C$ and $\delta^{15}N$ values of sequential samples taken from eight locks of hair recovered from sealed house floor contexts at the Nunalleq village site in southwestern Alaska to investigate how the diets of individuals varied over the period of sample growth (approximately one year). Given the seasonality of resources in the region, the relative stability of the isotopic patterns of four individuals was somewhat unexpected, but did make sense within the archaeological context, particularly when other lines of evidence from the site were considered. The presence of numerous salmon vertebrae on site, and storage vessels containing aquatic biomarkers, strongly suggested that summer salmon runs may have provided the bulk of dietary protein that *some* individuals consumed throughout the year, likely due to the storage of surplus salmon (Masson-McLean et al., 2019; Britton et al., 2018a; Farrell et al., 2014). Modelling of the human hair isotope data against faunal isotope data provided further supporting evidence for the role of salmon in the diets of Nunalleq villagers (Britton et al., 2018a; Britton et al., 2013). However, not all individuals consumed isotopically static diets: three locks of hair tracked an increase in either $\delta^{13}C$, or $\delta^{15}N$ and that persisted for several months of growth; a fourth featured covariance of $\delta^{13}C$ and $\delta^{15}N$ values over a period of approximately six months; and a fifth featured a significant decrease of $\delta^{15}N$ values, but little change in $\delta^{13}C$ values, prompting Britton et al. (2018a) to put forward several possible explanations for the observed variation. Increasing $\delta^{13}C$ and $\delta^{15}N$ values probably evidenced the consumption of higher trophic level marine protein; the rising and falling $\delta^{13}C$ and $\delta^{15}N$ values of another individual suggested a reliance on freshwater resources, such as fish or waterfowl, during part of the year followed by increasing contributions from marine protein; and finally, falling $\delta^{15}N$ values with static $\delta^{13}C$ values suggested consumption of shellfish or other low trophic level marine protein sources (Britton et al., 2018a). Taken together, the diversity of dietary patterns present in only eight locks of hair has implications for individual mobility patterns, social roles and social organization, and individual food choices at Nunalleq (Britton et al. 2018a). This study was unique for offering a glimpse into the lives of individuals, which are not always accessible using traditional archaeological methods, and is complementary to studies of population- or community-level trends.

Nelson, Lynnerup, and Arneborg (2012b) did not initially design their study to address questions relating to Inuit diets in Greenland, but rather planned to use Inuit stable isotope data to aid in the interpretation of diachronic isotopic data sets from

Greenlandic Norse skeletons. However, the resulting data offered a tantalizing glimpse into Inuit subsistence and revealed geographic and intra-population differences in the types of marine species hunted, and in the relative contribution of marine and terrestrial species to Inuit diets. For example, while diets rich in marine protein were the norm among individuals recovered from coastal sites in southwest Greenland, human bone collagen $\delta^{13}C$ and $\delta^{15}N$ values varied between 23 individuals recovered from the site of Assumiut (Nelson et al., 2012b). Ringed seal appeared to be the predominant source of dietary protein for the majority of individuals, but one adult female and a subadult may have received greater contributions of protein from narwhal, while a second subadult appeared to consume protein with stable isotope values consistent with harp seals (Nelson et al., 2012a; Nelson et al., 2012b). In northeastern Greenland, human bone collagen values plotted along a continuum of increasing contributions of marine-derived dietary protein, and multiple dietary patterns were present at the site of Dødemandsbugten (Nelson et al. 2012b). Nelson et al. (2012b) suggested that, in general, each Inuit community occupied its own territory and did not move widely around the landscape to obtain resources, but the presence of different dietary strategies implied by outlying collagen isotope values at several sites suggested movement of certain individuals who may have spent part of their lives elsewhere (Nelson et al. 2012b).

The patterns of inter-individual differences in diet uncovered by Britton et al. (2018a) and Nelson et al. (2012b) were also found by Coltrain et al. (2016) in their isotopic study of Nuvuk, the largest pre-contact mortuary site in Alaska. Within the site, the $\delta^{13}C$ values of adults ranged from –15.7‰ to –12.4‰ and the $\delta^{15}N$ values ranged from +17.7‰ to +22.4‰ (Coltrain et al., 2016). Some of this range in data may be attributable to biological sex: while the mean collagen $\delta^{13}C$ and $\delta^{15}N$ values of biological male and female skeletons did not differ significantly, the $\delta^{15}N$ values of male skeletons were more variable than those of females (Coltrain et al., 2016). Where osteological evidence of biological sex is available for assemblages of human remains in the Arctic, there are consistently no statistically significant differences in the mean $\delta^{13}C$ and $\delta^{15}N$ values of males and females (Coltrain et al., 2016; Nelson et al., 2012b; Coltrain, 2009; Coltrain et al., 2004). However, the breadth of results reported by Coltrain et al. (2016) suggests that some males may have had access to different types of marine protein, perhaps due to their involvement in different subsistence or trade activities.

6 Challenges and future prospects of stable isotope studies of arctic populations

In certain archaeological contexts stable carbon and nitrogen isotope ratio analysis of human biological tissues can yield important insights into past human lifeways, particularly in cases where faunal preservation is poor, or when inter- and intra-population dietary variation is under study. However, stable isotope analyses of bulk proteins in the Arctic, as elsewhere, are limited by problems of equifinality. For example, prey species may have overlapping isotope values so that relative contributions of one prey class versus another cannot be distinguished with isotope mixing models (Phillips et al., 2014), or it may not be possible to distinguish physiological influences on $\delta^{15}N$ values from dietary inputs (e.g. Britton et al., 2018a). Additional problems occur when attempting to assign human remains to an absolute chronological framework. For many years after the adoption of radiocarbon dating, the skeletons of archaeological marine hunter-gatherers were avoided as a source of radiocarbon dates in the Arctic (e.g. Dumond and Griffin, 2002; Morrison, 1989; Arundale, 1981; McGhee and Tuck, 1976), due to the uncertainty associated with the marine radiocarbon reservoir and with estimated contributions of marine carbon to human bone collagen. While a number of authors have developed methods for estimating the contribution of marine carbon to human bone collagen (e.g. Raghavan et al., 2014; Craig et al., 2013; Barrett and Richards, 2004; Arneborg et al., 1999), local deviations, termed the delta (Δ) R, in the offset between atmospheric ^{14}C concentrations and the marine radiocarbon reservoir remain a major source of uncertainty that must be included in the calibration of ^{14}C ages from human and marine faunal skeletal remains (Bronk Ramsey, 2008; Stuiver, 1986). A discussion of ongoing research on this topic is beyond the scope of this paper, but readers are encouraged to see Dyke et al. (2018), Krus et al. (2019), and Ledger et al. (2016) for an Arctic perspective on this issue. In the following section, we elaborate on some of the issues associated with equifinality, and present recently developed areas of research that have potential applications in Arctic archaeology.

6.1 Asking better questions: Community-led research and bioarchaeology in the Arctic

We begin by focusing on recent developments in Indigenous and community-led research in Arctic communities, as further bioarchaeological research cannot proceed without input and consent from descendent communities. With the development of the National Graves and Repatriation Act (NAGPRA) in the United States, and the adoption of similar provincial legislature in Canada, many of the skeletal assemblages that were collected during the 19th and 20th centuries are being returned to Arctic communities, and most bioarchaeological studies are no longer conducted without permission from descendent groups. Through the development of community-led interdisciplinary archaeology projects, such as those at Nunalleq Village and Nuvuk in Alaska, or the Traditions and Transition project in Labrador, considerable progress has been made to incorporate the priorities of Indigenous stakeholders into archaeological research design (Traditions and Transitions, 2019; Hillerdal, 2017; Jensen, 2012). Some Canadian universities, such as the University of Victoria, the University of British Columbia, and Memorial University of Newfoundland, are now developing and implementing Indigenous research paradigms, but much still needs to be done to incorporate the voices and concerns of Indigenous groups across the Arctic in the development of archaeological questions. The incorporation of traditional knowledge could lead to a much deeper, more nuanced understanding of local environments (past and present), and an overall better interpretation of archaeological data. For example, the development of partnerships between Indigenous informants and Western scientists to study biodiversity and conservation in the north has improved the quality and scope of data regarding the ways species and arctic environments are responding to climate change and to the intensification of human exploitation of land and sea resources (Thornton and Scheer, 2012; Krupnik and Ray, 2007; Stevenson, 1996). For bioarchaeologists practicing in the NAA, such an approach would aid in building bridges between academic disciplines and Indigenous communities which in turn would lead to more interesting and relevant research questions, and new ways of tackling old problems. The Inuit Tapiriit Kanatami has put forward a clear and concise guide to conducting research on Inuit lands in Canada which includes strict guidelines on the ethical conduct of researchers and open access publication of data. Compliance with published Indigenous research guidelines (e.g.

FNIGC, 2019; ITK, 2018) would only improve the scope and impact of future bioarchaeological studies, and the relationships between archaeologists and Indigenous groups across the Arctic.

6.2 Macronutrient routing and physiological inputs to human stable isotope values

As reviewed above, the diets of archaeological Arctic hunter-gatherers were composed predominantly of protein and fats derived from marine mammals, fish, and caribou, with limited sources of carbohydrate. The incorporation of these macronutrients into human tissues is a source of uncertainty that must be considered when conducting palaeodietary analyses of arctic populations. In laboratory settings high protein diets are associated with increased direct routing of dietary amino acids to proteinaceous tissues (collagen, hair, and blood), and a lower diet-collagen $\delta^{13}C$ offset (Jim et al., 2006). Conversely, the consumption of marine protein may actually increase nitrogen isotope diet-tissue offsets (Webb et al., 2016). These experimental findings may have implications for palaeodietary studies of Arctic hunter-gatherers, particularly with respect to estimations of trophic level. The high marine protein diets of Arctic peoples may increase the diet-collagen $\delta^{15}N$ offsets and render commonly used trophic discrimination factors inappropriate for this context (Hedges and Reynard, 2007). However, in most of the cases presented in this paper, the trophic discrimination factors applied to human isotope data appear to be appropriate, based on prior assumptions for the zooarchaeological and archaeological records (Gulløv, 2012; Nelson et al., 2012b; Coltrain, 2009; Coltrain et al., 2004), but further support from the application of newer generations of palaeodietary models (e.g. FRUITS [Fernandes et al., 2015]; or SIMMR [Parnell, 2016]) would be a welcome addition to Arctic stable isotope studies.

The contribution of carbon from dietary lipids to bone collagen is generally considered to be relatively minor (Fernandes et al., 2012). In other, lower latitude contexts, populations accessed wild and cultivated sources of carbohydrates that provided ready sources of energy for amino acid synthesis, however, energy sources in the Arctic are limited to seasonal, and regionally variable, contributions from greens, tubers, berries, and seaweed, with the bulk sourced from animal fats. The influence of dietary lipids, such as whale (*muktuk*) and seal (*nuktuk*) blubber, on collagen $\delta^{13}C$

values is uncertain: experimental work with other mammals has shown flexibility in the incorporation of dietary lipids into proteinaceous tissues, prompting some researchers to urge caution when designing stable isotope studies of animals (including humans) with high lipid diets as protein-only models may misinterpret the stable isotope data (Newsome et al., 2014; Newsome et al., 2010). As stable isotope studies of arctic populations have thus far been limited to the analysis of bulk proteins (collagen and keratin), the interpretations of resulting isotope data sets have, of necessity, been quite broad. A recent analysis of polar bear blood and adipose tissue samples determined that large-bodied prey (whales and walrus) provided the greatest contribution of dietary lipids, while smaller marine mammals provided the bulk of dietary protein to bears (Cherry et al., 2011). A similar approach using human skeletal remains would be challenging as the $\delta^{13}C$ analysis of archaeological bone lipids remains relatively unexplored (Colonese et al., 2015). Instead, the $\delta^{13}C$ analysis of non-essential amino acids found in bone collagen or hair keratin may offer a way forward. Non-essential amino acids can be divided into two groups by biosynthetic precursor: Glucogenic amino acids (glycine, alanine, serine) are synthesized from carbon precursors taken from dietary carbohydrates and lipids, while the ketogenic amino acids (glutamate and aspartate) can be synthesized from carbon sourced from all dietary macronutrients (Newsome et al., 2014). As sources of dietary carbohydrates are limited in most of the Arctic, glucogenic amino acids would largely reflect dietary lipid sources. Building from Cherry et al. (2011), it could then be possible, for certain hunter-gatherer populations, to model the contributions of lipid sources from, for example, bowhead whale, seal, or terrestrial sources of fat, using the $\delta^{13}C$ values of glucogenic, and potentially ketogenic amino acids, too. Further insights could then be gained through comparison with the $\delta^{13}C$ values of proline which may be routed directly from dietary protein (Jim et al., 2006).

Dietary stress was proposed as a possible influence on human stable isotope values in the Arctic (Coltrain et al., 2016). During periods of nutritional stress, protein synthesis in healthy adults tends to slow, but it does not cease completely (Mekota et al., 2006). When insufficient concentrations of amino acids are consumed, the body will catabolise amino acids from skeletal muscle, predominantly targeting glutamic acid and alanine, for tissue maintenance, leading to secondary enrichment in ^{15}N of body proteins (Neuberger et al., 2013; Mekota et al., 2006). Fuller et al. (2005) found evidence of this phenomenon, in the form of increasing $\delta^{15}N$ values, in modern

pregnant people suffering from morning sickness. The influence of dietary stress on collagen $\delta^{13}C$ values hypothesized by Coltrain et al. (2016) finds support in the work of Neuberger et al. (2013) who, in a study of $\delta^{13}C$ and $\delta^{15}N$ values in the hair of anorectic patients, posited that the catabolism of body fat would introduce ^{13}C depleted carbon back into the body's carbon pool, thereby reducing the $\delta^{13}C$ value of amino acids that can use lipid-derived carbon as a substrate. Beaumont and Montgomery (2016) observed this phenomenon in dentine serial sections from Irish Famine Victims. It may be premature to assume that hunter-gatherers in the Arctic were regularly afflicted by dietary stress. While there are recorded occurrences of starvation during the post-European contact period relating to illness and modern declines in Arctic prey species (Krupnik and Chlenov, 2013; Boas, 1964), there is insufficient evidence to assume that nutritional deficits were commonplace across the Arctic during prehistory. However, osteological analyses of skeletal remains from Alaska to Labrador do report skeletal markers that may be consistent with physiological stress, such as that caused by illness, or vitamin deficiencies caused by parasitic infection, or use of non-traditional foods provided by European whaling groups (Keenlyside, 1998; Keenleyside, 1990; Way, 1978). Physiological stress should be considered as a possible source of negatively covarying $\delta^{13}C$ and $\delta^{15}N$ values (King et al., 2018; Beaumont and Montgomery 2016; Beaumont et al., 2015), but the application of a blanket correction to palaeodietary models may not be necessary.

6.3 Food preparation and storage

Arctic peoples preserved hunted and gathered food resources in a variety of ways (stored in snowpack, mixed with oil or fat, air dried, or carefully fermented) for consumption throughout the year (Friesen and Arnold, 1995; see Yamin-Pasternak et al., 2014 for a modern example). In the case of large scale summer or fall hunts, such as caribou in their prime, beluga drives, salmon runs, or bowhead whales, the meat and (especially) fat these provided were often expected to last through the leanest months of winter, from February to April (Masson-MacLean et al., 2019; Betts and Friesen, 2013, 2006; Betts, 2005; Taylor, 1988). It has long been recognised that the subsistence systems of many arctic peoples fall into the category of "collecting" on the spectrum of complex hunting and gathering societies (Savelle, 2002b; Binford, 1980). This distinction, in opposition to patterns of "foraging", is an important one in that

collecting is characterised by a lower level of residential mobility, but a higher level of logistical (or task) mobility and storage of high-bulk focal resources (Woollett, 2007; Betts, 2005; Whitridge, 1999; Stenton, 1989; Binford, 1980). These collecting and storage patterns, combined with variable mobility practices, may have the effect of attenuating expected seasonal differences in isotopic composition of human tissues, even when examined at a finer scale, as suggested by Britton et al. (2018a).

Several stable isotope studies have also proposed that the process of decomposition may raise the $\delta^{15}N$ and $\delta^{13}C$ values of stored meat. Bada et al. (1989) analysed the effects of artificial protein hydrolysis on the stable isotope values of modern tendon collagen. The hydrolysed protein fragments became slightly enriched in $\delta^{15}N$, while the $\delta^{15}N$ values of 78nhydrolyzed protein increased by up to +20‰ (Bada et al., 1989), possibly due to selective loss of particular amino acids with lower $\delta^{15}N$ values. Recently Yurkowski et al. (2017) tested the effects of decomposition and the duration of cold storage on the isotope values of ringed seal meat, Greenland shark tissue, and fish, and suggested that cold storage at a consistent temperature did not have an appreciable effect on stable isotope values, however, decomposition in a closed environment increased ringed seal $\delta^{15}N$ values by up to +2‰ (Yurkowski et al., 2017). Further experimental archaeology studies may be required, but the effect on human $\delta^{15}N$ values would probably be minor and may only be visible in incrementally growing tissues such as hair keratin, or tooth dentine.

6.4 Isotope baselines

The faunal isotope baseline is a key component of any palaeodietary or radiocarbon study using human bone collagen as an analyte; ideally, human isotope values will be compared to a set of carbon and nitrogen isotope ratio measurements from local, contemporaneous archaeological animals (van Klinken et al., 2002). Shifts in the $\delta^{13}C$ and $\delta^{15}N$ values of primary producers are known to occur through time and over geographic space, and higher trophic level animals may also modify their feeding behaviours depending on local environmental conditions or hunting pressures (Bocherens et al., 2014; Casey and Post, 2011; Betts and Friesen, 2006). Several recent studies of modern and archaeological specimens have shown the influence of climate and other environmental factors on the $\delta^{13}C$ and $\delta^{15}N$ values of Arctic fauna. Szpak et al. (2019) have demonstrated significant differences in the $\delta^{15}N$ values of

ringed seal populations of the Central Canadian Arctic Archipelago over the past 2000 years. Historic and modern walrus populations of the Chukchi Sea had significantly lower $\delta^{15}N$ and $\delta^{13}C$ values than archaeological specimens (Clark et al., 2019), findings which echoed that of an earlier study conducted on multiple species of archaeological and modern marine mammals from the same region (Szpak et al., 2017). The extensive sampling protocols of the aforementioned studies exceed the scope of most human palaeodietary studies, but they serve to highlight the possibility of temporal differences in isotope baselines that should be considered when conducting human palaeodietary analyses. To date, it is difficult to conduct statistical comparisons of archaeological faunal isotope values across the Arctic due to the varying sizes of published data sets, and incomplete reporting of the archaeological context of the faunal remains used to construct isotope baselines. The increasing popularity of stable isotope analysis as a tool for palaeoenvironmental studies may reduce the sample size disparities in the future, but archaeological palaeodiet studies must still deal with issues arising from legacy collections stored in museums in North America and in Northern Europe. Some of these issues include changes in recovery methods of faunal material between the present and early 20th century (Betts, 2016); difficulties in accessing skeletal material in distant repositories that may or may not have complete inventories; and the recovery of mixed faunal assemblages from sites with multiple, overlapping, Pre-Inuit and Inuit or Yupik contexts, a common occurrence in the NAA (Park, 1993). Sampling protocols may also introduce a bias to the isotope baseline. For example, it has been proposed that in some Arctic and Sub-Arctic regions, hunter-gatherers preferred juvenile prey to adults, and that the nursing effect on $\delta^{15}N$ values of young prey animals may explain higher than expected $\delta^{15}N$ values of human bone collagen, but the bones of juveniles animals are often bypassed in favour of those from mature specimens (Nelson et al., 2012b) which are considered more representative of animal populations.

Compound specific isotope analysis of amino acids liberated from archaeological specimens, such as bone collagen, hair keratin, or baleen may alleviate some of the problems associated with equifinality or isotope baselines. Essential amino acids are transferred intact from dietary protein to human tissues, allowing the $\delta^{13}C$ and $\delta^{15}N$ values of these amino acids to be used as tracers as negligible isotopic fractionation occurs during transfer (Popp et al., 2007; Fogel and Tuross, 2003; McClelland and Montoya, 2002). The $\delta^{13}C$ values of essential amino acids, when combined in

statistical models, can identify the 'isotope fingerprints' associated with different sources of primary production allowing the relative contributions of multiple foodwebs to a consumer isotope value to be characterized (Elliott Smith et al., 2018; Wang et al., 2018; Larsen et al., 2013; Larsen et al. 2009). This method has potential for improving our understanding of arctic diets, particularly when the contributions of prey species are difficult to distinguish using bulk collagen $\delta^{13}C$ and $\delta^{15}N$ values alone. Two studies conducted in the past 10 years have revealed surprisingly variable $\delta^{13}C$ values (–21.2‰ to –26.3‰) of the amino acid phenylalanine ($\delta^{13}C_{Phe}$) from 10 archaeological Inuit mummies from the Nuusuuaq Peninsula in Greenland that otherwise had relatively homogenous bulk collagen $\delta^{13}C$ values (–13.9‰ to –12.6‰) (Honch et al., 2012; Raghavan et al., 2010). This exceeds the variation in $\delta^{13}C_{Phe}$ values measured in the collagen of hunter-gatherers from the coast of the Baltic Sea (–25.3‰ to –24.4‰) (Webb et al., 2016), or the hair of hunter-gatherers from Chile (–24.7‰ to –20.6‰) (Mora et al., 2016). These data suggest that the individuals from Nuusuuaq were either consuming different types of marine protein, or the same type of protein, but from regions with different isotopic baselines. Further analysis of faunal specimens is of course required, but even this small dataset is evocative of the potential of compound specific carbon isotope applications to arctic contexts with respect to human palaeodiet, social organization, and palaeoenvironmental reconstructions.

6.5 Breastfeeding and childhood diets

Decisions surrounding breastfeeding initiation, the time at which complementary foods are introduced, and the types of foods given to infants are strongly influenced by cultural attitudes toward female bodies, child rearing, and sexual politics (Palmer, 2009; Fildes, 1986). Breastfeeding and weaning practices, and the foods accessed by children, are closely linked to infant mortality and infection (Sankar et al., 2015), population size, social and economic roles of infant caregivers, and social concepts of childhood (Fildes, 1986). Stable carbon and nitrogen isotope analysis of bone and dental collagen is commonly used to study breastfeeding and weaning practices in disparate archaeological contexts around the world (e.g. Britton et al., 2018b; King et al., 2018; Eerkens and Bartelink, 2013; Nitsch et al., 2011; Herring et al., 1998), but to date such studies have not been attempted in Arctic contexts. There is little published information about the breastfeeding and weaning practices of Arctic caregivers in the

pre- or post-contact periods that can be used to understand the modern trajectory of infant care in the Arctic (McIsaac, 2014; Asuri et al., 2011). Bioarchaeological studies of breastfeeding of pre- and post-contact Arctic populations would be informative of infant and maternal health in the past (Beaumont and Montgomery, 2016). Through sequential sampling and isotopic analysis of human deciduous and permanent teeth it may be possible to identify sub-annual changes in maternal and infant diets (Beaumont et al., 2015), to estimate average breastfeeding practices and by extension, commonly-held attitudes about childrearing (Britton et al., 2018b), to relate breastfeeding practices to the social and economic roles of infant caregivers (Nitsch et al., 2011), and by comparing the diets of infants and adults, gain more insight into social constructions of childhood among arctic hunter-gatherers.

7 Conclusions

Archaeological research in the North American Arctic benefits from well-preserved faunal assemblages and a rich ethnographic record with which to reconstruct past human subsistence, but stable isotope analysis of human and faunal biological tissues still has a role to play by complementing site- and region-based analyses with data from individuals. The research discussed in this review demonstrates that stable isotope analyses of human bone collagen and hair keratin have yielded important insights into diachronic shifts in diet, food cultures, and aspects of social organization at the level of the individual, but stable isotope research still faces the same challenges in the Arctic as it does elsewhere; issues of equifinality pose a number of problems in the interpretation of isotope data sets from bulk and sequentially sampled human tissues. There is reason for hope: Arctic researchers are now combining stable isotope analysis with community-led research agendas, site-based interdisciplinary analyses, and are better able to contextualize human stable isotope data as a result. The application of additional methods, such as compound specific isotope analysis, or the isotopic analyses of breastfeeding and weaning practices, has considerable potential in the Arctic. Future research must continue to incorporate Indigenous voices and research priorities as this will only improve the quality of information gleaned from archaeological and bioarchaeological investigations in the Arctic.

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Chapter 4

Diversity in Labrador Inuit sled dog diets: Insights from $\delta^{13}C$ and $\delta^{15}N$ analysis of dog bone and dentine collagen

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Abstract

Sled dogs were an integral part of Labrador Inuit life from the initial expansion and settlement of northeastern Canada to the present day. Tasked with pulling sleds and assisting people with other subsistence activities in the winter, dogs required regular provisioning with protein and fat. In this paper, we conduct stable carbon and nitrogen isotope ratio analysis of the skeletal remains of dogs (n=35) and wild fauna (n=68) from sites located on the north and south coasts of Labrador to characterize dog provisioning between the 15th to early 19th centuries. In addition, we analyse bone (n=20) and dentine (n=4) collagen from dogs from Double Mer Point, a communal house site in Hamilton Inlet to investigate how dog diets intersected with Inuit subsistence and trade activities at a local level. We find that dog diets were largely

composed of marine mammal protein, but that dogs on the north coast consumed more caribou and fish relative to dogs from the central and south coast sites. The diets of dogs from Double Mer Point were the most heterogenous of any site, suggesting long-distance movement of people and/or animals along the coast.

1 Introduction

Biomolecular approaches to the zooarchaeology of dogs, including stable isotope analysis and ancient DNA (aDNA), can speak to canine population histories and human-canid relationships over the course of our shared history. In Inuit cultures, dogs provided traction, hunting assistance, food, fur, protection and companionship, and in exchange, required food. Historically, Inuit and related Yup'ik cultures inhabited a range of environments and engaged in regionally and culturally distinct subsistence activities with implications for dog provisioning (Britton et al., 2018; Betts, 2005; Savelle, 2002). For example, Alaskan communities of the pre-contact and modern eras provisioned dogs with salmon, a resource that could be acquired in bulk and dried (McManus-Fry et al., 2018; Loftus et al. 2014). Human-canine relationships and the position of dogs among communities of the western and central Arctic have been further examined using osteometric, archaeological, ethnographic and genetic data (Davydov and Klokov, 2018; Hill, 2018; Losey et al., 2018; Strecker, 2018; Pitulko and Kasparov, 2017; Brown et al., 2013; Coltrain et al., 2004; Park, 1987; Morrison, 1984) but to date similar research in the Eastern Arctic and Subarctic is limited in scope (Ameen et al., 2019; Woollett, 2003). In Labrador, Canada, food resources varied with the season and location; Inuit communities moved seasonally to access patchy resources and to engage in long distance trade networks. Dog diets may reflect the geographic and seasonal distribution of prey resources, and the need to provision dogs with foods that could be stored and transported, or easily acquired while on the move.

To understand the reciprocal interactions of human subsistence activities, dog provisioning, and labour, we conducted the first carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratio study of Labrador Inuit dogs from five archaeological sites spanning the Labrador coast. We contextualized the data against the isotopic composition of local wild fauna to identify possible dietary protein sources. We paired a regional survey of dog diet with an intra-site analysis of dog teeth and bones from the site of Double Mer

Point and consider these data with respect to the local environment, the seasonal subsistence base, and the role of Double Mer Point in Inuit coastal trade networks.

1.1 Archaeological context

The ancestors of Labrador Inuit left the western North American Arctic and rapidly explored and settled the Eastern Arctic (including the Canadian Arctic Archipelago and Greenland) during the first half of the 13th century (Friesen, 2019; McGhee, 2009). This territorial expansion was facilitated by an economic dependence on arctic marine mammals, and by Inuit mastery of long-distance travel over snow and ice using dog traction technology, and over water using skin-covered boats (*kajat* and *umiat*). The movement of Inuit into the Labrador peninsula has been dated to ~1450 at sites north of Nain (Whitridge, 2012, 2016; Kaplan, 1983), and between the late 16th and 17th centuries Inuit had expanded their seasonal settlement pattern as far south as the Quebec Lower North Shore (Fitzhugh, 2015, 2016 Rankin, 2015; Stopp, 2002). During this early period of exploration, Inuit constructed small, sometimes multi-lobed, semi-subterranean houses in the outer coastal areas of Labrador, and hunted large whales, multiple species of seal and fish, and terrestrial animals (Kaplan and Woollett, 2016). Inuit came into contact with traces of Basque whalers and French fishers who had established shore stations along the southern coast of Labrador for the intensive harvesting of Atlantic cod (*Gadus morhua*) and bowhead whales (*Balaena mysticetus*) (Pope, 2015;; McLeod et al., 2008; Rastogi et al., 2008; Stopp, 2002; Barkham-Huxley, 1984). Through informal trade and seasonal looting of abandoned whaling and fishing stations, Inuit incorporated European-manufactured materials (modified iron nails, roofing tiles, hardwood) into their toolkit (Rankin and Crompton, 2016a; Jordan, 1978). Inuit developed a long-distance trade network, powered by influential middlemen traders, to move European goods and Inuit-harvested raw materials (baleen, seal and whale oil) up and down the coast (Taylor, 1977). As European harvesting depleted the stocks of baleen whales and walrus, seal increasingly became the focus of Inuit subsistence (Fitzhugh, 2016). A change in architectural style, from single-family dwellings to large semi-subterranean dwellings with multiple sleeping platforms and lamp stands, occurred by the mid-17th century and was widely adopted during the 18th century (Rankin, 2014). The onset of this Communal House Phase may have been stimulated by cooperative seal hunting, or have been an effective means to trade

European goods, organize labour, and boost social status (Rankin and Crompton, 2016b; Fay, 2015; Woollett, 2003; Kaplan and Woollett, 2000; Jordan, 1978). Hamilton Inlet, the geographic focus of our study, was a prime locus for trade in the latter half of the 18th century. Inuit in Hamilton Inlet could enter into trade with Quebec-based and English merchants, who had several posts through the 18th century along the shores of Lake Melville and Hamilton Inlet, while maintaining access to the abundant food resources available in The Narrows (Bohms, 2018). Hamilton Inlet was also used by Inuit overwintering on trading journeys between northern and southern Labrador (Kaplan, 1983; Taylor, 1974). Following the 1763 Treaty of Paris, Labrador was ceded to the British, and French posts and stations were slowly abandoned (Rankin et al., 2012). Though British merchants were not at first permitted to settle, the Moravian Church was granted 100 000 acres of land in Northern Labrador, and established mission stations at Nain (1771), Okak (1776) and Hopedale (1782) to Christianize the Inuit and regulate Inuit-European interactions. More stations were opened to the north and south beginning in 1830, but these early stations were particularly important in the way they disrupted the previously-established north-south Inuit trade routes by providing an alternative, northern entry point for many (but not all) European-manufactured goods (Rollmann, 2011; Taylor, 1976).

1.2 Dogs and Inuit culture

Human-dog interactions in Arctic communities have historically represented a reciprocal relationship wherein dogs exchanged labour for food, and humans laboured to feed dogs. In Arctic contexts where food resources can be acquired in bulk, dogs are commonly known for pulling sleds and assisting with subsistence activities (Davydov and Klokov, 2018). In some communities it was acceptable to consume dog meat (Park, 1987), while in others this practice was taboo, or reserved for times of economic hardship (Rasmussen, 1929). Dogs provided durable, moisture-resistant fur for lining mittens, trimming the hoods of parkas, and forming the outer portion of sealskin boots (Issenman, 2011). Additionally, dogs were tightly integrated into Inuit cosmology and could hold social roles within their communities (Laugrand and Oosten, 2002).

The earliest evidence for circumpolar dog sledding, dating to c. 8000 BP, was found on Zhokhov Island in the Siberian High Arctic (Pitulko and Kasparov, 2017,

1996). Whitridge (2018) suggests that the complete dog traction kit, including the sled (*komatik*) and its components, trace buckles, lines, and whips arose in the western Canadian Arctic, effectively enabling the rapid Inuit expansion eastwards. At regional scales, dog sledding served to connect communities (Sheppard, 2004), leading Birket-Smith (1945) to categorize dog traction as a mode of communication in the Arctic. Dogs were critical players in the seasonal mobility practices of Labrador Inuit. Pulling sleds from December through June, dogs moved entire households between autumn-winter and spring habitation sites along the coast and carried caribou carcasses from hunting camps in the interior (Woollett, 2003). The possession of a dog team allowed greater participation in pre-19th century Inuit trade networks, and increased the status of middlemen traders (Fay, 2015). By the late 18th century, some Inuit families on the north coast were in possession of up to 28 dogs and were capable of moving a large amount of goods across the landscape (Taylor, 1974). Humans also relied on dogs to navigate the landscape and scent prey (Whitridge, 2018). When traveling between communities during bad weather, dogs could be relied upon to scent human habitation sites (Rasmussen, 1929). The use of dog teams for subsistence and trade activities continued until the adoption of snowmobiles in the 20th century (Smith, 1972), and is today a popular winter sport (LWGA., 2019). After the introduction of snowmobiles to northern communities, former dog team owners observed a change in their own behaviours to compensate for the loss of the sensory capabilities of dogs,

> "By using a skidoo as your machine for transportation, you tend to sharpen your own senses: smell, eyes, your sense of direction in the dark or in a storm, and your prediction of the weather. These things were not really sharp before, because you had dogs. If you were going to go somewhere, they would probably know which way to go anyway, because all the things you knew went to the leader, and he recorded where he had been before." (Brody, 1977: 322-323).

As one of the outcomes of domestication was the disruption of natural hunting behaviours (Zeder, 2012; Boitani and Cuicci, 1995), dogs are the only domesticate that, historically, needed to be provisioned with the flesh of other animals.

Domestication carries the obligation to feed (Losey, 2018) and dog team owners could incur significant financial and labour costs while doing so (Krupnik, 1993; Rasmussen, 1929). Sled dogs require diets rich in fat to meet the energy requirements of pulling sleds and to maintain body temperature (Lupo, 2019; McManus-Fry et al., 2018). Rasmussen (1929) observed that sled dogs fed caribou quickly grew lethargic while those fed walrus meat and blubber could work for longer periods of time, potentially biasing dog diets toward marine sources of protein.

1.3 Double Mer Point and Hamilton Inlet, Labrador

Hamilton Inlet is located on the central Labrador coast. It extends from the Labrador Sea inland to Lake Melville and encompasses the marine environments of Groswater Bay, Back Bay, Double Mer, and the Narrows. Double Mer Point (GbBo-02) is located near the town of Rigolet (Fig. 4.1) and is the site of three contiguous Inuit winter houses that, based on artefact typologies, were occupied in the latter half of the 18th century and abandoned by approximately 1840 (Pouliot, forthcoming; Bohms, 2018; Rankin, 2014; Jordan, 1974, 1977). Winters are long with abundant precipitation and land-fast ice occurs between late December and May/June (Ames, 1977; Fitzhugh, 1972). Swift tidal currents flow around Double Mer Point and provide areas of open water that persist during the winter, except under the coldest conditions (Fitzhugh, 1972). Ringed seals (*Pusa hispida*), a source of meat and hides, were present year-round and could be hunted through breathing holes on fast ice, caught in polynyas during the winter, or when basking in the spring (Woollett, 1999). Harbour seals (*Phoca vitulina*), prized for their hides (Elliott, 2017), were more numerous in the summer, but could be hunted during the winter around polynyas and at the ice floe edge (Woollett, 1999). Harp seals (*Pagophilus groenlandicus*) were sometimes taken in large numbers as they foraged in Hamilton Inlet on their southward autumn migration (Elliott, 2017; Woollett, 1999). Grey (*Halichoerus grypus*) and bearded seals (*Erignathus barbatus*) were less frequent, and the three small species of seal (Harbour, Harp, and Ringed) compose the majority of identified species in faunal assemblages from Hamilton Inlet (Jankunis, 2019; Bohms, 2018; Elliott, 2017; Brandy, 2013; Woollett, 1999). Other marine sources of dog food at Double Mer Point include capelin (*Mallotus villosus*), which could be collected *en masse* during summer spawning episodes, Arctic char (*Salvelinus alpinus*), Atlantic salmon (*Salmo salar*), and numerous species of

migratory and non-migratory waterfowl and their eggs (Elliott, 2017; Ames, 1977; Fitzhugh, 1972).

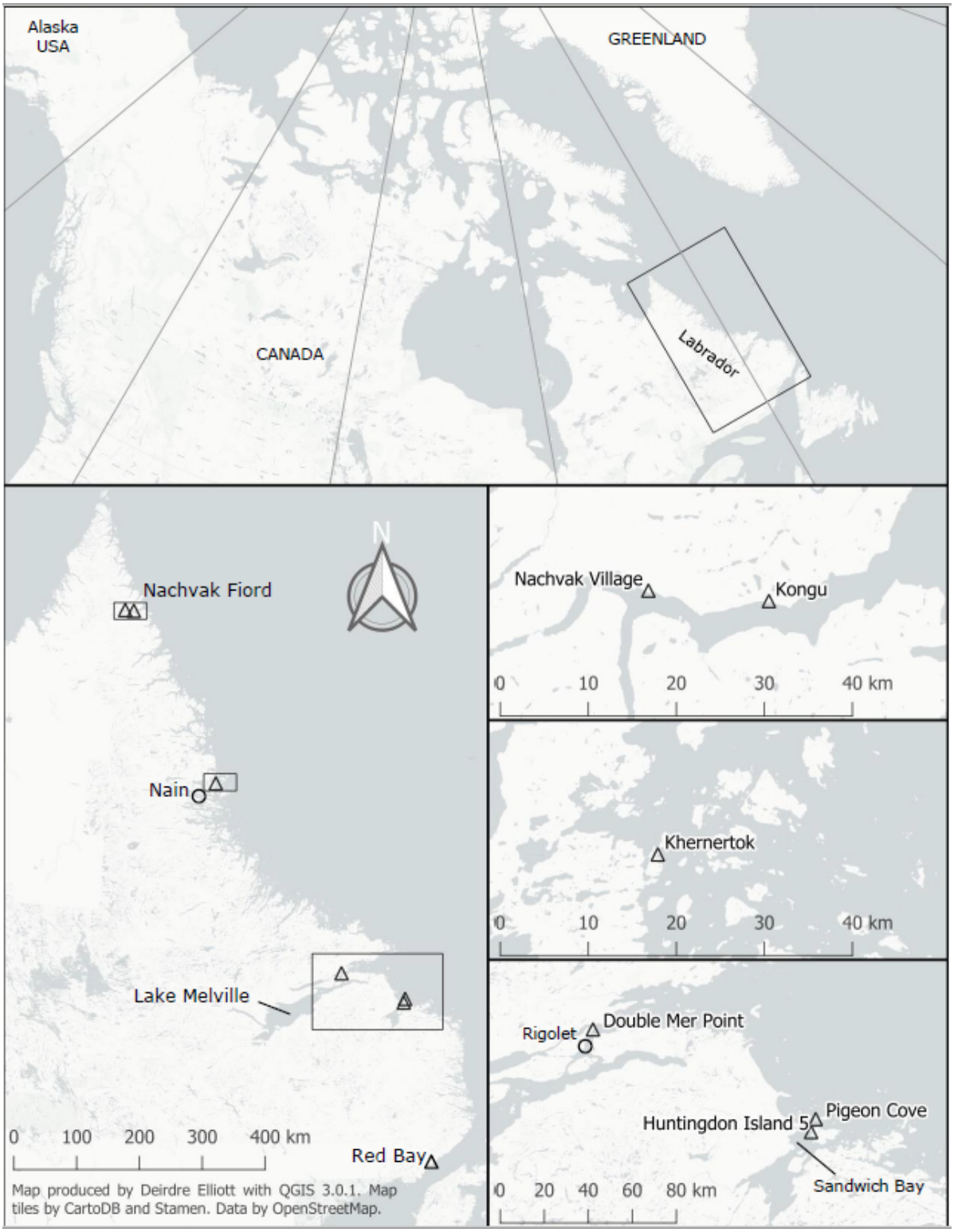

Figure 4.1. Map of study region with Inuit and Basque sample sites.

Caribou (*Rangifer tarandus*) and other terrestrial mammals were of secondary importance to the residents of Hamilton Inlet. Four caribou herds, including both barren ground and woodland types, were present in the spruce forests and tundra to the south and north of Hamilton Inlet during the mid-20th century (Fitzhugh, 1972). Caribou contributed antler and bone for tool making, and their hides were important for warm winter clothing, while foxes and other fur-bearers were trapped for furs, an activity that increased among the Inuit of Double Mer Point and Hamilton Inlet over the 19th century in response to European demand (Ames, 1977). Numerous varieties of berries grow on the exposed hillsides and islands near the site and include cloudberries (bakeapples), crowberries (blackberries), partridgeberries (redberries), and blueberries (Mitchell, 2014).

1.4 Stable isotope analysis and dog diets

Stable carbon and nitrogen isotope analysis of bone collagen is routinely employed to analyse the diets of archaeological humans and fauna as collagen reflects a long-term average of consumed dietary protein (Fernandes et al., 2012; Hedges et al., 2007). The turnover of dog bone collagen varies by dog skeletal element: approximately 30% of alveolar bone is replaced each year, while femoral bone collagen has a much slower turnover rate of 6% per year (Huja et al., 2006). Comparisons of different proteins, such as keratin and collagen, (e.g. McManus-Fry et al., 2018), or of different skeletal elements can be used to effectively study dog diets over multiple time scales. The permanent dentition of a dog develops during the first six to eight months of life, and by comparing the δ^{13}C and δ^{15}N values of dentine and bone collagen, it is possible to identify dietary continuity or change at different periods in a dog's life.

In Arctic and Subarctic contexts, δ^{13}C values distinguish marine and terrestrial sources of protein as mid- and high-latitude marine species have higher δ^{13}C values than terrestrial species (Schoeninger and DeNiro, 1984). Measured δ^{13}C values from archaeological seal, fish, and seabirds from Eastern Arctic and Subarctic contexts range from –10‰ to –16‰, while the δ^{13}C values of caribou and other terrestrial game are, on average, lower than –18‰ (Harris et al., 2019; Guiry and Grimes, 2013; Guiry et al., 2012; Nelson et al., 2012). Bone collagen δ^{13}C values are offset from diet by approximately +5‰ but this number can vary between +2‰ and +10‰ with dietary regime (Ambrose and Norr, 1993). This source of uncertainty can be circumvented by a direct comparison of consumer and prey bone collagen δ^{13}C values as these are

offset by approximately +1‰ (Bocherens and Drucker, 2003). Trophic interactions can be estimated by comparing the $\delta^{15}N$ of different taxa as consumers have higher (+3 to 5‰) $\delta^{15}N$ values than their prey (Hedges and Reynard, 2007; Bocherens and Drucker, 2003; van Klinken et al., 2002; Shoeninger and DeNiro, 1984). The $\delta^{15}N$ value of collagen can also be affected by an animal's nitrogen balance. Episodes of physiological stress (illness, injury, malnutrition) can prompt skeletal muscle to release amino acids back into the amino acid pool for tissue synthesis (Mekota et al., 2006). This increases collagen $\delta^{15}N$ values and may also decrease $\delta^{13}C$ values if body lipids are increasingly used for amino acid synthesis (Neueberger et al., 2013).

Marine foodwebs are typically longer than terrestrial foodwebs, and marine carnivores, such as polar bears, may have $\delta^{15}N$ values greater than +18‰, while terrestrial herbivores and carnivores have $\delta^{15}N$ values below +12‰ (Bocherens et al., 2016; Nelson et al., 2012; Cherry et al., 2011). Freshwater species were of less economic importance in coastal Labrador, but anadromous fish species, such as Arctic char and Atlantic salmon were seasonally accessible from coastal locations (Ames, 1977; Brice-Bennett, 1977). The $\delta^{15}N$ and $\delta^{13}C$ values of anadromous fish species vary with age; smolts yet to winter in the ocean have lower $\delta^{13}C$ values than adults returning from the marine environment (Dixon et al., 2012).

Stable isotope investigations of domestic dog diets in Alaska, the Aleutian Islands, and Nunavut found broad dietary similarities between dogs and humans (McManus-Fry et al., 2018; West and France, 2015; Coltrain et al., 2004) and we anticipated similar results in Labrador. The skeletal remains of marine mammals dominate faunal assemblages throughout the coastal region (Elliott, 2017; Brandy, 2013; Swinarton, 2008; Woollett, 2003), and we expected that dog diets would carry strong marine stable isotope signatures indicative of marine protein-based diets. However, as the distribution of marine species is uneven between the north and south coasts, we could not rule out geographic differences in dog diets among coastal regions. To that end, we conducted $\delta^{13}C$ and $\delta^{15}N$ analysis on the skeletal remains of dogs from north, central and south coast sites to determine, 1) Was there geographic variation in the types of foods fed to dogs? and, 2) How did the diets of dogs at Double Mer Point compare to archaeological and zooarchaeological evidence for human subsistence activities at the site? To facilitate our interpretation of dog diets, we also developed the first archaeological isotope baseline for Labrador using the skeletal remains of wild animals collected from Inuit and Basque sites.

2 Materials

Domestic dogs were identified using the comparative collection of Memorial University of Newfoundland (Swinarton, 2008). Where possible, we sampled the same skeletal element to ensure that no dogs were sampled twice, but we also relied on element size, archaeological site context, and isotope values (Appendix 2, SI Table 2) to distinguish individuals. Given that sled dog lives were relatively short (Woollett, 2003), and we primarily sampled long bones or mandibles, the sampled elements should have broadly similar collagen turnover rates. In addition to domestic dog skeletal remains, each of the sites in our study (except the Red Bay sites) produced archaeological evidence of dog sled traction in the form of dog harness and sled components (Bohms, 2018; Elliott, 2017; Fay, 2016; Rankin, 2015). While none of the sampled bones featured pathology suggestive of dog sledding (which occurs mainly on the vertebrae, maxillae, and crania [e.g. Losey et al., 2014; Park, 1987]), given the importance of dog sledding to historical Labrador Inuit culture (section 1.2), it is likely that the sampled dogs played a role in traction.

We sampled six dogs from the pre/proto-contact site of Nachvak Village; five dogs from the post-contact communal house site of Kongu; four dogs from the communal house site of Khernertok; five dogs from the communal house site of Pigeon Cove; and 10 dogs from the communal house site of Huntingdon Island 5. In addition to sampling 22 dog mandibles from Double Mer Point, we also sampled mandibular canine dentine from four individuals. The deciduous dentition of domestic dogs begins to erupt between three and four weeks of age (Shabestari et al., 1967) and weaning begins shortly afterwards. The permanent canines begin to form below the gumline while the deciduous canines are still in situ (Shabestari et al., 1967). The permanent canine erupts between four and five months of age but at this time the root of the canine has not yet closed. In their analysis of a permanent premolar from the Mesolithic Blick Mead dog, Rogers et al. (2019) assumed that following the eruption of the premolar, it would take approximately seven weeks for the root apex of the tooth to close. We were unable to find similar data for the canine but given the size of the tooth relative to dog premolars, it may take longer for the root to close. We anticipate that following the eruption of the canine, the root will continue to grow for at least another seven weeks and thus the entire tooth may incorporate dietary information over approximately the first seven months of life.

We included nine canid specimens that could only be identified as dog/wolf under the assumption that domestic dogs could be distinguished isotopically from wild canid species due to the consumption of significant amounts of marine protein. We obtained wild faunal samples from each site except Huntingdon Island 5 and included two shipwreck contexts associated with the Basque whaling site of Red Bay. Further site context and sampling details are presented in Appendix 2, SI File 1 and summarized in Figure 4.2.

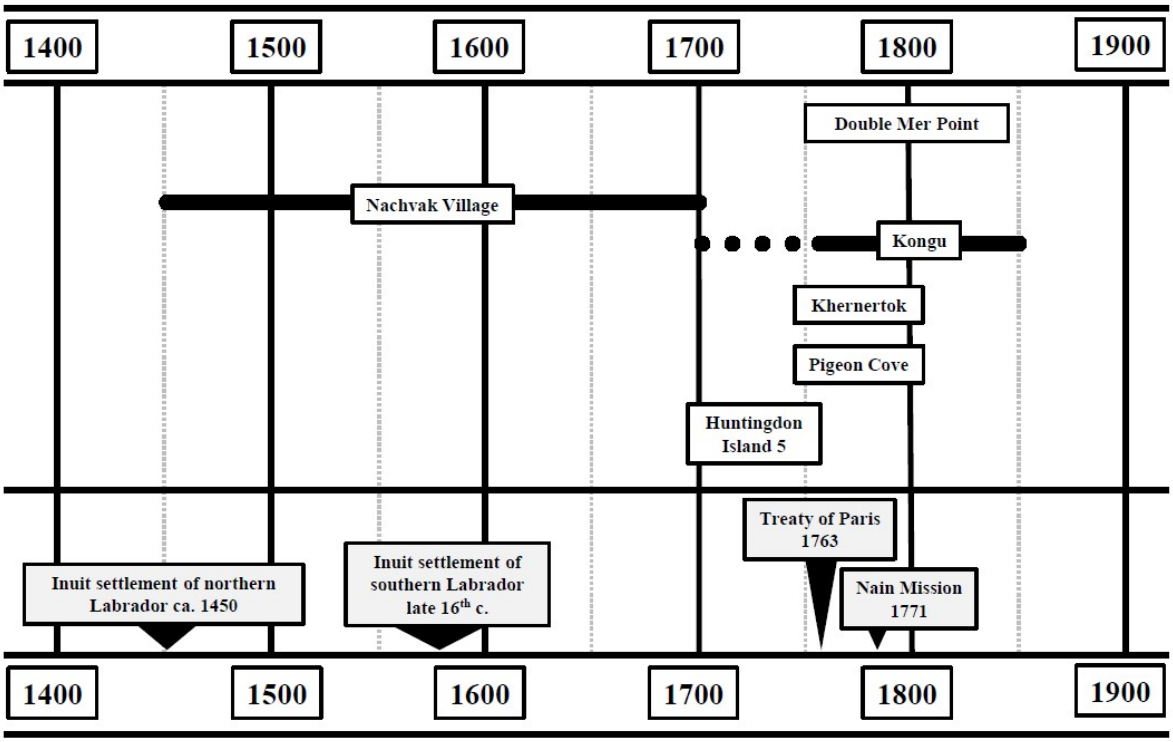

Figure 4.2. A timeline of key events in Labrador history mentioned in the text (grey boxes) with approximate date ranges for each Inuit sample site (white boxes). All dates are given as AD.

3 Methods

3.1 Collagen extraction

The collagen samples were prepared at four laboratories: The Memorial Applied Archaeological Science lab (MAAS) of Memorial University (MUN), the Archaeological Research Laboratory of Stockholm University (SU), BioArCh of the University of York, and at the Department of Anthropology of the University of British Columbia (UBC). Each collagen extraction procedure used similar modifications of the Longin (1971) method. Bone chunks of ~200 mg were cut from skeletal elements using a hand-held

Dremel tool. The bone chunks were demineralized in chilled (MAAS, SU) or room temperature (UBC) 0.5 M hydrochloric acid. Additional pretreatment steps were employed to remove humic contaminants. The demineralized bone samples from Huntingdon Island and Double Mer Point were placed in chilled 0.025 M sodium hydroxide (NaOH), and the NaOH solution was refreshed at 10-minute intervals until the solution remained clear, after which time the bone samples were rinsed with 0.1 M HCl, and then rinsed to neutrality with deionized water. No sample was exposed to NaOH for longer than 40 minutes. The bone samples from the Red Bay shipwreck contexts were soaked in 0.1 M NaOH in a sonic bath and the solution was refreshed every 15 minutes until the solution remained clear. The samples were then rinsed to neutrality with Type 1 water. Gelatinisation procedures were similar across all labs: the demineralized bone samples were placed in a dilute HCl solution (pH 3) and heated to 70℃. After 48 hours, the samples were removed from heat and filtered with E-Zee filters (pore size 40-90 μm, Elkay, UK). Filtered samples were then frozen and lyophilised. Gelatinized samples from Red Bay were centrifuged to isolate solubilised collagen from solids, and frozen and lyophilised. The mandibular canines from Double Mer Point were sectioned in half, parallel to the growth axis, using a diamond-bladed bandsaw. From one half of the tooth, we cut a small wedge of dentine, of approximately 30 mg, 5 to 8 mm beneath the crown for isotopic analysis. The canine samples were demineralized in chilled 0.6 M HCl, gelatinized (80℃, 48 hours), filtered with E-Zee filters, frozen and lyophilised.

3.2 Stable isotope analysis of collagen samples

The collagen stable isotope data were obtained from four laboratories: The TERRA Facility of the CREAIT Network, Department of Earth Sciences of MUN, UBC, BioArCh, and a commercial laboratory, IsoAnalytical (IA). The samples were calibrated to the V-PDB (carbon) and AIR (nitrogen) scales using standard reference materials. The instrumentation and standards for each laboratory are presented in SI File 2. We calculated analytical accuracy, precision, and uncertainty using the methods of Szpak et al. (2017a). These calculations are presented in SI File 2 and SI Tables 6-12 (Appendix 2). Analytical accuracy was better than ±0.3‰ for $\delta^{13}C$ measurements and ±0.2‰ for $\delta^{15}N$ measurements. Analytical precision was less than ±0.1‰ for $\delta^{13}C$ measurements and ±0.2‰ for $\delta^{15}N$ measurements. Total analytical

uncertainty could only be calculated for BioArCh and UBC and was better than ±0.2‰ for $\delta^{13}C$ and $\delta^{15}N$ measurements. Using this method, we could not calculate analytical accuracy or total uncertainty for the samples analysed at IsoAnalytical, but the maximum differences between the measured and accepted values of the calibration and check standards included in the run were 0.1‰ for $\delta^{13}C$ and 0.2‰ for $\delta^{15}N$.

3.3 Statistical analysis

Statistical analyses were conducted with SPSS v. 23. Extreme outliers were identified as data points exceeding 3× the interquartile range as calculated using Tukey's Hinges. We were unable to compare the distribution of $\delta^{13}C$ and $\delta^{15}N$ values between sites due to inconsistent and small sample sizes, but we did compare the distribution of $\delta^{13}C$ and $\delta^{15}N$ values between dogs from the Double Mer Point houses 2 and 3 using Mann-Whitney U tests with an alpha of 0.5.

3.4 Palaeodietary modelling

We estimated the contribution of three protein sources to dog diets using SIMMR (Parnell et al. 2013; Parnell et al. 2010) in R v. 3.5. Stable isotope mixing models estimate the relative contributions of dietary sources to an isotope mixture (the consumer) but produce a range of estimates rather than a unique solution. The number of dietary sources available to a consumer tends to exceed the number of isotope ratios that can be measured which leaves the model mathematically underdetermined, but newer Bayesian models, such as SIMMR, constrain some of this uncertainty by assigning probabilities to the range of possible solutions (Parnell et al. 2010). The accuracy of a model depends on appropriate trophic discrimination factors and accurate identification and isotopic characterization of the food sources (Parnell et al., 2010). We limited the number of dietary sources to three (Table 4.1) as there was considerable overlap in the isotopic values of different prey taxa. For example, the mean marine mammal $\delta^{13}C$ and $\delta^{15}N$ values are nearly identical to published archaeological codfish data ($\delta^{13}C$: –14.5 ± 0.6‰; $\delta^{15}N$: +15.2 ± 0.6‰) from Newfoundland (Guiry et al., 2012). Only the dog bone collagen data were included as isotope mixtures.

Table 4.1. The mean $\delta^{13}C$ and $\delta^{15}N$ values of food groups used in the SIMMR palaeodietary model.

Food group	N	Mean $\delta^{13}C$ (‰)	SD	Mean $\delta^{15}N$ (‰)	SD
Marine mammals	44	–14.1	1.0	+15.7	1.5
Fish	241	–15.9	0.6	+10.2	0.7
Caribou	8	–18.4	0.4	+2.5	0.7

The marine mammals group included ringed, harp, harbour and bearded seals, and baleen whales. The fish group included published data from the bones of modern Arctic char, scales of Atlantic salmon, and muscle tissue of capelin, corrected for the Suess effect. While fish bones are not generally well-preserved at Labrador archaeological sites (Woollett, 2007; Whitridge, 2001), these species were chosen based on modern ethnographic reports of dog provisioning practices (e.g. Ames, 1977), and proximity of Double Mer Point, Nachvak Village and Kongu to productive salmon and Arctic char rivers. The third group consisted of caribou. We grouped the dog isotope data by site and removed one extreme outlier (3x IQR) from the Double Mer Point dataset and one data point from the Huntingdon Island 5 site that fell within 0.1‰ of being an extreme outlier. We assigned trophic discrimination factors of +1 ± 0.2‰ and +4 ± 1‰ for carbon and nitrogen, respectively, after Darimont and Reimchen (2002), McManus-Fry et al., (2016), and Bocherens and Drucker (2003). We adjusted the $\delta^{13}C$ values of muscle from modern capelin collected from coastal Newfoundland (Sherwood and Rose, 2005), Iceland (Thompson et al., 1999), and Greenland (Marcoux et al., 2012) by +2.7‰ and the $\delta^{15}N$ values by –1.2‰ which reflect published muscle-collagen isotopic offsets for fish (Dury et al., 2018; Robson et al., 2012). We corrected the modern fish data, including the modern salmon scale data from Newfoundland and Labrador, for the Suess Effect using the equation below, after Hilton et al. (2006), and as modified by Misarti et al. (2009):

$$\text{Suess Effect Correction Factor (SECF)} = a^{*}\exp^{(b^{*}0.027)}$$

Where a is the maximum annual rate of decrease in the $\delta^{13}C$ of the global oceans, estimated by Eide et al. (2017) to be –0.016‰; *b* is the difference between the year of death/collection and AD 1850, and 0.027 represents the exponential curve established by Gruber et al. (1999) for the change in the $\delta^{13}C$ of the global oceans between 1945

and 1970. The SECF ranged from a minimum of –0.8‰ for capelin collected in 1995 (Thompson et al., 1999) to a maximum of –1.3‰ for Arctic char collected in 2014 (Guiry et al. 2016). These corrections are consistent with those of Mackensen (2013) for the Arctic Ocean. We evaluated the performance of the model by comparing the breadth of the credible intervals for each food source, and by using matrix plots to refine our interpretation of the model results. Strong negative or positive correlations indicate that the model could not distinguish the contributions of different sources (Parnell and Inger, 2019).

4 Results

The $\delta^{13}C$ and $\delta^{15}N$ values of dogs, and dog/wolf specimens from each site are presented in full, with accompanying collagen quality indicators, in SI Table 13 (Appendix 2). The isotope data from local faunal specimens are presented in SI Table 14 (Appendix 2). The results of the SIMMR model are presented in SI File 3 (Appendix 2). Four of the dog and faunal sample C/N ratios exceeded 3.6 and were excluded from further analyses. The bone samples treated with NaOH had slightly lower mean C:N ratios (n=75, 3.20 ± 0.20) than those not treated (n=66, 3.33 ± 0.08). This suggests that NaOH may remove non-collagenous contaminants more effectively than pre-treatment methods that do not incorporate an alkaline wash (Szpak et al. 2017b), but such a small change is unlikely to make an interpretable difference in the stable isotope values of this particular dataset.

4.1 Wild fauna

The distribution of the $\delta^{13}C$ and $\delta^{15}N$ values of wild fauna (Fig. 4.3) was consistent with published isotope data from other Arctic and Subarctic contexts (Harris et al., 2019; McManus-Fry et al., 2018; Szpak et al., 2017c; Britton et al. 2013; Guiry et al., 2012; Coltrain et al., 2004). The lowest $\delta^{13}C$ and $\delta^{15}N$ values were measured in small terrestrial herbivores, ptarmigan and hares. Eight caribou had mean $\delta^{13}C$ and $\delta^{15}N$ values of –18.4 ± 0.4‰ and +2.5 ± 0.7‰, respectively. Harp, ringed, and bearded seals had similar $\delta^{15}N$ values of ~ +15.5‰, but we found some slight differences in the $\delta^{13}C$ values among seal species. Harbour seals had $\delta^{15}N$ values that were approximately +2‰ higher than those of other seal species. Baleen whales had

slightly lower $\delta^{13}C$ and $\delta^{15}N$ values, reflecting their consumption of low trophic level invertebrates (Lowry, 1993).

By using the isotopic data from foxes and wolves we can estimate the types of foods that would be available to dogs without direct provisioning by Inuit, while polar bears represent diets that are known to be dominated by marine mammals (Cherry et al., 2011; Thiemann et al., 2008). Arctic and red foxes had overlapping $\delta^{13}C$ and $\delta^{15}N$ values, ranging from –19.8‰ to –17.1‰ (mean –18.7 ± 1.1‰), and +3.3‰ to +10.4‰ (mean +6.9 ± 2.5‰). Consistent with ecological observations, the foxes with $\delta^{15}N$ values approaching +10‰ may have eaten some marine or anadromous protein. Foxes are known to hunt for seabird eggs, denning ringed seal pups, and scavenge polar bear kills in Labrador, Newfoundland, Iceland, and northern Norway (Roth, 2002; Angerbjörn et al., 1994; Sklepkovych, 1986; Andriakshek et al., 1985). The four wolf specimens had $\delta^{13}C$ values ranging from –18.8‰ to –15.0‰ (mean –17.5 ± 1.7‰), and $\delta^{15}N$ values ranging from +7.0‰ to +13.5‰ (mean 9.1 ± 3.0‰). The two wolf specimens from Pigeon Cove had $\delta^{13}C$ values and $\delta^{15}N$ values that differed by 0.3‰ and 0.1‰, respectively, suggesting only one individual is represented. The range in wolf $\delta^{13}C$ and $\delta^{15}N$ values can be attributed to the high $\delta^{13}C$ and $\delta^{15}N$ values of the specimen from Huntingdon Island 5. Wolves in British Columbia and Alaska are known to opportunistically take spawning salmon or scavenge marine mammals (Milakovic and Parker, 2011; Darimont and Reimchen, 2002). Isotopic compositions (n=22, $\delta^{15}N$ =10.8±1.6, $\delta^{13}C$ –15.3±0.8 (Guiry, et al. 2016)) of archaeological Atlantic salmon which are comparable across their range (Guiry, 2019), are consistent with this possibility. Archaeologists also observed wolves and their tracks along the shore of the mainland adjacent to Huntingdon Island during the excavation of the site. The three polar bears in our study, from Nachvak Fiord and Red Bay, had $\delta^{13}C$ values ranging from –14.1‰ to –12.7‰ (mean –13.5 ± 0.7‰), and $\delta^{15}N$ values ranging from +18.1‰ to +19.7‰ (mean +18.8 ± 0.8‰).

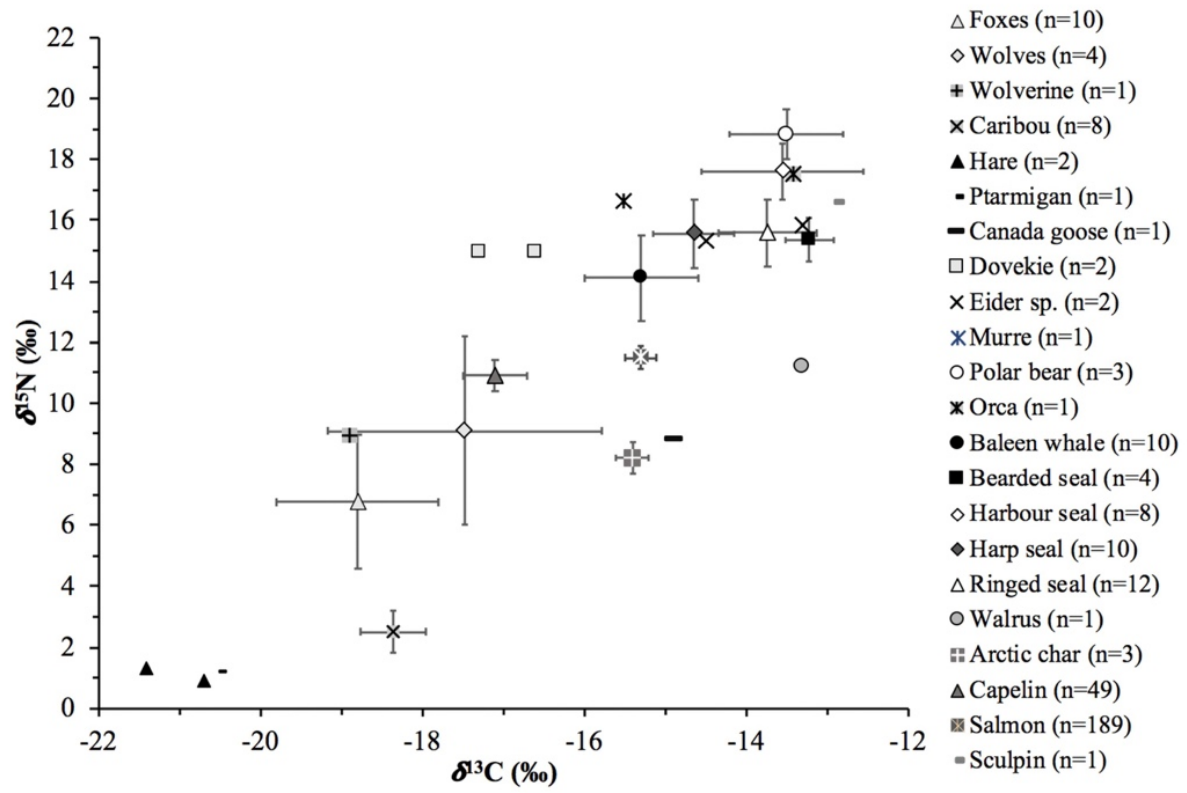

Figure 4.3. Baseline $\delta^{13}C$ and $\delta^{15}N$ values of wild fauna from Labrador. Published isotope data from Arctic char (Guiry et al., 2016) and salmon scale collagen (Dixon et al. 2012) and capelin muscle tissue, corrected to bone collagen values (Marcoux et al., 2012; Sherwood and Rose, 2005; Thompson et al., 1999) added for comparison.

4.2 Domestic dogs and dog/wolves

The specimens identified as *Canis* sp. or dog/wolf (n=9) had $\delta^{13}C$ values ranging from –19.9‰ to –12.4‰ and $\delta^{15}N$ values ranging from +5.3‰ to +21.3‰. All but one of the dog/wolf specimens grouped with the domestic dogs (Fig. 4.4), suggesting that in Labrador, isotopic composition may be used as a robust indicator of domestication status based on the premise that dogs were provisioned with foods that are typically less available to their non-domestic counterparts. The dog/wolf specimens that isotopically grouped with domestic dogs from each site were combined for subsequent analysis (Table 4.2). We observed some geographic patterning between the dogs from the north, central, and south coasts of Labrador (Fig. 4.5) that will be explored in greater detail on a site by site basis.

Table 4.2. Mean $\delta^{13}C$ and $\delta^{15}N$ values of bone collagen from domestic dogs and dog/wolves from Labrador Inuit sites, presented to 1 SD. The interquartile ranges (IQR) were calculated using Tukey's Hinges and were used to identify outliers (3xIQR).

Site	N	$\delta^{13}C$	SD	IQR	$\delta^{15}N$	SD	IQR
Double Mer Point	19	–13.3	0.8	0.6	+18.3	1.5	1.3
Nachvak Village	6	–14.2	0.2	0.2	+16.5	1.2	1.3
Kongu	6	–13.4	0.6	0.9	+17.7	0.8	1.1
Khernertok	5	–13.4	0.2	0.2	+16.8	0.5	0.9
Pigeon Cove	5	–13.7	0.5	0.6	+18.4	0.7	1.2
Huntingdon Island 5	11	–13.5	0.6	0.5	+18.9	0.7	1.2

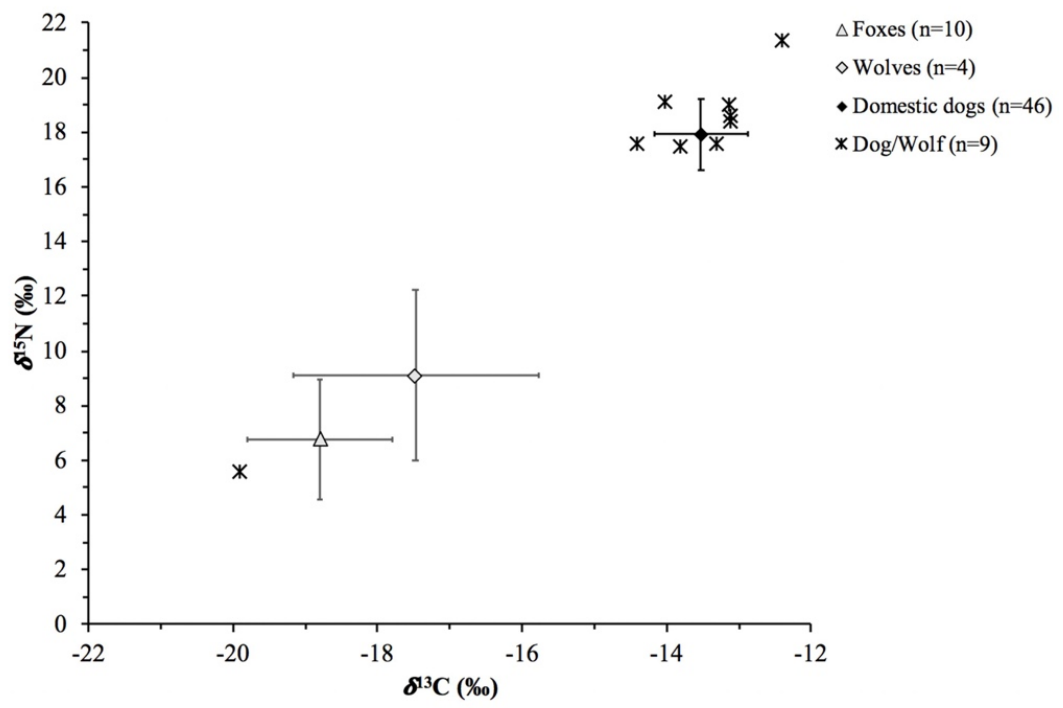

Figure 4.4. Mean $\delta^{13}C$ and $\delta^{15}N$ values of fox, wolf, and domestic dogs from coastal Labrador plotted with specimens identified as "Dog/wolf".

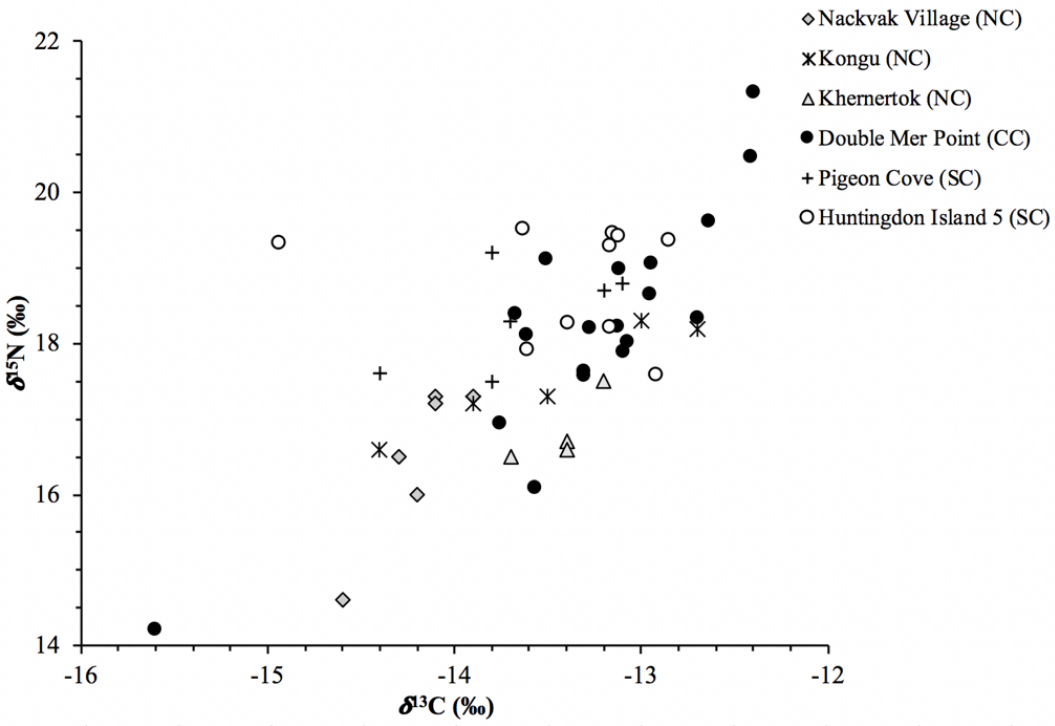

Figure 4.5. Dog and dog/wolf bone collagen samples presented by site.

The $\delta^{13}C$ values of dogs from the north coast sites (Nachvak Village, Kongu and Khernertok) ranged from –14.6‰ to –12.7‰ (mean –13.8 ± 0.5‰), and the $\delta^{15}N$ values ranged from +14.6‰ to +18.4‰ (mean +16.9 ± 0.9‰) (Fig. 4.6). The dogs from House 2 at Khernertok form a tight cluster, and two of the five samples (MARC 2004 and 2063) may represent the same individual.

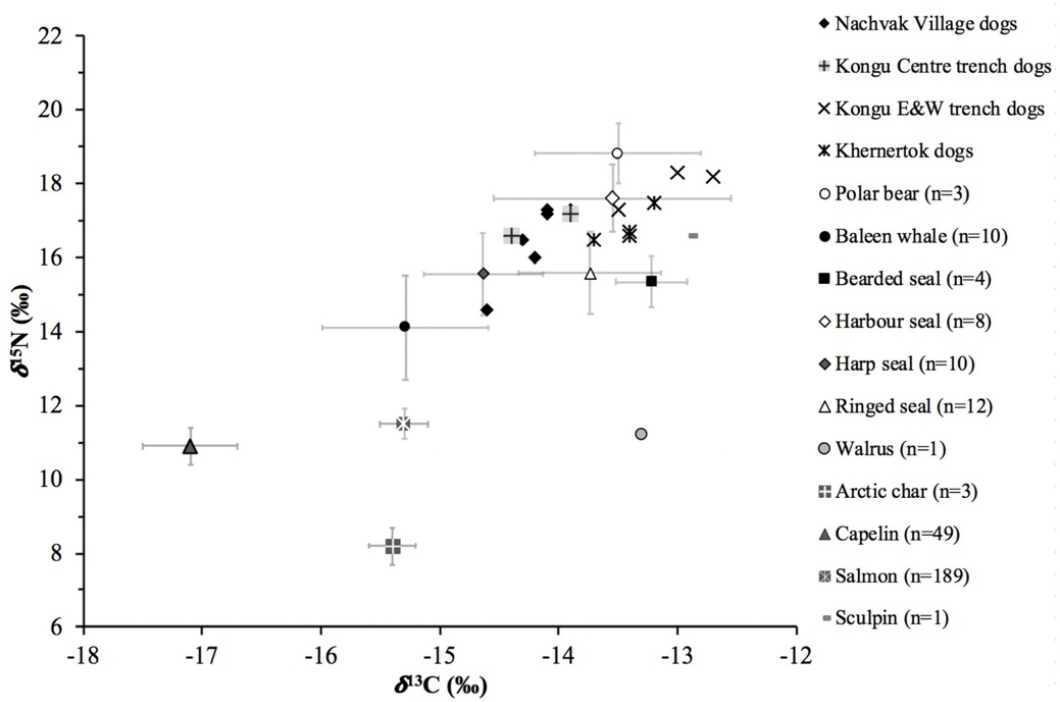

Figure 4.6. The $\delta^{13}C$ and $\delta^{15}N$ values of domestic dogs from Nachvak Village, Kongu, and Khernertok plotted with possible food sources. Published isotope data from Arctic char bone (Guiry et al., 2016), salmon scale collagen (Dixon et al., 2012) and corrected capelin muscle tissue (Marcoux et al., 2012; Sherwood and Rose, 2005; Thompson et al., 1999) added for comparison.

We obtained well-preserved collagen from 19 of the 22 mandibles and from the four canines from Double Mer Point. The $\delta^{13}C$ values of the dog bone collagen range from –15.6‰ to –12.4‰ (mean –13.4 ± 0.8‰), and the $\delta^{15}N$ values range from +14.2‰ to +21.3‰ (mean +18.3 ± 1.5‰) (Fig. 4.7). One dog, DMP 11, had an outlying $\delta^{13}C$ value of –15.6‰ and a relatively low $\delta^{15}N$ value of +14.2‰, suggesting that it was fed differently than the majority of the dogs from the site. The dogs recovered from the barrier between Houses 1 and 2, potentially dating to the early 19th century, had higher mean $\delta^{13}C$ (–12.9 ± 0.6‰) and $\delta^{15}N$ (+19.4 ± 1.2‰) than the dogs from Houses 2 and 3 which had similar mean $\delta^{13}C$ and $\delta^{15}N$ values. The dogs from House 2 had the most variable $\delta^{13}C$ and $\delta^{15}N$ values, with SDs of 0.9 and 1.9, respectively, but no statistically significant differences were noted between the $\delta^{13}C$ (U = 26.5, p = 0.384), or $\delta^{15}N$ (U = 30.5, p = 0.631) values of dogs from House 2 or 3.

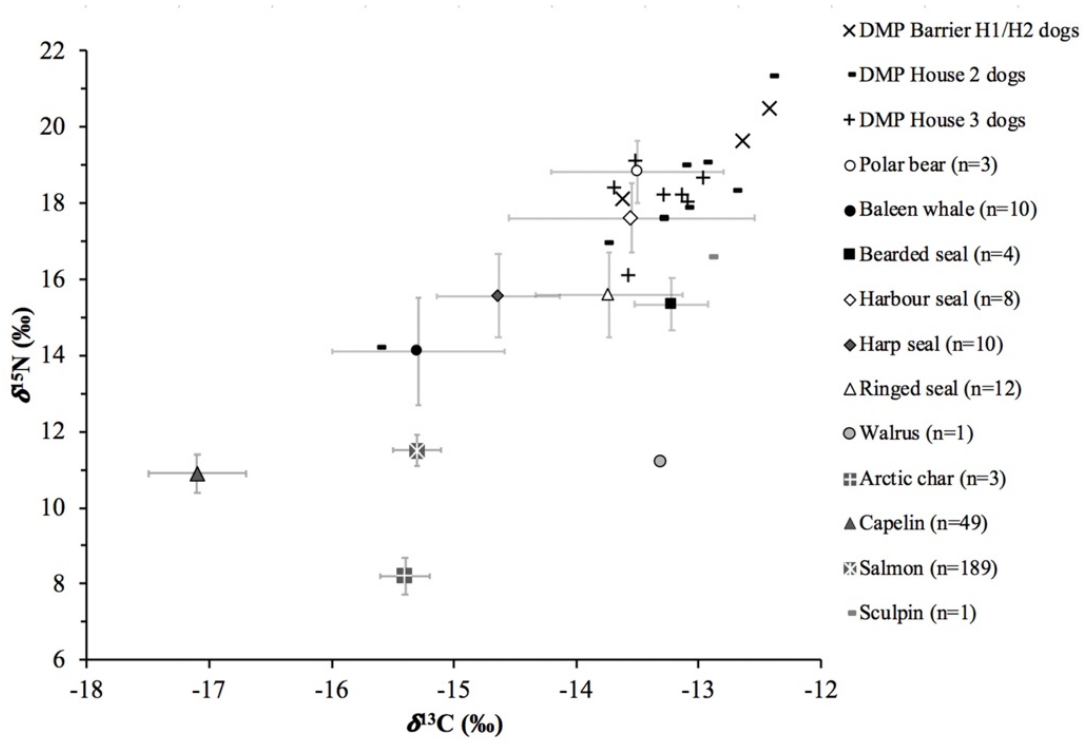

Figure 4.7. The $\delta^{13}C$ and $\delta^{15}N$ values of Double Mer Point dogs, separated by house, plotted with possible food sources. Published isotope data from Arctic char bone (Guiry et al., 2016), salmon scale collagen (Dixon et al., 2012) and capelin muscle corrected to bone collagen values (Marcoux et al., 2012; Sherwood & Rose, 2005; Thompson et al., 1999) added for comparison.

The stable isotope values of the mandibles and mandibular canines of four dogs are compared in Table 4.3. The offset in $\delta^{13}C$ values between the paired samples from DMP04, 17, and 24, did not exceed ± 0.1‰. The canine $\delta^{15}N$ values were high relative to mandibular values, with $\Delta^{15}N_{C\text{-}M}$ ranging from +1.0‰ to +1.6‰. A negative offset of –0.7‰ occurred between the $\delta^{13}C$ values and of –1.5‰ between the $\delta^{15}N$ values of the canine and mandible of DMP02.

Table 4.3. Double Mer Point mandibular and canine $\delta^{13}C$ and $\delta^{15}N$ values, and the offsets between the canine ©and mandible (M).

Sample ID	Element	$\delta^{13}C$	$\Delta^{13}C_{C-M}$	$\delta^{15}N$	$\Delta^{15}N_{C-M}$
DMP02	Mandible	–12.4		+20.5	
	Canine	–13.1	–0.7	+19.0	–1.5
DMP04	Mandible	–12.6		+19.6	
	Canine	–12.5	+0.1	+20.6	1.0
DMP17	Mandible	–13.5		+19.1	
	Canine	–13.6	–0.1	+20.7	1.6
DMP24	Mandible	–13.1		+18.0	
	Canine	–13.0	+0.1	+19.4	1.4

The 17 specimens from the sites in Sandwich Bay had $\delta^{13}C$ values ranging from –14.9‰ to –12.9‰ (mean –13.5 ± 0.6‰), and $\delta^{15}N$ values ranging from +17.5‰ to +19.5‰ (mean +18.7 ± 0.7‰), (Fig. 4.8). The distribution of $\delta^{13}C$ values was similar between Pigeon Cove and Huntingdon Island 5, however one dog from Huntingdon Island 5 had a relatively low $\delta^{13}C$ value of –14.9‰.

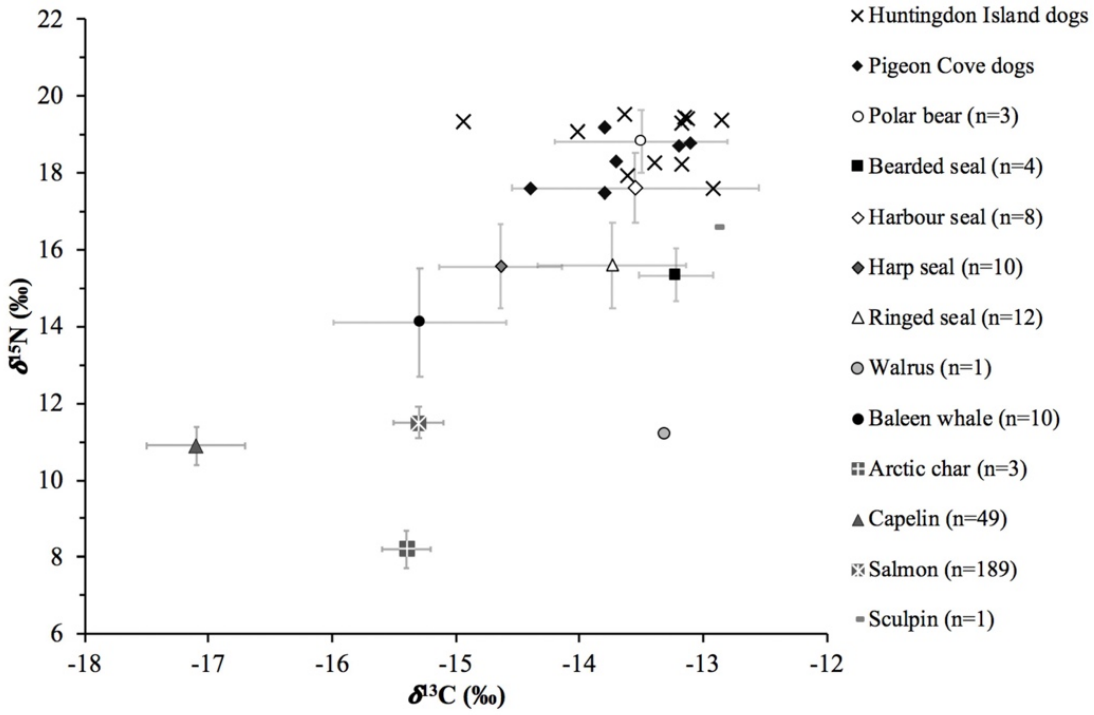

Figure 4.8. The $\delta^{13}C$ and $\delta^{15}N$ values of domestic dogs from Huntingdon Island and Pigeon Cove plotted with possible food sources. Published isotope data from Arctic char bone (Guiry et al., 2016), salmon scale collagen (Dixon et al., 2012) and capelin muscle corrected to bone

collagen values (Marcoux et al., 2012; Sherwood & Rose, 2005; Thompson et al., 1999) added for comparison.

SIMMR estimates of the probability of different contributions from three food sources to dog diets are presented in Figures 4.9 and 4.10. The credible intervals were the narrowest for caribou, but the mean and median estimates showed good agreement for all food sources and all of the standard deviations fell below 0.15 with the majority less than 0.10.

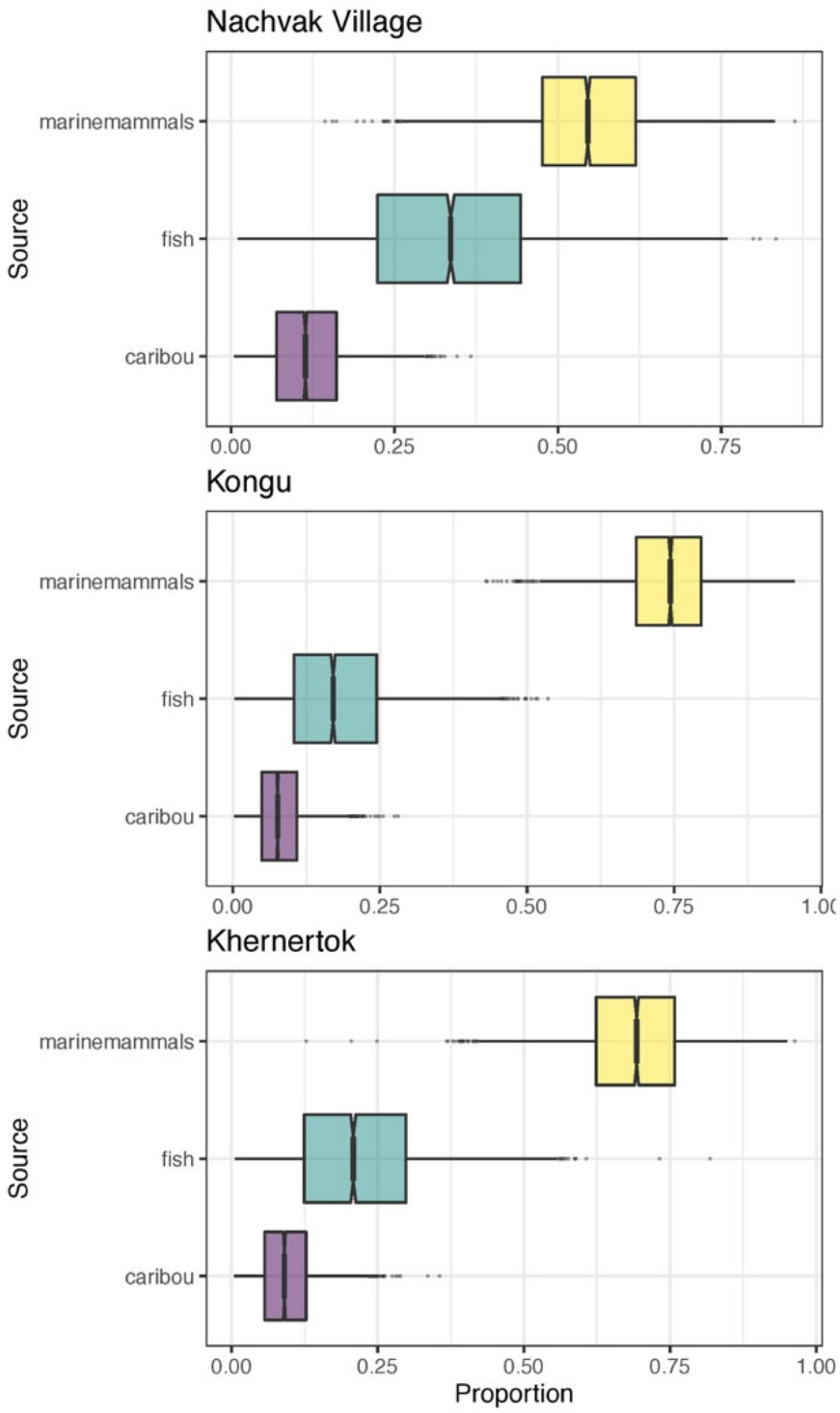

Figure 4.9 Bayesian estimates of the probability of the contributions of protein types for north coast sites: Nachvak Village (n=6), Kongu (n=6), and Khernertok (n=5).

Across all sites, the relative proportions of fish and marine mammals were negatively correlated (–0.9) indicating that either fish or marine mammals composed the primary contribution to diet, but both could not have contributed equally over the time span represented by bone collagen (Inger et al., 2015). The model could not

distinguish the relative contributions of sources to the diets of Nachvak Village dogs, as indicated by negative correlations between fish and caribou (–0.8) and between fish and marine mammals (–0.9). Consistent with our preliminary interpretation of the stable isotope data marine mammals were the greatest contributor to diet across all sites. Dogs of the central and south coast sites consumed the greatest proportion of marine mammals with very minor contributions from caribou and fish, while dogs at Nachvak Village and Khernertok likely ate a significant amount of fish and/or caribou in addition to marine mammals.

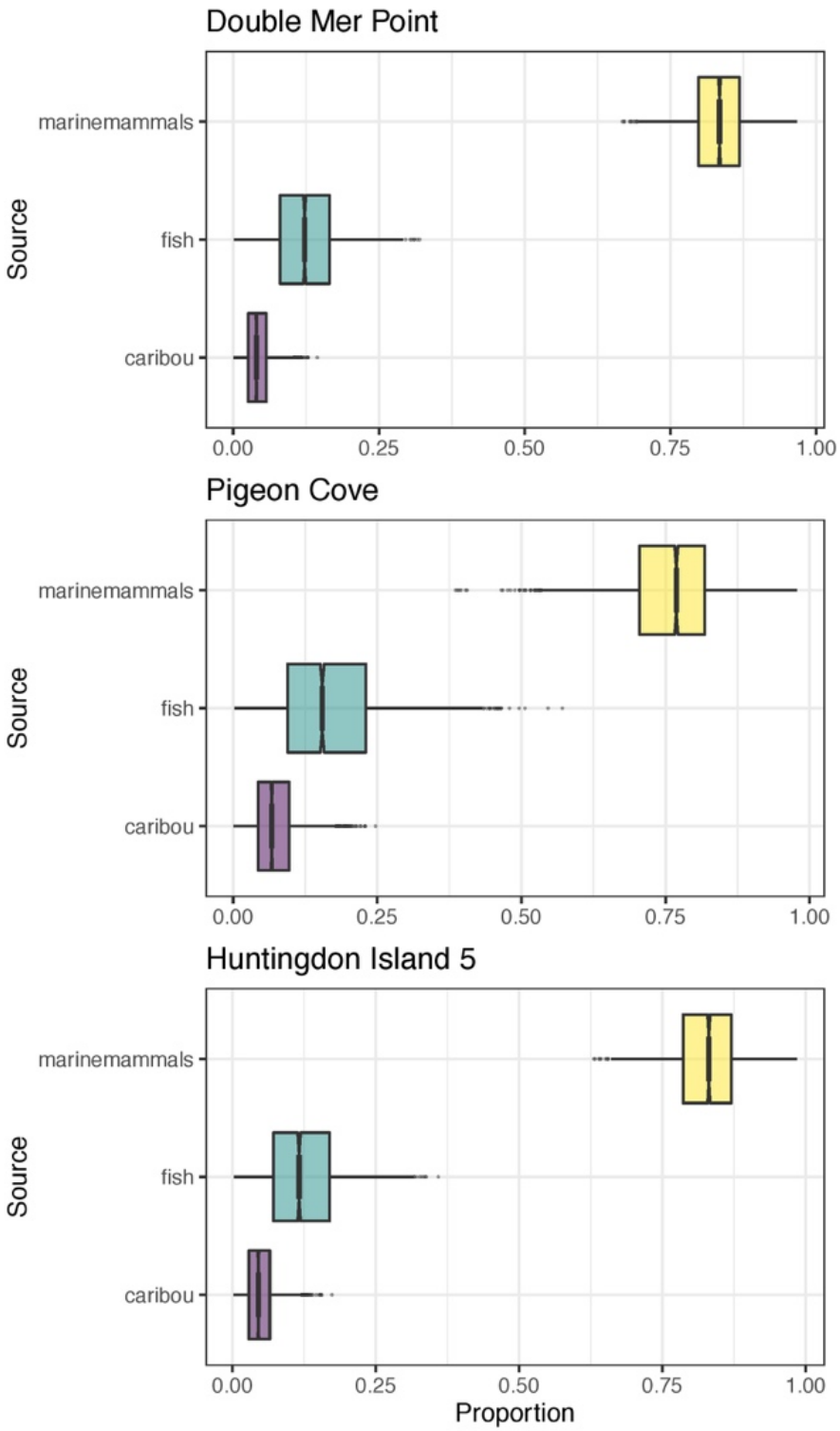

Figure 4.10. Bayesian estimates of the probability of the contributions of protein types for central and south coast sites: Double Mer Point (n=19), Pigeon Cove (n=6), and Huntingdon Island 5 (n=11) dogs.

5 Discussion

5.1 Palaeodietary analysis of Labrador sled dogs

Through the analysis of dog diets, we can better understand the subsistence activities required to provision sled dogs and facilitate Inuit mobility and trade in coastal Labrador between the 15th and 19th centuries. Sled dog diets were dominated by marine mammal protein, but the possibility that codfish may have played a minor role in dog diets cannot be excluded based on the similarity between the isotopic composition of codfish and marine mammals. Regional variation occurred among dog diets that may have been rooted in the geographic distribution of Inuit habitations and land use patterns relative to that of prey species. For example, Nachvak Village is situated within easy reach of navigable routes to inland caribou herds, and while poor bone preservation conditions may have differentially impacted fish remains, the site is located next to a famously productive Arctic char river. Dogs may have been partially provisioned, perhaps in the warm months when they were not working, with locally available caribou and fish. Working sled dogs require at least 10 000 calories per day and thrive when >50% of those calories are sourced from fat, most easily acquired from blubberous marine mammals (Loftus et al., 2014; Case et al., 2000; Kuhnlein et al., 1991). With mean $\delta^{13}C$ and $\delta^{15}N$ values of –14.2‰ and +16.7‰, respectively, the Nachvak Village dogs may have received approximately half of their protein from marine mammals. This is in contrast to dogs from the East and West trenches of Kongu which were provisioned largely with marine mammals year-round. These dogs, associated with the middens of two communal houses, had higher $\delta^{13}C$ values than dogs from the trench associated with the possible older feature. The Centre Trench at Kongu may relate to the earliest Inuit occupation of the site, by former residents of Nachvak Village (Elliott, 2017), so the lower isotopic values of the Centre Trench dogs may reflect foods obtained from the environment around Nachvak Village. Due to insufficient evidence, we are unable to say with certainty that the difference between Nachvak Village and the communal houses of Kongu was not due to broad changes in Inuit subsistence practices over time due to factors such as climate and shifting economic foci. Kaplan (1983) found that seal and whale were consistently important across outer coastal sites in Northern Labrador and Woollett's (2003) analysis of subsistence over ~300 years of Inuit occupation in Hamilton Inlet found little change

in types of prey targeted until the mid-19th century, when inland trapping became an important economic activity.

The sled dogs at Khernertok consumed similar diets to one another, but with a mean δ^{15}N value of +16.8‰, similar to Nachvak Village dogs, and were fed less seal than dogs at Kongu or at sites further south. At –13.4‰, the mean δ^{13}C value is high relative to fish (–16.3‰) and caribou (–18.3‰) making it unlikely that the diets of Khernertok dogs were supplemented with caribou or Arctic char to the same extent as Nachvak Village dogs. Archaeological walrus in the Eastern Arctic have low δ^{15}N values (~ +12‰) relative to seals and δ^{13}C values of approximately –13‰ (Nelson et al., 2012; Coltrain et al., 2004), and when compared with dog isotope values, may have been a source of protein at Khernertok.

The diets of dogs from Huntingdon Island 5 and Pigeon Cove were dominated by marine mammals, most likely seal. Huntingdon Island 5 lies adjacent to a polynya where seals could have been hunted in the winter and the Inuttitut name for Sandwich Bay translates as the Place of Many Ringed Seals (Rankin, 2015). Seal were important throughout the occupation of Huntingdon Island 5 and featured prominently in the middens from Houses 3 and 4 (Rankin, 2015; Brandy, 2013).

5.2 Dog provisioning at Double Mer Point

Double Mer Point is located in one of the best studied regions of Labrador and is almost fully excavated giving us the opportunity to contextualize the isotopic data with archaeological and zooarchaeological evidence. The domestic dogs at Double Mer Point were provisioned with marine foods with minor contributions from sources such as Arctic char, Atlantic salmon, or caribou. Jordan and Kaplan (1980) observed that ringed and harbour seals negatively covary in faunal assemblages from Hamilton Inlet and harbour seals may have been more commonly hunted during the 18th century (Woollett, 1999). This may have occurred at other sites in Hamilton Inlet, but is unlikely at Double Mer Point. With several exceptions, the majority of the dogs have δ^{15}N values falling at or below the mean harbour seal δ^{15}N value. These values are consistent with diets of ringed or harp seals and align with the site's zooarchaeological assemblage, which predominantly features ringed and harp seal (Elliott and Swinarton, in press). Ringed seals could be hunted during the winter in the open water

off the coast of Double Mer Point, or caught denning in the ice of Double Mer to the north and west of the site.

The paired canine and mandible samples taken from four dogs recorded a change in diet that may relate to seasonal availability of food resources. As the permanent canine begins to form between one-three months after weaning (Shabestari et al., 1967), it should not be strongly influenced by a nursing isotope signal. The positive $\Delta^{15}N_{C\text{-}M}$ and negligible $\Delta^{13}C_{C\text{-}M}$ observed for three dogs suggests that as the canine root grew, the three dogs were consuming higher trophic level food than was reflected in mandibular bone collagen. Puppies born in the early spring could have been fed the meat of ringed or harbour seals (including juveniles of both species), seabirds and their eggs, and later, in the summer, they may have been provisioned with salmon or capelin (Ames, 1977). Several months of eating the meat of adult and juvenile seals may have elevated canine $\delta^{15}N$ values relative to the average sources of dietary protein throughout the year which would be recorded in mandibular collagen. We observed negative $\Delta^{15}N_{C\text{-}M}$ and $\Delta^{13}C_{C\text{-}M}$ for a fourth dog which suggests a diet composed of lower trophic level foods, like fish or caribou, during puppyhood followed by increasing contributions of seal meat later in life.

While there were no significant differences in the mean isotope values between dogs from Houses 2 and 3, the dogs from House 2 had more variable isotope values which may relate to Inuit trading activities. The human occupants of House 2 had more European manufactured goods and may have been heavily involved in coastal trade networks (Jankunis, 2019; Bohms, 2018) which could have necessitated travel throughout the year (Fay, 2015). During long-distance trips, sled dogs could be exchanged or purchased, or could perish at sites far from their place of birth. A dog (DMP11) with stable isotope values consistent with a mixed diet of fish, seal and caribou may have originated from the north coast where such diets appear more common. Another dog (DMP06) with a $\delta^{13}C$ value of –12.4‰ and $\delta^{15}N$ value of +21.4‰ was provisioned with very high trophic level foods, or perhaps shallow water fish, which may indicate access to a different resource base than was available at Double Mer Point.

Palaeodietary studies rely on the tested assumption that bone collagen predominantly reflects the isotopic composition of dietary protein (Fernandes et al., 2012; Froehle et al., 2010; Ambrose and Norr, 1993; Tieszen and Fagre, 1993) and cannot be used to effectively study sources of dietary fat. By measuring the $\delta^{13}C$

values of blood and lipids, Cherry et al. (2011) showed that polar bears obtained dietary protein from ringed and other small species of seal, while large species of seal, whale, and walrus contributed significant amounts of dietary energy that would have been invisible through the analysis of polar bear proteins alone. We might find similar results were we to analyse dog bone lipids, or the $\delta^{13}C$ values of amino acids synthesized from non-protein carbon sources and would be better positioned to speak to past dog husbandry practices among Labrador Inuit.

We did not identify any clear isotopic markers of nutritional or physiological stress (e.g. negatively covarying $\delta^{13}C$ and $\delta^{15}N$ values [Beaumont and Montgomery, 2016]) among the sampled dogs, but this possibility should be considered in future studies of sled dogs. Reduced or intermittent summer feeding of dogs has been documented ethnographically (Boas, 1974), and suggested by osteological evidence (Losey et al., 2014). Physiological stress may be possible in dogs that carry a heavy intestinal parasite load due to the ingestion of contaminated animal meat, including that of other dogs (Goyette et al., 2014; Salb et al., 2008; Connell, 1949; Cameron et al., 1940). Further studies employing incremental sampling protocols may identify episodes of dietary or physiological stress in dogs that could be further investigated through parasitological or proteomic/genetic analyses of dog coprolites recovered from Inuit sites.

6 Conclusion

The $\delta^{13}C$ and $\delta^{15}N$ values of dogs and wild fauna from coastal Labrador form the first investigation of dog provisioning practices of Labrador Inuit and act as a complimentary line of evidence for understanding dog husbandry in Eastern Canada. There was some geographic variation in the types of foods that dogs could access between sites. All dogs consumed marine mammals, but dogs on the north coast were additionally provisioned with fish, caribou, and potentially walrus. Caribou and Arctic char were accessed at the site of Nachvak Village, but the predominance of marine mammals in the diets of dogs confirms the importance of these animals to the performance of working dogs in cold environments. To the south, the diets of dogs closely aligned with the zooarchaeological assemblages, suggesting that humans and dogs subsisted on similar protein sources, such as ringed seal. This does not represent a complete picture of diet, however, as lipids may have contributed upwards

of 50% of the calories in dog diets, and Inuit may have consumed imported European goods, such as salt pork or flour, that would not have been given to dogs.

Double Mer Point was situated within a productive environmental region where seals could be hunted year-round, and local dogs predominantly ate small species of seal (ringed and harp), but with some minimal seasonal variation in the trophic level of prey. The human occupants of House 2 were heavily involved in coastal trade networks and this may be reflected in the dietary variation of dogs recovered from the house. Our analysis of paired mandibular and canine samples yielded evidence for seasonal variation in dog diets and suggests the potential of future applications of this method to understand dog provisioning in seasonal environments.

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Supporting Information: Appendix 3

Supporting information file 1: Site contexts and samples
Supporting information file 2: Standards and Instrumental Analyses
Supporting information file 3: SIMMR model results
Supporting information tables 1–6: Check and calibration standards
Supporting information table 7: Stable isotope values and collagen quality indicators of domestic dogs and 'dog/wolves' from Labrador, Canada
Supporting information table 8: Stable isotope values and collagen quality indicators of wild Labrador fauna

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Chapter 5

Archives of human-dog relationships: Genetic and stable isotope analysis of Arctic fur clothing

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Abstract

Among Indigenous populations of the Arctic, domestic dogs (*Canis familiaris*) were social actors aiding in traction and subsistence activities. Less commonly, dogs fulfilled a fur-bearing role in both the North American and Siberian Arctic. Examples of garments featuring dog skins were collected during the 19th-20th centuries and are now curated by the National Museum of Denmark. We sequenced the mitochondrial genomes of macroscopically identified dog skin garments. We conducted stable carbon and nitrogen isotope ratio analysis of the dog furs and of fur samples from contemporaneous pelts of Arctic (*C. lupus arctos*) and grey (*C. lupus*) wolves. Despite the presence of biocides used to protect the fur clothing during storage, we extracted well-preserved DNA using a minimally invasive sampling protocol. Unexpectedly, the mtDNA genomes of one-third of the samples were consistent with wild taxa, rather than domestic dogs. The strong marine component in the diets of North American dogs distinguished them from Greenland and Canadian wolves, but Siberian dogs

consumed diets that were isotopically similar to wild species. We found that dog provisioning practices were variable across the Siberian and North American Arctic, but in all cases, involved considerable human labour.

1 Introduction

Bioarchaeological approaches to the human-dog relationship are becoming increasingly commonplace. Previous studies have employed stable isotope analysis (carbon, nitrogen, sulphur) of dog bone collagen to investigate dietary relationships (Rogers et al., 2019; McManus-Fry et al., 2018; Monagle et al., 2018; Guiry and Grimes, 2013; Rick et al., 2011; Tankersley and Koster, 2009; Cannon et al., 1999; Burleigh and Brothwell, 1978), and genetic and radiogenic isotope analysis of preserved hard and soft tissues to track population movements (Ameen et al., 2019; Ní Leathlobhair et al., 2018; Ollivier et al., 2018; Fillios & Taçon, 2016; Laffoon et al., 2015; Brown et al., 2013). Dogs are frequently used as a proxy for human diet (Guiry, 2012) under the assumption that dogs could access similar foods as those consumed by humans either directly through provisioning, or indirectly through scavenging. Furthermore, by assuming that dogs travel in the company of their owners, human migrations and/or cross-cultural interactions are revealed by tracking shifts in haplotypes or allele frequencies of dogs over geographic space (Ameen et al. 2019; Ollivier et al. 2018). While these approaches have received critique for oversimplifying human-dog dietary relationships (Perri et al., 2019; Eriksson & Zagorska, 2002), when biomolecular methods are combined with recent developments in social zooarchaeology, there is considerable potential to yield new insights into human-environment interactions (McGrath et al., 2019).

The Canine Surrogacy Approach (Edwards et al., 2017; Guiry, 2012; Cannon et al., 1999) to dog diets and later modifications that may characterize population genetic studies, lack sensitivity to the often-fraught history of dogs in colonial North America and Siberia. During European exploration and settlement of these regions, the colonial agendas of Western geopolitical powers were furthered through the use of racially-charged language that positioned indigenous Arctic dog breeds as a metaphor for human Indigenous populations (Riche, 2015); control of domestic dog populations and forced resettlement policies further undermined traditional Indigenous lifeways (Lévesque, 2010; Tester, 2010; Laugrand & Oosten, 2002). Recent calls in

anthropology and archaeology to reject anthropocentrism are creating more nuanced understandings of humans and their relationship to domestic dogs, wild canids, and at a broader scale, historical and modern landscapes and ecological webs (Losey et al. 2018a; Overton and Hamilakis, 2013; Conneller, 2004; Viveiros de Castro, 1998). Social zooarchaeology repositions human beings relative to other species and focuses on the social, sensory, and environmental facets constituting the consumption of animals and their secondary products (Overton and Hamilakis, 2013).

In the world view of Inuit and Yup'ik cultures, humans share the landscape with non-human beings who are in possession of a spirit known as *inua* (Fitzhugh and Kaplan, 1983). Animals known to possess inua include dogs, seals, whales and wolverines, as well as a number of other beings (Bodenhorn, 1990; Fitzhugh and Kaplan, 1983). Reliant on animals for both food and raw materials, northern peoples were constantly engaged in social interactions with non-human beings. These relationships were maintained through the careful observance of food taboos and ritualized behaviours (Hill, 2011; Bodenhorn, 1990; Rasmussen, 1931, 1929). Dogs were unique in Inuit and Yup'ik cosmology; they were given names at birth, they received and wore amulets, they took part in ritual activities, and were considered to be members of society (Hill, 2018; Whitridge, 2018; Laugrand and Oosten, 2002). In contrast, wolverines did not behave according to the strict rules set out by arctic societies and represented dangerous and subversive figures (Laugrand, 2017).

Relational ontology and animism (Descola, 2013) have provided useful avenues to understand how the worldviews of arctic peoples are expressed in material culture. Connecting ontological perspectives with ecology is the concept of *habitus.* Habitus describes the corporeal bodies of humans and non-humans as 'an assemblage of affects or ways of being' (Viveiros de Castro, 1998). A habitus is constituted by the physical characteristics of a being that allow it to exist within an environment, and the interactions with other living and non-living things that shape its experiences and construct its perspective (Descola, 2013). The concept of habitus can provide similar insight into the use of fur clothing by arctic peoples. The functional properties of furs allow humans to inhabit the world in similar ways to wild species, literally providing humans with a 'second skin' (Bodenhorn, 1990) and through biomolecular analyses of the furs, it is also possible to glimpse aspects of the habitus of the non-human arctic beings, namely those relating to diet. In the present study, we sought to access human-canid relationships through the combined methods of ancient mitochondrial

DNA and stable carbon and nitrogen isotope analysis. We applied shallow DNA sequencing to genetically identify the source of the fur and verify macroscopic species identifications. These results were combined with stable isotopic analysis to yield new insights on regional variation in the diets of domestic dogs and wild species.

2 BACKGROUND

2.1 Dogs in the Arctic

Human occupation of arctic environments was made possible through the use of domestic dogs for traction, hunting aids, companionship, and as a source of fur and food (Strecker, 2018; Laugrand and Oosten, 2014; Morey, 2010). North American Arctic and Subarctic dogs were historically relied on for sled traction, assistance with scenting seal-breathing holes and hunting polar bears (Whitridge, 2018; Rasmussen, 1931). The uses of dogs among Siberian Arctic cultures were more variable. Among the Nenet and Khanty reindeer herders of Western Siberia, dogs were used for traction, herding reindeer (caribou, *Rangifer tarandus*), and hunting wild game (Losey et al., 2018b; Dwyer and Istomin, 2008; Handford, 1998; Fitzhugh, 1997). Dogs were tasked with pulling sleds in the coastal Kamchatka Peninsula until the introduction of domestic reindeer, 100 years ago (Strecker, 2018).

The presence of domestic dogs among Siberian and North American Indigenous communities is increasingly the focus of genetic and osteological research (Ameen et al., 2019; Perri et al., 2019; Losey et al., 2018c; Losey et al., 2018b; Brown et al., 2013). Dogs fall into seven identified mitochondrial clades, A-F and the recently identified X clade (Ameen et al., 2019; Ní Leathlobhair et al., 2018; Thalmann et al., 2013; Pang et al., 2009; Savolainen et al., 2002;). Arctic dogs from Eastern Siberia and North America predominantly belong to the mitochondrial A-clade, based on samples ranging from the Early Holocene through to the current day (Ameen et al., 2019; Ní Leathlobhair et al., 2018; Brown et al., 2015, 2013). Specific A-clade haplotypes of North American dogs likely accompanied successive migrations of human groups from Siberia into the North American continent (Ameen et al., 2019; Ní Leathlobhair et al., 2018).

2.2 Dog fur clothing

The expert fabrication of fur clothing is regarded as a key adaptation to arctic environments (Issenman, 2011). Historically, the use of different furs was dependent upon a number of factors: the availability of species; trade with other northern groups (Arnold, 2016); the value of different furs as trade commodities; and opportunistic encounters with other species, such as polar and grizzly bear, while trapping foxes for European and Euro-American markets (Oakes, 1988). Generally, clothing across the North American and Siberian Arctic regions was made from the pelts of reindeer/caribou, harp seal (*Pagophilus groenlandicus*), or ringed seal (*Pusa hispida*) (Issenman, 2011; Carlsen et al., 1995; Hatt and Taylor, 1969). The furs of dogs, wolverines, and other species with dense fur, were used as a trim or ruff on the borders of clothing such as parkas, coats, and boots (Issenman, 2011; Hatt and Taylor, 1969; Krasheninnikov and Crownhart-Vaughan, 1955). The long guard hairs shared by these animals were useful for controlling temperature and humidity (Issenman, 2011). In subzero temperatures, the condensation from breath can collect on the fur trim around the hood and freeze, but this condensation can be shaken or brushed free from furs with long guard hairs (Issenman, 2011). When these furs line the edge of a hood, they can block the wind and aid in maintaining a warm environment around the face (Issenman, 2011; Cotel et al., 2004). Carnivore fur, such as dog, have a longer use-life as the fur is more resilient to fluctuations in humidity and moisture, whereas when the same processes occur to caribou fur, the fragile, hollow hairs will shed (Issenman, 2011; Hatt and Taylor, 1969; Steller, 1774). In some regions, certain dog furs were valued over others, for example in Kamchatka white fur from long-haired dogs was held in the highest regard (Strecker, 2018; Krasheninnikov & Crownhart-Vaughan, 1955). Dog fur has also been used in other regions outside of the Arctic such as the Salish coast where dog fur was woven into blankets up until European contact (Solazzo et al., 2011).

2.3 Canid diets and stable isotope analysis

The care and provisioning of domestic animals represent an investment, or storage of human labor, in return for assistance with subsistence activities, raw materials, and secondary products (Gudeman, 1977). As carnivores, dogs are one of the few domestic species that must be provisioned with meat and sources of dietary lipids

(Losey et al., 2018a). In the Arctic, dogs were, and continue to be provisioned with readily available food sources, such as salmon or seal, which can be acquired in bulk and stored. In Greenland, the Canadian Arctic Archipelago, and coastal Labrador, between the 15th and 20th centuries, dogs were provisioned with seal, fish, shark, and caribou depending on the local availability of particular taxa (Coltrain et al., 2004; Hantzsch, 1977; Jensen, 1961; Freuchen, 1921). Pre- and post-European contact populations of the Aleutian Islands and coastal Alaska harvested salmon and marine mammals to feed domestic dogs (McManus-Fry et al., 2018; West and France, 2015; Dunlap et al., 2007; Andersen, 1992). For at least 300 years, salmon has been a staple food for sled dogs of the Kamchatka Peninsula while hunting dogs were fed birds (Strecker, 2018; Krasheninnikov and Crownhart-Vaughan, 1955; Steller, 1774). Among the Nenets and Khanty of the Northern and Polar Urals, dogs were, and still are, fed reindeer meat and seasonal, locally available freshwater fish (Svoboda et al., 2011), which may demonstrate historical continuity with prehistoric practices (Losey et al., 2018d). Frequently, it is the scarcity of provisions for dogs that is responsible for the decline in their populations, in addition to epidemics of rabies and canine distemper virus (Strecker, 2018; Degerbøl and Freuchen, 1935; Hjortlund, 1907).

The day-to-day practices, such as feeding, that reinforced human-dog relationships in the Arctic have only recently begun to receive academic attention (Losey et al., 2018a). Stable carbon and nitrogen isotope ratio analysis provides an effective means to estimate the sources of dietary protein. Stable carbon isotope ratios (δ^{13}C values) can distinguish between the three main photosynthetic pathways used by different plant taxa (O'Leary, 1988), and between marine and terrestrial environments (Schoeninger and DeNiro, 1984). Cumulative enrichment occurs in ^{15}N between trophic levels linking stable nitrogen isotope ratios (δ^{15}N values) to a consumer's trophic position and environment (Minagawa and Wada, 1984). Higher δ^{15}N values are measured in marine consumers (McManus-Fry et al., 2018; Britton et al., 2013; Guiry et al., 2012; Nelson, Møhl, et al., 2012; Byers et al., 2011; Szpak et al., 2009; Coltrain et al., 2004) as aquatic food chains are longer than those of terrestrial environments.

Fur keratin is used as a dietary proxy in both modern and archaeological studies of diet (McManus-Fry et al., 2018; Milakovic and Parker, 2011; Urton and Hobson, 2005; Darimont and Reimchen, 2002;) as it incorporates amino acids sourced from the diet during growth and, once formed, is metabolically inert (Petzke et al., 2005).

Isotopic fractionation occurs in the metabolic processes that transform dietary amino acids, and those already found in the body, into new proteinaceous tissues, such as keratin (Macko et al., 1987). Diet-fur discrimination factors of +2 – +2.6‰ for $\delta^{13}C$ and +3.4‰ for $\delta^{15}N$ were originally determined for red foxes (Roth and Hobson, 2000) and appear to be appropriate for wolves (Milakovic and Parker, 2011; Urton and Hobson, 2005; Darimont and Reimchen, 2002). By comparison, bone collagen, the most common analyte in palaeodietary studies, tends to be elevated in $\delta^{13}C$ and $\delta^{15}N$ relative to diet by +5‰ and +3 – +5‰, respectively (Bocherens and Drucker, 2003; Ambrose and Norr, 1993). Bone collagen and fur keratin record diet over different time periods of an animal's life; bone collagen reflects the average protein sources consumed across a dog's lifespan while fur keratin records dietary inputs only over the period of growth, approximately 14 to 15 weeks (Diaz et al., 2004). The growth rate of dog fur across different dog breeds is not thoroughly understood and can be expected to fluctuate seasonally (Diaz et al., 2004; Al-Bagdadi et al., 1977). Isseman (2011) reports that the husky's winter fur, containing a mixture of long guard hairs and short wool-like underfur, would add a warm, moisture-resistant layer to clothing. We do not associate the sampled furs in the study with a particular season, but we assume that the fur samples would have grown over a period of three to four months.

3 MATERIALS AND METHODS

3.1 Fur clothing samples

The samples studied in this project were obtained from the ethnographic collections curated by the National Museum of Denmark (Supplementary Table 1). The fur clothing was collected from Indigenous cultures across the North American and Siberian Arctic during the late 19th and early 20th centuries. The Fifth Thule Expedition, 1921–1924, purchased additional items in 1927 from Siberia (the so-called Eugen Alexander collections) that are currently curated by the National Museum. Further details can be found on the SkinBase database http://skinddragter.natmus.dk/Clothing (Schmidt, 2016). The year of collection, the name of the Indigenous culture and location are recorded for some of the garments, but others are only associated with a general location, such as Alaska and the Aleutian Islands, or Kamchatka Krai. For this reason, we were unable to link the samples to

particular locations or cultures and refer to the samples only by the general location of acquisition, which in some cases necessitated the use of colonial language.

Fur clothing or garments macroscopically identified as being dog/wolf fur were selected for inclusion in this study. We further collected paired samples from four additional garments with visually different ‘dog’ fur. A small sample of skin was removed from the garment roughly the size of a grain of rice with the fur intact upon the skin. The fur was removed from the skin using a sterile scalpel whereupon the fur and skin were processed for isotopic analysis and DNA sequencing, respectively. Mitochondrial genomes have been published from 11 dog furs in this collection from arctic communities spanning from St. Lawrence Island (Alaska) to Greenland (Ameen et al., 2019). The published mitochondrial genomes from these specimens were combined with samples included in this study to broaden the geographic range to western Siberia, test the macroscopic species identification, and to increase the coverage of published samples (Ameen et al., 2019).

3.2 Wolf pelt samples

The historical wolf samples from Greenland and Canada used in this study have been provided by the Natural History Museum of Denmark, the Natural History Museum, University of Oslo and the Danish Museum of Hunting and Forestry and were sampled from stuffed specimens or complete hides collected and listed as wolves.

3.3 Ancient DNA analysis of skin samples

DNA was extracted from skin samples (n=68) using a protocol, specific to ancient soft tissues, that removed inhibitors such as the biocides used to treat the garments in the museum collections (Ameen et al., 2019; Gilbert et al., 2007). The samples underwent a brief predigestion step to remove surface contaminants in an EDTA and proteinase K buffer for 30 minutes, followed by overnight digestion to extract the DNA. Purification of the extraction was performed according to (Ameen et al., 2019; Ersmark et al., 2015). Library building was conducted as per the BEST protocol for libraries (Ameen et al., 2019; Carøe et al., 2018). The amplified libraries were sequenced on the Illumina HiSeq2500 sequencing platform at Science for Life Laboratory in Stockholm, Sweden and further sequencing of previously published samples was conducted at the BGI sequencing facilities in Shenzhen, China on the BGISEQ-500 platform.

Libraries prepared for sequencing on the BGISEQ-500 platform also follow the BEST protocol with the only alteration being the use of platform-specific sequencing adapters and indexes (Carøe et al., 2018).

The sequenced reads from each sample were initially mapped to the reference genome for the dog, CanFam3.1 under the assumption that the fur was of dog origin as indicated by the macroscopic assessment (Li and Durbin, 2009; Lindblad-Toh et al., 2005). The reads were also aligned to the NCBI NR protein database (14th Nov. 2019) using DIAMOND (Buchfink et al., 2015) to test whether the furs could have originated from other taxa. Briefly, DIAMOND aligns nucleotide data against a reference database composed of protein sequences from all three domains of life (bacteria, eukaryotes, and archaea). The taxonomic composition of a sample is computed based on these alignments using the LCA algorithm with MEGAN (Huson et al., 2016, 2007).

Subsequently, each sample was mapped to a concatenated panel of 28 mitochondrial reference genomes. These correspond to local mammalian taxa from the region which are reported to have been used for clothing (Issenman, 2011; Hatt and Taylor, 1969;). Related species were used when mitochondrial references were not available, for example, the only relevant mitochondrial reference available for Arctic rodents were the Daurian ground squirrel and Siberian chipmunk mitochondrial genomes but ethnographic records also report the use of other ground squirrel species (Issenman, 2011). Each sample was mapped to the panel of mitochondrial reference genomes using BWA (Li and Durbin, 2009). A concatenated reference panel was used to mitigate the repeated mapping of the same reads to conserved or repetitive regions of the mitochondrial genomes. The alignments were then filtered to remove all reads with mapping quality below 30 and PCR duplicates were removed with Picard tools (http://broadinstitute.github.io/picard/) (Supplementary Table 2, Appendix 2). The reads mapping to each mitochondrial reference in the concatenated reference panel were then extracted and quantified. Consensus sequences were called for samples that possessed complete mitochondrial genomes for the identified taxa with HTSbox (https://github.com/lh3/htsbox). Four of the previously published samples have increased coverage as a result of additional sequencing (Ameen et al., 2019). A maximum-likelihood tree of dogs and wolves was constructed with 1000 bootstrap replicates using RAxML (Stamatakis, 2006) from samples with at least 3x mean coverage of the mitochondrial genome, with publicly available dog and wolf

mitochondrial genomes using a coyote as the outgroup (Ameen et al., 2019; Ní Leathlobhair et al., 2018; Frantz et al., 2016; Thalmann et al., 2013; Pang et al., 2009). A maximum-likelihood tree was also constructed for fox samples following the same procedure, using one mitochondrial fox genome generated in this study and publicly available arctic fox (n=3) and red fox (n=6) mitochondrial genomes using the dog mitochondrial reference genome (NC002008.4) as an outgroup (see Supplementary Fig. 1, Appendix 2, for a list of NCBI accession numbers for fox mitochondrial genomes). For samples identified as dogs, and in cases with enough sequenced reads, biological sex was identified in cases through the comparison of reads mapping to the X chromosome in comparison to chromosome 1, which is similar in length (Skoglund et al., 2013, 2015).

Furthermore, we used FastQ Screen (Wingett and Andrews, 2018), a tool for searching against a reference panel to determine species source or metagenomic composition, with the same 28 mitochondrial genomes plus the human mitochondrial reference genome to evaluate the source of the furs. Due to the lack of complete whole genome references for all the candidate species, mitochondrial references were used to limit the disproportionate reference size for taxa with whole genome references available. FastQ Screen has been implemented on similar datasets to identify the animal source of clothing for Ötzi, the Tyrolean Iceman (O'Sullivan et al., 2016) and to assess the animal of origin for medieval vellum samples (Fiddyment et al., 2015). The FastQ Screen run was implemented also using BWA to align the sequenced reads to the reference panel. The results of FastQ Screen were visualised for the dataset used in the study with MultiQC (Ewels et al., 2016).

3.4 Isotope analysis of fur samples

The samples macroscopically identified as dog fur were pretreated at the Archaeological Research Laboratory, Stockholm University. The samples were cleaned by ultrasonication in a 2:1 chloroform-methanol solution (3 x 15 minutes). The solvent treated samples were then rinsed with deionized water and air-dried for 24 hours. Between 0.7 mg and 1 mg of each fur sample was tightly folded into a tin capsule (5x9 mm, Säntis Analytical, Switzerland) for stable carbon and nitrogen isotope analysis. The fur samples were analyzed at the Jan Veizer Laboratory, University of Ottawa, Canada. Ten percent of the samples were analyzed in duplicate.

The samples were combusted in a Vario EL Cube (Elementar, Germany) EA-IRMS interfaced via Conflo IV to Delta Advantage isotope ratio mass spectrometer (Thermo, Germany). The raw isotope data were referenced to the VPDB (carbon) and AIR (nitrogen) scales using six calibration standards (IAEA-N1, IAEA-N2, USGS-40, USGS-41, NBS-22, and IAEA-CH-6). Three internal check standards were included in the analytical run: C-51 (δ^{13}C: –23.0‰; δ^{15}N: +0.1‰), C-52 (δ^{13}C: –11.9‰; δ^{15}N: +16.6‰), C-54 (δ^{13}C: –16.6‰; δ^{15}N: –34.5‰). Analytical error was monitored using a blind standard (C-55, Glutamic acid, δ^{13}C: –4.0‰; δ^{15}N: –28.5‰) run in triplicate and was better than $\pm$0.1‰ for carbon and nitrogen.

The wolf fur samples were pretreated and analyzed at BioArCh, University of York. The samples were ultrasonicated in deionized water for 1 hour to remove dirt and other debris. The samples were then soaked in a 7:1 dichloromethane/methanol solution (Tankersley and Koster, 2009) for 14 hours after which time the solution was removed and the excess solvent allowed to evaporate. The samples were then ultrasonicated in deionized water (3×30 minutes) (Britton et al., 2013) and oven-dried (40°C, 24 hours). Each dried sample was then homogenized using sterilized scissors. The samples (0.9 mg–1.1 mg) were weighed in duplicate into tin capsules and combusted in a Sercon GSL Sample Preparation System module coupled to a Sercon 20-22 mass spectrometer. The raw isotope values were calibrated to the VPDB and AIR scales using international standards (Caffeine [IAEA 600] δ^{13}C: –27.8$\pm$0.1‰, δ^{15}N: +1.0$\pm$0.1‰; Cane sugar [IA-R006] δ^{13}C: –11.6$\pm$0.1‰; and IAEA-N-2 δ^{15}N: +20.3$\pm$0.2‰). Replicates of an internal fish gelatin standard (δ^{13}C: –15.2$\pm$0.1‰, δ^{15}N: +15.3$\pm$0.2‰) were run between every six samples to correct for instrumental drift. Three additional fish gelatin standards were used as check standards. Analytical error on replicate analyses of the samples was $\pm$0.2‰ or better for δ^{13}C and δ^{15}N.

We assessed sample preservation by comparing the atomic C/N ratios of the fur to published modern data sets from humans. In the papers we surveyed C/N ratios from the fur of modern canids included in stable isotope studies are rarely published. The C/N ratios of modern hair range from 3.0 to 3.8 (O'Connell et al., 2001; O'Connell & Hedges, 1999a), and are typically used to assess the preservation of human and non-human archaeological samples (McManus-Fry et al., 2018).

3.5 Isotope data treatment

The challenge with interpreting stable isotope data from a wide geographic area lies in finding suitable comparative baseline data sets against which the target isotope data can be contextualized and interpreted (Casey and Post, 2011). As our samples date to the late 19th and early 20th century, the Suess effect on the $\delta^{13}C$ values of the samples was minimal and approximated analytical error. Therefore, we compared our samples to archaeological datasets and did not correct the fur data for the Suess effect. However, published modern salmon scale data (Satterfield and Finney, 2002) used in the paleodiet interpretation were corrected for the Suess effect after (Misarti et al., 2009) modified from (Hilton et al., 2006). This resulted in the addition of +0.7‰ to the salmon $\delta^{13}C$ values. This value is only an approximation of the change in $\delta^{13}C$ in the Pacific Ocean, as we did not account for changes due to phytoplankton productivity, sea surface temperature, and atmospheric CO_2 concentration. However, we deemed this acceptable because our intention was not to produce a comprehensive model of paleodiet.

Much of the comparative archaeological data available for arctic fauna is sourced from bone collagen, therefore, for ease of comparison, we adjusted the $\delta^{13}C$ and $\delta^{15}N$ values of dog fur specimens by +1.4‰ and +0.9‰, respectively, after (O'Connell et al., 2001). These discrimination factors were determined through experimental research on modern humans, but to the best of our knowledge, such data do not yet exist for domestic dogs, however, similar offsets have been used in dietary analyses of wolf fur and bone collagen (Kays and Feranec, 2011) and palaeodietary analyses of domestic dog fur and collagen (McManus-Fry et al., 2018).

4 Results

4.1 Genetic species identification of fur clothing

Samples were taken from 68 specimens to initially confirm the macroscopic species identification in order to ensure the appropriate interpretation of the isotopic results as well as to increase the number of complete mitochondrial genomes from historical arctic dogs in context with dietary data. Of the 68 specimens sampled, DNA data from 11 of these specimens were previously acquired and published by Ameen et al., (2019). In the previously published dataset two samples were identified as having

been derived from animals with wolf mitochondrial haplotypes (Ameen et al., 2019); however, samples with low *Canis* sp. DNA content were excluded from analysis due to insufficient coverage of the mitochondrial genomes and as such were not tested for originating from non-*Canis* sources.

Based on mitochondrial and protein sequences, taxonomic assignment was possible for 36 of the samples from this study, and we confirmed the taxonomic assignment of the 11 published specimens (Fig. 5.1A,C). Four samples included in previously published studies underwent further sequencing improving the mitochondrial genome coverage (Ameen et al., 2019). The results of the alignment to the concatenated panel of mitochondrial genomes and the FastQ Screen results produced complimentary results after filtering out reads with low mapping quality and reads with no hits or hitting multiple genomes, respectively, see Appendix 2, Supplementary Fig. 2 and Supplementary Tables 2 and 3. We were able to confidently identify 31 specimens as dogs or wolves on the basis of their DNA, including the 11 published individuals. A further 8 samples were identified genetically as wolverine fur (*Gulo gulo*). Fox fur was identified on three of the garments; it was possible to identify one specimen (TRF.02.12) as a red fox (*Vulpes vulpes*) using phylogenetic tree construction, see Supplementary Fig. 1 (Appendix 2). However, insufficient data was available for the other two specimens to provide confident species-level assignments. Two specimens showed the most reads mapping to the reindeer/caribou mitochondrial genome and both also had reads aligning to ruminant proteins in the DIAMOND analyses, see Supplementary Fig. 3 and Supplementary Table 4 (Appendix 2). Individual samples were also identified as a lynx (*Lynx lynx*) and a rodent related to the Durian ground squirrel (*Spermophilus dauricus*). Concatenated reference panel alignment and the FastQ Screen analyses both showed the greatest proportion of reads aligned to the Ursus genus for one specimen, TRF.02.39. The light colour of the fur, a high δ^{15}N value, and higher volume of reads mapping to the *Ursus maritimus* mitogenome over the *Ursus arctos* mitogenome, together suggest the fur originated from a polar bear. Due to an insufficient amount of data, with less than 50,000 reads, a confident taxonomic assignment was not possible for eight of the sequenced samples. For three additional samples with between 95,648 and 435,734 reads sequenced, no species in the mitochondrial panel or DIAMOND analysis could be identified as the taxa of origin for the fur. This likely occurred as the result of biases in the protein database which contained a disproportionate amount of data from dogs

relative to other taxa of interest – even in the samples confidently identified as wolverine or fox, DIAMOND identified them as dog. Of the specimens confidently identified as dog, the endogenous DNA content ranged between 14-60% (mean 52.4%).

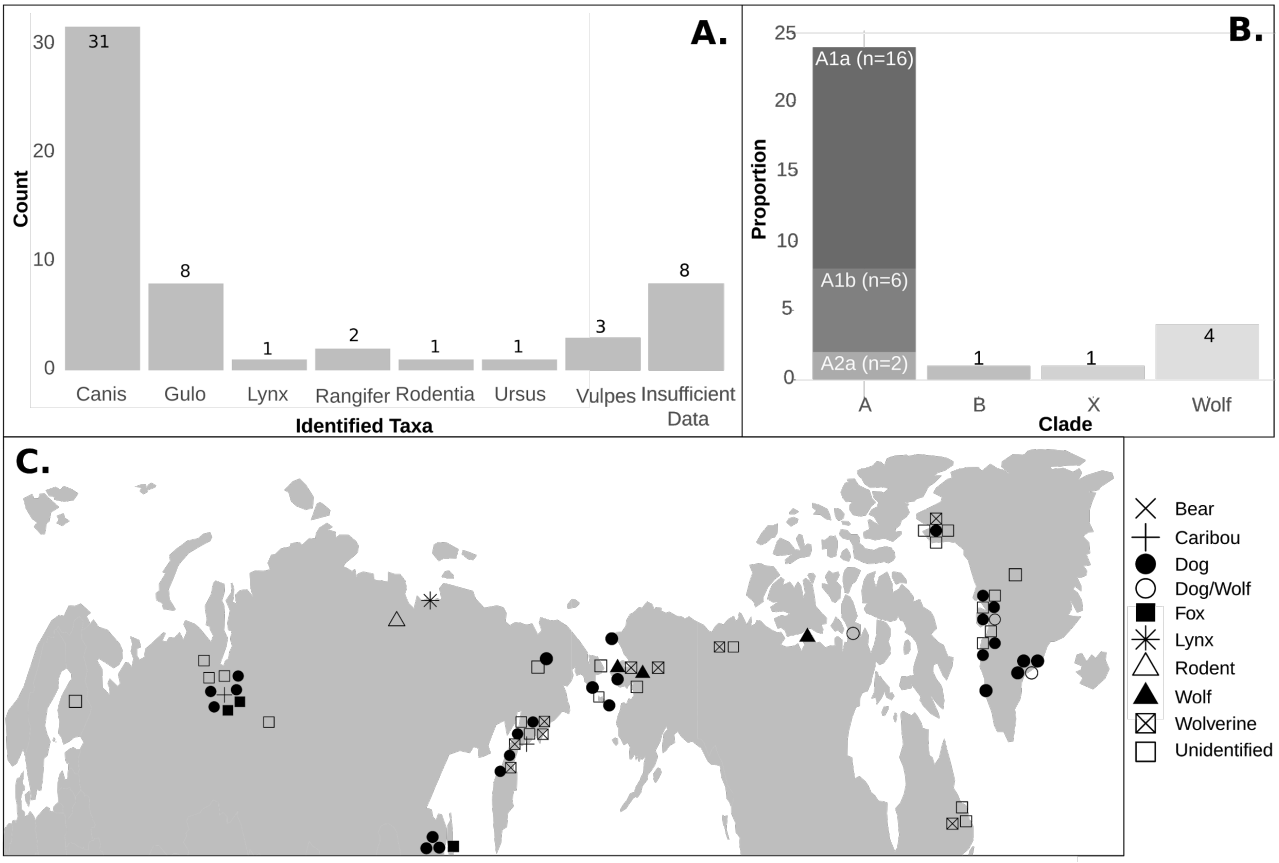

Figure 5.1 Genetically identified taxa from fur samples. A) Counts taxa identified genetically from this study and the published samples from the collection (Ameen et al., 2019). B) Counts of dog/wolf haplotypes carried by dogs/wolves in the collection. C) Genetically identified fur samples mapped to the region of collection.

Complete mitochondrial genomes, where at least 90% of the sites had a mean coverage of 3x, were obtained from 17 dogs, one fox, one lynx, and six wolverines out of the 47 total samples sequenced. A phylogenetic tree was constructed with the dog/wolf mitochondrial genomes from this study and combined with 344 published mitochondrial genomes and the four previously discussed published mitogenomes with improved coverage (TRF.02.04, TRF.02.14, TRF.02.16, and TRF.02.29). Phylogenetic analysis revealed that only the two published samples were wolves (TRF.02.27 and TRF.02.28), the 17 previously unpublished mitochondrial genomes

were all phylogenetically identified as dogs (Supplementary Fig. 4). One of the previously unpublished dog mitochondrial genomes, from a Nenets/Khanty coat, was found to have a mitochondrial genome from the B clade in the phylogenetic tree while the remaining 16 samples fell into the A clade. The A-clade dogs fell into three of the main A-subclades: A1a (n=10), A1b (n=4), and A2a (n=2) (Fig.1B).

4.2 Paleodiet of Arctic and Subarctic dogs, wolves, and wolverines

All but one of the samples met with published preservation criteria (O'Connell and Hedges, 1999b), with atomic C/N ratios ranging from 3.3 to 3.8. One sample (TRF-2-43), with exceedingly high weight % carbon and nitrogen, was removed from further analysis. The stable isotope data and preservation indicators from the samples genetically identified as *C. l. familiaris* and the wolf pelts are shown in Tables 5.1-5.2 and Figure 5.2. Stable isotope results and preservation indicators from fur clothing samples genetically identified as wild species or with insufficient data for genetic identification are shown in Table 5.3.

Table 5.1. Stable isotope results and preservation indicators from fur clothing samples genetically and macroscopically identified as *C. l. familiaris* (domestic dog).

Sample ID	MT. Cov.	Location	Year of collection	Sex	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	%C	%N	C/N
TRF-2-53	149.5	Kamchatka Krai, Russia	1961	M	–19.8	+6.5	45.3	14.7	3.5
TRF-2-54	14.7	Kamchatka Krai, Russia	1961	M	–20.4	+12.3	44.3	14.8	3.5
TRF-2-57	14.7	Kamchatka Krai, Russia	1961	F	–18.0	+7.3	44.1	14.7	3.5
TRF-2-23	29.7	Northern/Polar Urals, Russia	1927	M	–19.8	+7.1	44.3	14.6	3.5
TRF-2-25	44.5	Northern/Polar Urals, Russia	1927	M	–20.3	+8.5	43.7	14.2	3.6
TRF-2-14	73.2	Point Hope, Alaska	1926	M	–16.2	+14.6	40.6	13.3	3.6
TRF-2-29	101.2	Alaska/Aleutian Islands	1945	M	–16.5	+13.4	44.8	14.5	3.6
TRF-2-16	155.4	St. Lawrence Island, Alaska	1939	F	–14.2	+18.3	44.7	14.5	3.6
TRF-2-65	0.9	Nunavut, Canada	No date	F?	–16.1	+14.0	44.2	14.0	3.7
TRF-2-37	10.9	Tasiliak, Greenland	1911	M	–15.3	+16.4	44.3	14.4	3.6
TRF-2-70	12.0	Tasiliak, Greenland	1911	F	–14.7	+17.8	50.2	15.8	3.7
TRF-2-47	36.4	Uummannaq, Greenland	1926	F	–15.4	+19.8	39.6	13.1	3.5

TRF-2-41	4.0	West Greenland	1980	F	–16.5	+17.8	46.9	14.9	3.7
TRF-2-44	2.2	West Greenland	No date	M	–15.1	+18.3	40.0	12.8	3.6
TRF-2-45	2.2	West Greenland	No date	M	–14.6	+15.8	44.5	14.3	3.6

Table 5.2. Stable isotope results and preservation indicators from wolf pelts.

Sample ID	Location	Region	Year of collection	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	%C	%N	C/N
1766	Itivleriaq, East Foxe Basin	Nunavut, Canada	1922	–20.9	+7.5	44.7	15.0	3.5
2046	Itibdjeriang, East Foxe Basin	Nunavut, Canada	ca. 1928	–20.6	+7.6	43.2	14.8	3.4
2047	Itibdjeriang, East Foxe Basin	Nunavut, Canada	ca. 1928	–21.0	+7.4	43.5	14.8	3.4
2043	Southampton Is.	Nunavut, Canada	1922	–20.2	+8.2	43.8	15.0	3.4
2044	Wilson Lake	Nunavut, Canada	1922/23	–20.2	+8.0	44.2	15.3	3.4
2048	Back River	Nunavut, Canada	1923	–21.3	+7.9	43.9	15.1	3.4
2049	Back River	Nunavut, Canada	1923	–19.5	+12.3	43.5	15.0	3.4
2050	Back River	Nunavut, Canada	1923	–19.7	+12.0	43.4	15.0	3.3
1458	Axel Heiberg Is.	Nunavut, Canada	1912	–23.1	+5.9	43.6	15.0	3.4

1460	Axel Heiberg Is.	Nunavut, Canada	ca. 1914	–22.9	+6.5	41.7	14.4	3.4
4093	Axel Heiberg Is.	Nunavut, Canada	1940	–21.7	+8.9	43.1	14.8	3.4
4094	Axel Heiberg Is.	Nunavut, Canada	1940	–21.5	+8.2	43.7	15.1	3.4
Eunr	Ellesmere Is.	Nunavut, Canada	1919	–23.0	+8.4	45.2	15.1	3.5
3456	Ellesmere Is.	Nunavut, Canada	1919	–22.8	+6.6	45.4	15.5	3.4
1921	Rosenvinge	Greenland	1925	–22.4	+5.4	44.9	15.4	3.4
1237	Hvalrosodden	Greenland	1922/23	–22.5	+5.6	43.4	14.9	3.4
4903	Kap Graah	Greenland	1926	–21.6	+5.8	42.9	14.7	3.4
8.1	East coast	Greenland	1901	–22.7	+7.0	43.7	14.9	3.4
1240	Skibshavnen	Greenland	1908	–19.4	+13.2	44.7	15.4	3.4

Table 5.3 Stable isotope results and mtDNA coverage from samples genetically identified as wild species or with insufficient data for identification.

Sample ID	Macroscopic species ID	Genetic species ID	Location	MT. Cov.	Year of collection	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	%C	%N	C/N
TRF-2-27	*C. l. familiaris*	*C. lupus*	Alaska/Aleutian Is., USA	4.9	1945	–19.1	+6.8	45.3	15.0	3.5
TRF-2-28	*C. l. familiaris*	*C. lupus*	Alaska/Aleutian Is., USA	10.7	1945	–19.3	+6.7	44.7	14.1	3.7
TRF-2-69	*C. l. familiaris*	*C. lupus*	Kent Peninsula, Canada	38.0	1927	–18.5	+7.8	43.7	14.5	3.5
TRF-2-03	*C. l. familiaris*	*Gulo gulo*	Kamchatka Krai, Russia	0.4	1966	–20.2	+6.7	52.7	17.6	3.5
TRF-2-50	*C. l. familiaris*	*Gulo gulo*	Kamchatka Krai, Russia	0.1	1961	–21.0	+6.6	45.3	15.1	3.5
TRF-2-55	*C. l. familiaris*	*Gulo gulo*	Kamchatka Krai, Russia	5.4	1961	–17.1	+11.9	44.2	14.6	3.5
TRF-2-56	*C. l. familiaris*	*Gulo gulo*	Kamchatka Krai, Russia	4.3	1961	–18.9	+8.2	38.0	12.6	3.5
TRF-2-32	*C. l. familiaris*	*Gulo gulo*	Labrador, Canada	4.5	1924	–16.6	+13.6	44.4	14.9	3.5
TRF-2-35	*C. l. familiaris*	*Gulo gulo*	MacKenzie Delta, Canada	1.7	1936	–20.4	+6.9	42.1	13.9	3.5
TRF-2-30	*C. l. familiaris*	*Gulo gulo*	Alaska/Aleutian Is. USA	10.0	1945	–22.0	+6.3	44.3	14.4	3.6
TRF-2-39	*C. l. familiaris*	*U. maritimus*	Kap York, Greenland	0.0	1905	–15.0	+18.5	49.1	16.1	3.6
TRF-2-62	*C. l. familiaris*	*V. lagopus*	Northern/Polar Urals, Russia		1927	–22.2	+9.1	45.6	14.7	3.6

TRF-2-61	*C. l. familiaris*	*V. lagopus?*	Northern/Polar Urals, Russia	1927	–19.4	+11.9	44.4	14.2	3.6
TRF-2-66	*C. l. familiaris*	-	Kap York, Greenland	1905	–15.2	+15.9	36.9	12.1	3.6
TRF-2-33	*C. l. familiaris*	-	Labrador, Canada	1922	–13.8	+19.7	43.8	14.6	3.5
TRF-2-34	*C. l. familiaris*	-	Labrador, Canada	1922	–14.4	+18.3	45.2	14.5	3.6
TRF-2-72	*C. l. familiaris*	-	MacKenzie Delta, Canada	1926	–21.9	+11.4	44.5	14.4	3.6
TRF-2-52	*C. l. familiaris*	-	Kamchatka Krai, Russia	1961	–20.0	+7.9	45.0	15.0	3.5
TRF-2-63	*C. l. familiaris*	-	Northern/Polar Urals, Russia	1881	–23.2	+8.7	45.5	14.6	3.6
TRF-2-67	*C. l. familiaris*	-	Northern/Polar Urals, Russia	1927	–23.4	+7.5	45.4	14.1	3.8
TRF-2-17	*C. l. familiaris*	-	West Greenland	No date	–14.9	+18.3	45.2	14.5	3.6
TRF-2-43	*C. l. familiaris*	-	West Greenland	No date	–15.0	+15.7	77.3	29.4	3.1
TRF-2-46	*C. l. familiaris*	-	West Greenland	1870	–16.2	+13.6	44.3	14.1	3.7

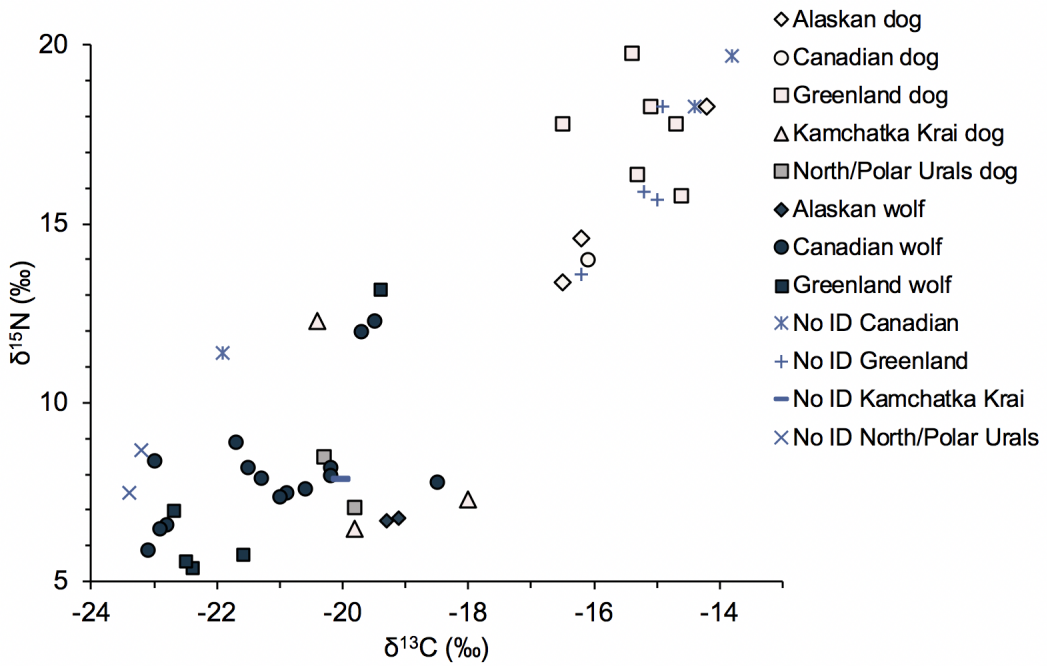

Figure 5.2. The δ^{13}C and δ^{15}N values of genetically identified dog and wolf fur samples, and samples lacking a genetic species identification.

We observed a broad range of δ^{13}C (–20.4‰ to –14.2‰) and δ^{15}N values (+6.5‰ to +19.8‰) in the dog fur samples, suggesting that dietary resources from marine, terrestrial, and potentially freshwater sources were used to provision dogs across the Arctic. The fur samples identified macroscopically as *C. l. familiaris* but for which no genetic identification could be obtained had a broader δ^{13}C range of –23.4‰ to –13.8‰, and δ^{15}N values ranging from +7.5‰ to +19.7‰.

The wolf pelts collected in Canada in the early 20th century had δ^{13}C values ranging from –23.1‰ to –18.5‰, and δ^{15}N values ranging from +5.9‰ to +12.3‰. The Greenland wolf pelts had δ^{13}C values ranging from –22.7‰ to –19.4‰, and δ^{15}N values ranging from +5.4‰ to +13.2‰. The genetically identified wolf fur samples from two Alaskan parka hoods had similar δ^{13}C values of –19.1‰ and –19.3‰, and δ^{15}N values of +6.8‰ and +6.7‰. The wolf samples are separated by latitude and plotted in Figure 5.3. The Canadian wolf samples from high latitudes (>75°N) generally had lower δ^{13}C values than those from lower latitudes, but the sample size was too small for statistical testing. One Greenland wolf pelt collected from a latitude above 75°N had a very high δ^{15}N value and higher δ^{13}C value relative to the other Greenland

wolves. This suggests some dietary contributions from marine or anadromous species.

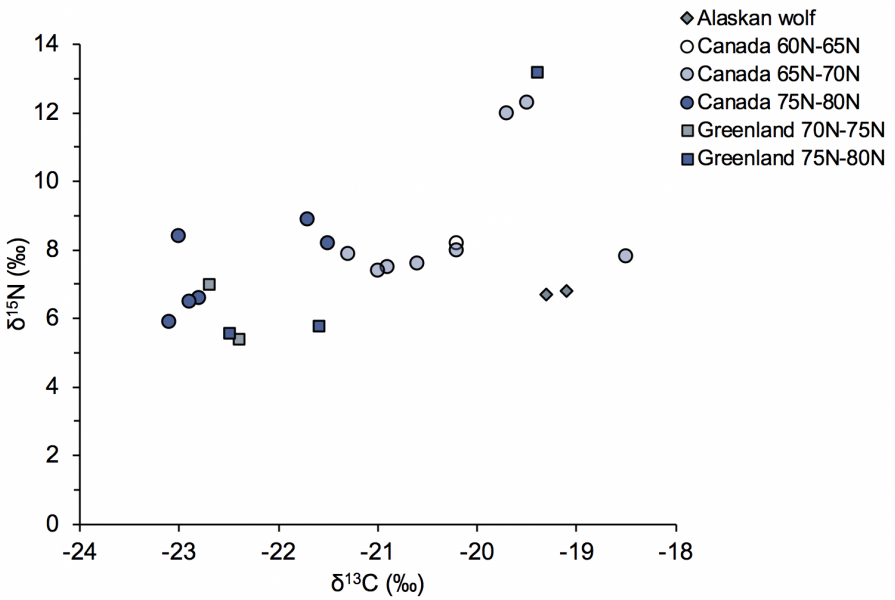

Figure 5.3 The $\delta^{13}C$ and $\delta^{15}N$ values of early 20th century wolves plotted according to latitude.

The ~5‰ range in $\delta^{13}C$ values and ~7‰ range in genetically identified wolverine $\delta^{15}N$ values was a surprising result of our study (Fig. 5.4). Wolverines have not been the subject of frequent isotopic study but the existing published bone collagen data from Alaska is tightly clustered around –20‰ reflecting a diet of terrestrial herbivore protein (Dalerum et al., 2009a). Wolverine diets are typically comprised of hunted and scavenged terrestrial ungulates (Dalerum et al., 2009b; Koskela et al., 2013), but the isotopic values of two wolverines from Kamchatka and Labrador are suggestive of inputs of protein from marine or anadromous species.

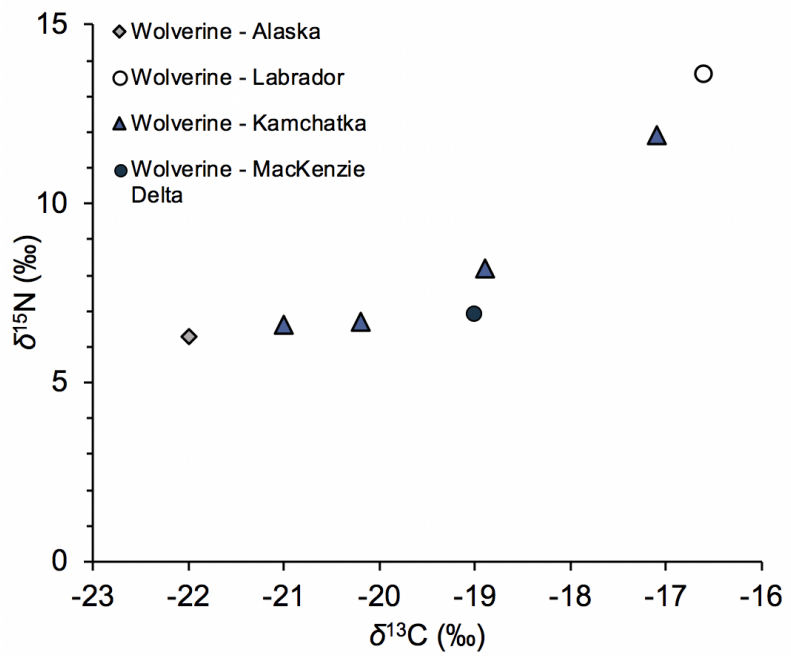

Figure 5.4 The $\delta^{13}C$ and $\delta^{15}N$ values of fur from genetically identified wolverines from Canada (Labrador and MacKenzie Delta), Alaska, and Kamchatka Krai.

5 Discussion

Fur clothing acts as a material archive and mnemonic of the social interactions between humans, dogs, and other species (Overton and Hamilakis, 2013). Living dogs were simultaneously working with each other alongside humans to sustain life in the Arctic and, among some communities in Kamchatka, being tended to as a future source of fur. As the fur was expertly fashioned into warm clothes it may have acted as a reminder of the owner-dog relationship during life and continued to testify to the interactions of the dog with other species via their consumption, and to the long-term genetic history of domestic dogs among Arctic cultures. The following section will review the methodological implications of this study, followed by a discussion of the results with respect to the reciprocal interactions of humans and dogs, and, as a contrast, the adversarial relationship between people and wolverines.

5.1 DNA analysis of fur clothing

Until the 1970s, the National Museum of Denmark routinely treated fur garments with chlorinated biocides to preserve the furs from insects, but despite this treatment, we were still able to extract sufficient endogenous DNA for analysis. The preservation of DNA in the skin samples proved to be very good in most cases. In cases where the

endogenous content of dog DNA appeared to be low (<10% dog DNA) closer investigation showed this to be the result of incorrect macroscopic identification rather than poor preservation. However, low endogenous content alone cannot distinguish between dog/wolf and non-dog/wolf samples. Samples with between 10-56% endogenous 'dog DNA' were, in turn, either dog samples with reduced preservation or from other carnivore species with similar DNA sequences, such as foxes and bears.

The phylogenetic analysis showed that, with only two exceptions, the dog mitogenomes from the collection all fall into the A clade. This is consistent with previous studies that show that Arctic dogs, prior to European colonization over the last century, possess mitochondrial haplotypes within this clade (Ameen et al., 2019; Brown et al., 2015, 2013). One of the exceptions is a Nenets/Khanty dog with a B clade haplotype, suggesting that this dog likely has at least some ancestry from outside of the Arctic where this haplotype is prevalent. Unfortunately, a sufficient amount of hair was unavailable for isotopic analysis, therefore we cannot compare the isotopic composition of the individual to other dogs from the region. The second exception is a dog carrying an X-clade haplotype as identified previously (Ameen et al., 2019). The specimens with A clade haplotypes generally cluster geographically, with dogs from Greenland grouping with other dogs from Greenland, and the different regions of Siberia clustering together.

The paired samples from garments with visually different dog fur provided some insight into the use of dogs in arctic communities. The coat featuring fur from the B clade haplotype had dog fur of two different colours, both of which were sampled and sequenced. The white fur possessed the B clade haplotype, while the sample with black fur carried an A clade haplotype demonstrating that dogs with both haplotypes were contemporaneously present in the region. Two individuals, male and female, were identified in a second set of paired samples taken from a coat made predominantly of dog skin. In the third set of paired samples the mitochondrial and sex data were insufficient to determine if the fur originated from different individuals. In the final set of paired samples both were identified as C. lupus with no phylogenetic distinction between the two and neither sample could be confidently assigned a sex. It appears that as dogs worked together to pull sleds, they were physically united after death, frequently with wild animals, in the task of protecting human bodies from the Arctic environment. Although domestic dogs were in possession of a unique perspective, and occupied a distinct position in the cosmology of arctic peoples

(Laugrand and Oosten, 2014), from the perspective of humans, the similarities between wild and domestic species may have been more important when choosing furs for clothing.

5.2 Isotopic analysis of fur clothing

Isotopic analysis of the sampled furs provided further characterization of the species composing the clothing of Arctic hunter-fisher-gatherers and herders. For samples with insufficient genome coverage, we hypothesized that diet may provide an indication of canid species, but this proved to be highly context dependent. Domestication is associated with behavioral, morphological, genetic change and, in the case of dogs, increasing dependence on humans for food, shelter, and protection (Zeder, 2006). In the archaeological past, and among modern societies with limited access to commercial dog food, dogs could have accessed locally available foods, either through scavenging or direct provisioning by their owners (Guiry, 2012). Dietary dependence would be particularly apparent among the dogs of mobile or semi-sedentary coastal arctic hunter gatherers. In such communities, marine resources were collected in bulk and dried or frozen to serve as dog food (Strecker, 2018; Ames, 1977), and these practices are revealed in the stable isotope values of archaeological dogs (McManus-Fry et al., 2018; West & France, 2015; Coltrain et al., 2004).

To enable comparison with published bone collagen data, the domestic dog, wolf, and unidentified fur samples were adjusted to estimated bone collagen values. The Greenland dog samples (Fig. 5.5A) plotted with local marine mammals suggesting these formed a dominant dietary component, similar to archaeological humans in the same region (Nelson et al., 2012). Four of the wolf samples had diets consistent with terrestrial sources of protein, while the fifth may have consumed a mixed marine-terrestrial diet. Greenland-based studies of Arctic wolf scat show that musk ox, hare, lemmings, and Arctic foxes feature in wolf diets (Dalerum et al., 2018; Maquard-Peterson, 1998). The unidentified samples from Greenland and Labrador (Fig. 5.5B) plot among the genetically identified dogs and published dog bone collagen samples. Dogs from the central and south coasts of Labrador were historically provisioned with small species of seal (ringed, harp and harbor) which would result in high $\delta^{13}C$ and $\delta^{15}N$ values relative to local marine species (Harris et al., 2020). Two of the dog fur samples from Alaska (Fig. 5.5C) are consistent with published dog bone collagen data from coastal Alaska and the Aleutian Islands and suggest a mixed salmon-marine

protein diet, while the third dog consumed food more consistent with a diet of marine mammals (Ameen et al., 2019; McManus-Fry et al., 2018; West and France, 2015). The two wolf fur samples had much lower $\delta^{13}C$ and $\delta^{15}N$ values relative to marine taxa and genetically identified dogs. The wolf fur samples (Fig. 5.5D) from Nunavut had isotopic compositions consistent with a diet of terrestrial protein, while the $\delta^{13}C$ and $\delta^{15}N$ values of the domestic dog were consistent with a marine protein-based diet (Coltrain et al., 2004). The unidentified fur sample from the MacKenzie Delta plotted among the wolf samples. These results suggest that the unidentified samples with isotopic values consistent with marine environments may be from domestic dogs, but similar isotopic values from polar bear fur (Table 5.3) ultimately undermine this assumption. However, future isotopic studies of canid bones from the Eastern Arctic may reasonably assume that diet can be used as a general indicator of behavioral domesticity.

The diets of the Kamchatka Krai (Fig. 5.5E) and Northern and Polar Ural (Fig. 5.5F) dogs were less indicative of dietary dependence. The dogs from Kamchatka Krai had isotopic compositions inconsistent with a diet of salmon, which was unexpected given the abundant literature describing the salmon-rich diets of Kamchatkan sled dogs (Strecker, 2018; Krasheninnikov & Crownhart-Vaughan, 1955). Instead the results suggested a mixed diet of terrestrial and perhaps protein from salmon (Satterfield and Finney, 2002). This could be attributed to seasonal variation in the types of foods fed to sled dogs, or the fur samples may have been taken from hunting dogs, who were reportedly fed with birds, rather than fish (Strecker, 2018; Krasheninnikov and Crownhart-Vaughan, 1955). The dogs from Nenet and Khanty communities in the Urals occupied a region of isotopic space between anadromous fish and reindeer which also suggests a mixed diet. The two unidentified samples (TRF-2-63 & TRF-2-67) potentially consumed freshwater fish which could be caught in the Ob River that passes through the traditional territories of the Nenets and Khanty, or other terrestrial game.

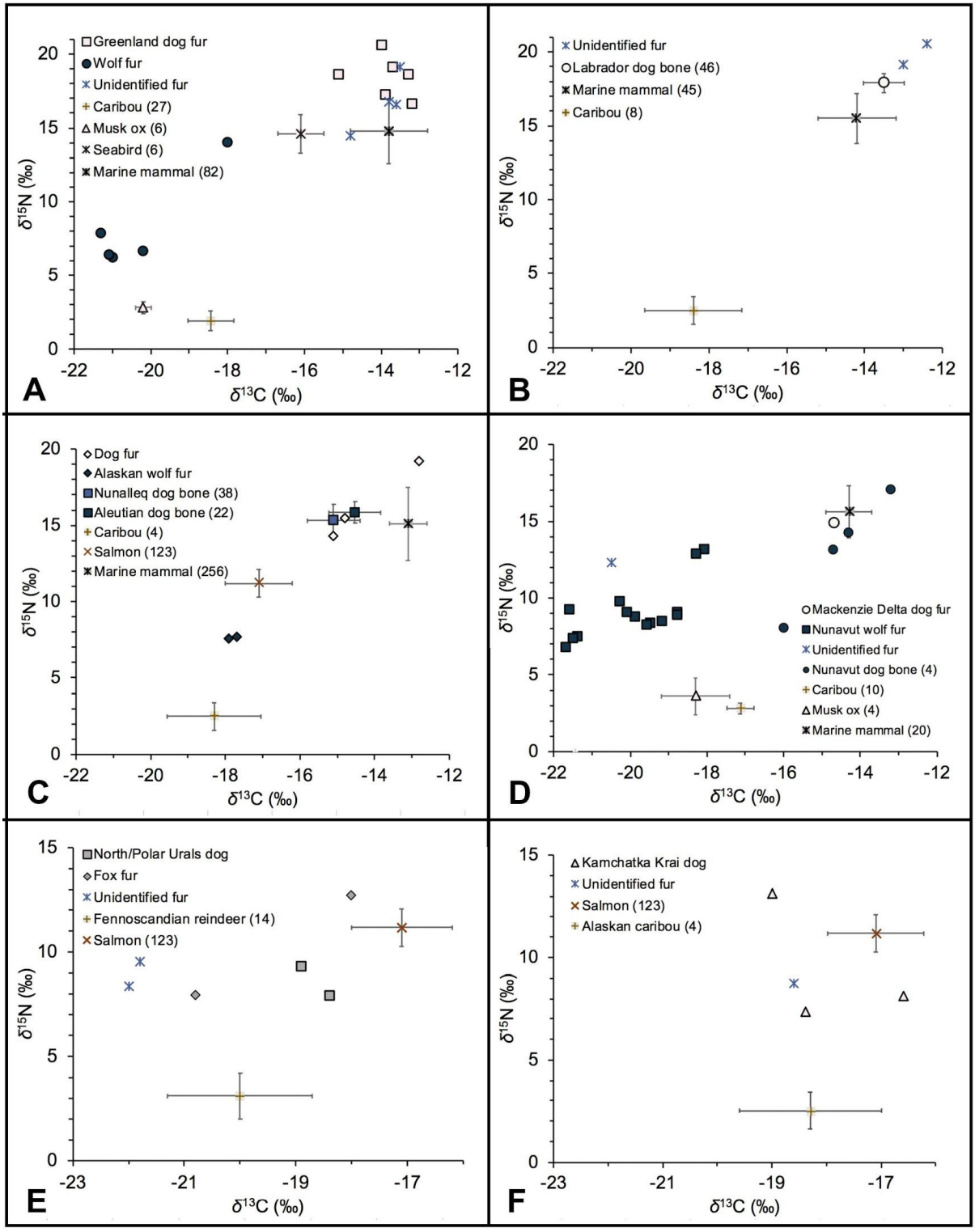

Figure 5.5. Fur samples adjusted to bone collagen isotope values per geographical region: A) Greenland B) Labrador C) Alaska D) Nunavut E) Urals F) Kamchatka. Published comparative bone collagen data were taken from the following sources: Greenland - (Nelson et al., 2012); Labrador - (Harris et al., 2020), modern Arctic char - (Guiry et al., 2016); Hudson Bay - (Coltrain et al., 2004); Alaska - (Clark et al., 2019; McManus-Fry et al., 2018; Szpak et al., 2017; West and France, 2015; Britton et al., 2013), Pacific salmon data - (Satterfield and Finney, 2002); Fennoscandian data - (Dury et al., 2018).

Some of the interactions that reinforce domestication and underpin human-dog relationships are revealed here through biomolecular analyses of ethnographic collections. In the North American Arctic, humans engaged in reciprocal relationships with dogs and other species (Hill, 2011); dog-human interactions were characterized by labor on behalf of both parties to procure marine mammals, fish, and caribou (McManus-Fry et al., 2018; West and France, 2015; Coltrain et al., 2004). The effort was well-spent as properly nourished sled dogs helped to maintain connections between communities in winter, and increased access to geographically dispersed resources (Taylor, 1974). In Siberia, herders provisioned dogs with reindeer and fish remains, and devoted significant energy to the actions involved in preparing dog food (Svoboda et al., 2011; Tuisku, 2001). The fish and reindeer soups prepared for dogs required not only the ingredients of the dish but also the collection of firewood and water (Tuisku, 2001). Dog provisioning was not an afterthought, but a critical component of daily life. While it is not possible to determine what proportion of food was acquired through direct feeding versus scavenging, the available isotopic data reveal a correspondence between human and dog diets (McManus-Fry et al., 2018; Coltrain et al., 2004). As sled dogs consumed food, they were engaging in social relationships with their owners, with other dog team members, and with other animals (Whitridge, 2018).

A complex relationship with a dietary element also existed between humans and wolverines, but it was not characterized by the reciprocity or cooperation as between dogs and people. Like humans, wolverines relied on the flesh of other animals for survival but unlike humans and other wild animals possessing inua, the wolverine violated the social contract by stealing food from meat caches and scavenging (Laugrand, 2017). The range of isotopic composition among the wolverine furs sampled in this study suggest that wolverines could have been encountered in a variety of locales, and through careful observation of these animals within their environment hunters could discern where best to place traplines. Despite the contempt fostered by the wolverine's assaults on carefully constructed meat caches, amulets made of wolverine teeth and claws were believed to imbue the wearer with strength (Laugrand, 2017), and wolverine pelts were prized among the Canadian Inuit for their warming and protective properties (Cotel et al., 2004; Oakes, 1988). The mixed marine-terrestrial isotope signatures of two wolverines may have resulted from

consumption of cached marine mammal meat or fish signifying the tenacity of this species, and its presence in arctic communities.

The aim of this research was to consider the social relationships of humans and dogs using biomolecular methods and there are two important limitations to the data that require consideration. The curated assemblage of clothing reflects the collection practices and interests of 19th and early 20th century ethnographers and anthropologists. Therefore, the frequency of garment components made from dog pelts may not be a reflection of the frequency with which dog pelts were actually used among arctic communities. Dogs were crucial for life in the Arctic, but their major contribution was labour, not furs. At the National Museum of Denmark, the items that include dog fur only constitute about 100 pieces of approximately 1650 garments in the collections (ranking fourth after seal, caribou, and polar bear). Secondly, while we found that species of some of the furs were misidentified by macroscopic examination, the study was not designed as an explicit test of morphoscopic methods. Further research designed to examine the rate of error in morphoscopic methods and the conditions under which error is more likely to occur may be warranted, but we cannot, at this point, quantify the failure rate associated with macroscopic identification of animal fur.

6 Conclusion

Many of the properties of animal skins allowed, in a very literal sense, the limitations of the human body to be transcended by co-opting some of the physical characteristics of dogs and wild species. Of the samples with sufficient data for genetic identification which had been macroscopically identified as dogs, 34% were revealed to be sourced from other taxa, highlighting the limitations in identifying small pieces of fur in clothing macroscopically. The generally excellent preservation of DNA in these skin samples, some of which were collected in the late 19th century, attests to the potential of this DNA reservoir for the investigation of population genetics before globalisation. Stable isotope analysis of the furs allowed the exploration of short term provisioning practices and revealed the diversity of dog diets across the Arctic region. Museum-curated ethnographic collections are a largely untapped resource as that can, using minimally invasive methods, form the basis for a range of ecological and cultural studies.

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Supporting Information: Appendix 3

Supplementary Tables 1–3

Supplementary Figures 1–2

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Chapter 6

Feeding infants at the Arctic Circle: Incremental isotope analysis of dentine and amino acids of Bering Sea hunter-gatherers

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Abstract

In this paper, we present novel results of compound specific $\delta^{15}N$ analysis of incremental dentine serial samples to characterize the breastfeeding and weaning practices of prehistoric Bering Sea hunter-gatherers at the site of Ekven (600–1000 CE). The Old Bering Sea culture was one of the earliest fully marine adapted cultures of northeastern Siberia and St. Lawrence Island, Alaska. We sampled the permanent first molars of adults and subadults. We measured isotopes of carbon and nitrogen in bulk collagen extracted from incremental dentine samples, then selected samples from two individuals were hydrolysed and the constituent amino acids derivatized for analysis via GC-C-IRMS. The Ekven amino acid data were compared to Alaskan fauna

and to three European individuals with terrestrial diets. The results showed that infants began to consume weaning foods within six months following birth, but the duration of breastfeeding and the weaning process varied among individuals. Approximately half of the sampled individuals were fully weaned between one to two years of age, while the remaining individuals completed weaning between three and five years of age. The isotopic analysis of single AAs may be useful for distinguishing systemic stress from influences of maternal or seasonal diet on infant δ^{15}N values. We were surprised to find that the δ^{15}N values of glutamic acid were not sensitive indicators of the introduction of weaning foods; the δ^{15}N values of proline appeared to track the introduction of supplementary foods, likely due to the role of this AA in arginine synthesis

1 Introduction

Bioarchaeological analyses of breastfeeding can act as a point of departure for inquiries into the experience of gender in the past. The care and feeding of infants vary cross-culturally and are integrated with cultural attitudes toward female bodies, social hierarchies, ritual and religious practices, and economic and social positions (Palmer, 2009; Dettwyler, 2004, 1995; Fildes, 1986). Maintenance activities are those that support life and society, including, but not limited to, childcare, food production and preparation, cleaning, caring for the elderly and infirm, textile and pottery production, dwelling maintenance, and caring for domestic animals (Sánchez Romero et al., 2008). In Arctic societies, many of these activities were shared between males and females or performed exclusively by women (Braymer-Hayes et al., 2020; Frink, 2009; Bodenhorn, 1990). Gendered division of labour in a number of Inuit and Yup'ik societies was geared towards ensuring and maintaining reciprocal social relationships with prey animals. Many of the tasks performed by women served the purpose of drawing prey animals to male hunters and placating the spirits of those animals after death (Bodenhorn, 1990). Infant feeding practices were integrated within this system as the types of foods consumed by pregnant and lactating females had the potential to affect the family's food security and the infant's future relationships with non-human beings (Rasmussen, 1931).

Stable isotope-based approaches to infant feeding practices in the past are becoming increasingly common in archaeology, particularly with the development of

new incremental dentine sampling protocols (Czermak et al. 2018; Beaumont et al. 2013). The dentine in permanent and deciduous teeth forms incrementally during infancy and childhood and provides an isotopic record of diet over the period of formation (Beaumont et al., 2013; Howcroft et al., 2012; Eerkens et al., 2011; Fuller et al., 2003). The interpretation of dentine isotope data is complicated by the issue of equifinality; in addition to dietary inputs, the isotopic composition of tooth dentine can also be influenced by periods of nutritional and/or physiological stress, and by maternal diet (King et al., 2018; Beaumont and Montgomery, 2016). The novel isotopic analysis of dentine amino acids (AAs) may help to distinguish between physiological and dietary inputs by comparing the isotopic values of 'trophic' and 'source' amino acids with bulk collagen carbon and nitrogen isotope values.

This study has two main aims: to investigate the infant feeding practices of hunter-gatherers associated with the Old Bering Sea culture at the site of Ekven, Chukotka; and, to explore the potential of compound specific isotope analysis (CSIA) of amino acids isolated from dentine increments as a tool for distinguishing dietary and physiological inputs to the nitrogen isotope signals measured in human teeth. The study employs stable carbon and nitrogen isotope ratio analysis of dentine increments from the permanent first molars of 22 individuals (subadults and adults). The bulk collagen data are combined with nitrogen isotope analysis of dentine amino acids to provide further information on the timing of the introduction of weaning foods and the interaction between infant nitrogen isotope values, physiology, and diet. The data are interpreted relative to ethnographic data from northern Alaska and Canada.

2 Background

2.1 Archaeological context

The Old Bering Sea (OBS) culture represents the first fully marine adaptation in Northeastern Siberia and is ancestral to present-day Inuit and Yup'ik populations of the Siberian and North American Arctic (Flegontov et al., 2019; Fitzhugh, 2016; Raghavan et al., 2014; Ackerman, 1998). Early expressions of OBS date to ~500 CE, with the majority of human mortuary activities at Ekven occurring between 600–1000 CE (Dury et al., in prep; Mason and Rasic, 2019). The timing of the intensive marine adaptation of the OBS coincided with, and may have prompted, the development of a

sedentary or semi-sedentary settlement pattern along the coasts of the Bering and Chukchi Seas (Fitzhugh, 2016). Subsistence practices of the OBS people varied with site location; on St. Lawrence Island, OBS settlements were situated near walrus haul outs, while bowhead whales may have featured heavily in the subsistence of communities located on the Bering Sea coast of the Siberian mainland (Whitridge 1999; Mason 1998).

The Ekven settlement and mortuary site is located in Chukotka on the Bering Sea coast (Fig. 6.1). The burials were located in the 1960s and excavations were carried out periodically in the succeeding decades, finally coming to a close in the mid-1990s. Adult and subadult individuals were interred in topsoil, above the modern permafrost layer, across two hillsides near the Ekven settlement (Arutiunov and Sergeev, 1975). The burials were elaborately constructed and featured whale bone frames and covers, log platforms in some cases, and numerous utilitarian (toggling harpoon heads, bolas, needles, scrapers) and non-utilitarian grave offerings (carved figurative objects, amulets, ochre), as well as the bones of birds and other animals (Arutiunov and Sergeev, 1975). Burials were single or multiple, and the human skeletons were found in both extended supine and flexed positions (Arutiunov and Sergeev, 1975). A comprehensive radiocarbon dating protocol is ongoing at the site and thus far indicates that the burial ground was in use between 600–1000 CE (Dury et al., in prep).

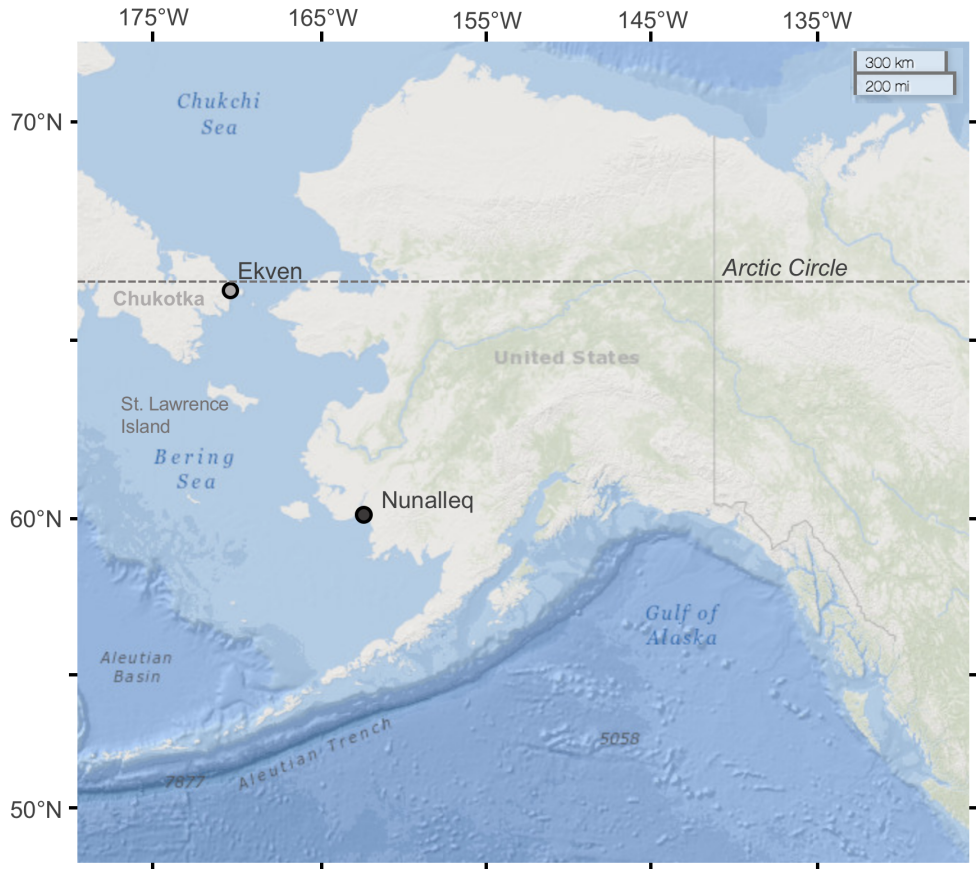

Figure 6.1. Ekven, the study site, and Nunalleq, the source of the comparative faunal material used in the analysis. Map made using the NatGeo Mapmaker Interactive tool. https://mapmaker.nationalgeographic.org/

The duration of breastfeeding and the choice of weaning foods are strongly influenced by culture on a community level, and by the social resources available to individual nursing females (Winterburn et al., 2003; Macadam and Dettwyler, 1995). After Katzenberg et al., (1996), we define exclusive breastfeeding as the period when infants only receive breastmilk, either from their biological mother or from a wet nurse. The onset of the weaning process occurs when supplementary foods are introduced to the infant alongside continued breastfeeding, and the weaning process is complete when the infant ceases to ingest human breastmilk (Katzenberg et al., 1996). Breastfeeding and weaning can be classified as maintenance activities because, while the ability to breastfeed is a biological characteristic common to all mammals, lactating people benefit from guidance from more experienced individuals as the activity is associated with a number of obstacles, such as breast infection or latching difficulties. Breastfeeding practices, and the foods considered appropriate for infant consumption vary by culture, time period (Fulminante, 2015), and even within families, therefore

infant feeding represents the transmission of knowledge between individuals and across human generations.

Arctic cultures have historically been associated with an extended duration of breastfeeding, i.e. longer than two years. Oral tradition and ethnographic research suggests that prior to Western colonisation, infants were breastfed for two to three years, but broths and premasticated foods could be introduced within the first few months of life, or as soon as an infant could hold up its head (Hildes and Schaefer, 1973; Maynard and Hammes, 1970; Heller et al., 1967; Rasmussen, 1931). The transmission of infant- and childcare knowledge began relatively early in a female's life. Among the Inuit of northern Canada and Greenland, girls between the ages of five and eight were instructed by older female relatives to attend to the biological and social needs of infants (Billson and Mancini, 2007; Guemple, 1995) and this instruction would be reflected in the way that they subsequently chose to care for their own children. In this way, social change could be reflected in infant feeding practices.

2.2 Stable isotope analysis and infant diets

Stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope ratio analysis is commonly used to investigate past breastfeeding and weaning practices among archaeological populations (See reviews in Britton et al., 2018; Tsutaya and Yoneda, 2015). Carbon and nitrogen isotope values are recorded in the collagen of bones and teeth, a protein which tends to survive well over archaeological timescales (Dobberstein et al. 2009). The isotopic composition of collagen is directly related to the isotopic composition of dietary protein, with some input from dietary carbohydrates and lipids (Fernandes et al., 2012; Ambrose and Norr, 1993). The average time span represented by the $\delta^{13}C$ and $\delta^{15}N$ values measured in bone collagen will vary by skeletal element and the age of an individual: rib collagen has a higher turnover rate than femoral collagen, and collagen turnover is higher during the rapid growth periods of infancy and childhood than during adulthood (Tsutaya and Yoneda, 2013; Hedges et al., 2007; Parfitt, 2002). Human teeth develop incrementally and preserve the isotopic values of protein consumed over the period of growth (Hillson, 2005).

Stable carbon isotope ratios track the source of primary production in a food web and are useful for distinguishing marine protein-based diets from terrestrial diets, or between C_3 and C_4 ecosystems. Carbon isotope values undergo a small (~1‰)

positive trophic shift between mother and infant during breastfeeding, however, $\delta^{13}C$ values may be more sensitive to the introduction of weaning foods and, among consumers of C_3 diets, have been shown to decline more quickly than $\delta^{15}N$ values following the introduction of weaning foods (Beaumont et al., 2018; Craig-Atkins et al., 2018; Fuller et al., 2006, 2003).

A stepwise increase in $\delta^{15}N$ values of +3 to +5‰ occurs between trophic levels, with further variation occurring in relation to the quality of dietary protein, an individual's growth and nutritional status, pregnancy, and general health (Webb et al., 2016; Warinner and Tuross, 2010; Fuller et al., 2005, 2004; Katzenberg and Lovell, 1999). Nursing infants are understood to occupy a trophic position above their mothers due to the consumption of breastmilk with an average offset of +2 to +3‰ observed between co-forming tissues of mother-infant pairs (Howcroft, 2013; Romek et al., 2013; de Luca et al., 2012; Fuller et al., 2006; Fogel et al., 1989). This is slightly less than the usual offset observed between consumers and their diets, which can be as high as +6‰ (O'Connell et al., 2012), and may be due to the presence of ^{15}N-depleted urea in breastmilk, the rapid growth rate and positive nitrogen balance of infants, among other reasons (see Tsutaya and Yoneda [2015] for a review).

Studies employing incremental analysis of the dentine of deciduous first molars have shown that dietary and physiological variation during pregnancy can also influence maternal and fetal $\delta^{15}N$ values (Beaumont et al., 2018; Beaumont and Montgomery, 2016). Deciduous teeth begin to form in utero and thus record isotopic evidence of maternal diet and, potentially, instances of maternal nutritional and physiological stress during the third trimester of pregnancy (King et al., 2018; Beaumont et al., 2015). Protein catabolism may lead to a ^{15}N enrichment in new forming tissues (Fuller et al. 2005) which can mimic or mask the effect of breastfeeding on infant $\delta^{15}N$ values. This effect has been recorded in the earliest forming increments of deciduous molars (Craig-Atkins et al. 2018; King et al. 2018). Maternal or infant physiological stress may also be associated with peak $\delta^{15}N$ values of permanent molars that exceed the mean $\delta^{15}N$ value in collagen from females from the same group by greater than two standard deviations, or >+3‰ (Beaumont and Montgomery, 2016).

Shown in Table 6.1, the $\delta^{15}N$ values of collagen amino acids vary depending on the biosynthetic pathway and the number of enzyme-catalysed reactions required to synthesize a particular AA (McMahon and McCarthy, 2016). The enzymes that facilitate the transfer of amino groups between AAs are known as transaminases and

discriminate against heavy isotopes (e.g. ^{15}N, ^{13}C) (Macko et al., 1987). Amino acids that are synthesized from the body pool of nitrogen, known as 'trophic' amino acids, will be depleted in ^{15}N relative to the substrate (usually glutamic acid) (Kendall et al., 2018; O'Connell, 2017). Due to its role in the synthesis of other trophic AAs, Glu undergoes stepwise enrichment in ^{15}N between trophic levels, earning it the title of the 'canonical trophic AA' (McMahon and McCarthy, 2016). Amino acids that are routed directly from diet (source AAs) undergo little to no subsequent isotopic fractionation and have $\delta^{15}N$ values that approximate those of primary producers (McClelland and Montoya, 2002). Gly and Ser were initially classified as source amino acids (Popp et al., 2007), but are now known to behave as trophic amino acids among some higher trophic level consumers. Like the trophic AAs, they can be linked to the body's central nitrogen pool (McMahon and McCarthy, 2016). Thr is unique among collagen AAs as it becomes progressively depleted in ^{15}N with trophic level and $\delta^{15}N_{Thr}$ is shown to be negatively correlated with the concentration of dietary protein (Fuller and Petzke, 2017). It has been called the 'metabolic' AA, but as O'Connell (2017) notes, all AAs are metabolic.

Table 6.1. Classification of amino acids, after O'Connell (2017), and their contribution of nitrogen to the collagen molecule. Post-translational modifications to proline are not included.

Amino Acid	Abbreviation	Classification	% collagen residues	# N atoms	%N in collagen
Alanine	Ala	Trophic	11.03	1	9.21
Arginine	Arg	Trophic	5.10	4	17.04
Asparagine/Aspartic acid*	Asx (Asn + Asp)	Trophic	4.38	2	3.65
Glutamine /Glutamic acid*	Glx (Gln + Glu)	Trophic	7.13	1	5.95
Glycine	Gly	Source or trophic	33.10	1	27.62
Histidine	His	Source	0.57	3	1.43
Isoleucine	Ile	Trophic	1.01	1	0.85
Leucine	Leu	Trophic	2.41	1	2.01
Lysine	Lys	Source	3.39	2	5.66

Methionine	Met	Source	0.60	1	0.50
Phenylalanine	Phe	Source	1.33	1	1.11
Proline	Pro	Trophic	21.69	1	18.10
Serine	Ser	Source or trophic	3.49	1	2.91
Threonine	Thr	Metabolic	1.74	1	1.46
Tyrosine	Tyr	Source	0.41	1	0.34
Valine	Val	Trophic	2.60	1	2.17

*During hydrolysis, asparagine residues are converted to aspartic acid and glutamine residues are converted to glutamic acid. GC-C-IRMS measurements thus measure N from both AAs and the resulting measurements are written as Asx or Glx, respectively.

Infant amino acid requirements differ from adults due to differences in amino acid biosynthetic pathways (Bertolo and Burrin, 2008) and to the demands of protein synthesis. The concentration of AAs delivered via the placenta is in excess of that required for protein synthesis (Heine, 1991); in contrast, breast milk contains high concentrations of Glu, Pro, and Leu to meet the requirements of the rapidly developing infant gut, but Ala, Arg, and Gly are present in low concentrations (Davis et al., 1994).

CSIA may help to circumvent the issue of equifinality affecting the interpretation of maternal and infant $\delta^{15}N$ values mentioned in section 2.2. Nutritional stress and pathological states are known to influence the isotopic composition of collagen and other proteins (Mekota et al. 2006; Fuller et al. 2005). To date, very few isotopic analyses of infant amino acids have been conducted. Tea et al. (2013) and Romek et al. (2013), unexpectedly, did not find a predictable trophic relationship between AAs from infant hair and breastmilk from exclusively breastfeeding mother-infant pairs. Romek et al. (2013) cited unknown metabolic factors as the cause of lower than expected $\delta^{15}N$ values of the trophic AAs Val, Ala, and Asx in infant hair relative to breastmilk. Consistent with expectations derived from other AA studies of consumer-diet relationships, the average $\delta^{15}N_{Glu}$ and $\delta^{15}N_{Pro}$ values were elevated in baby hair relative to milk (Romek et al., 2013).

The potential of CSIA to tease apart some of the interpretative issues in bioarchaeological approaches to breastfeeding remains largely unexplored. In this study, we combine $\delta^{13}C$ and $\delta^{15}N$ analysis of bulk collagen and amino acids from dentine extracted from incrementally sampled deciduous and permanent first molars

to ask: 1) *How long were infants breastfed in prehistoric Arctic societies?*; 2) *What was the rate of weaning?*; and 3) *Can $\delta^{15}N$ analysis of dentine AAs lead to a greater understanding of sources of nitrogen isotope variation in infant bone collagen*

3 Materials and methods

3.1 Skeletal assemblages

This study was conducted on human remains from the Ekven site in coastal Chukotka, but the data were interpreted through comparison with human remains from the United Kingdom, dating to the 18th century, and an individual from Russia, dating to the Medieval period. Age and sex were estimated using standard methodology. Age estimation was based on dental development (Al Qatahni et al., 2010) and epiphyseal fusion (Scheuer and Black, 2000). This allowed the ages of subadults to be determined with greater precision than adults. Where possible, sex was estimated using gross morphological traits of innominate bones of adults or of those in late adolescence (Buikstra and Ubelaker, 1994). Further details are presented below and provided in Table 6.2.

3.1.1 The Ekven mortuary site

We sampled bones and teeth from adult and subadult individuals from Ekven. Approximately one half of the excavated skeletal assemblage from the site is currently curated by the Institute of Archaeology, Russian Academy of Science (IARAS) in Moscow, Russia. The other half resides at Moscow State University. We sampled the skeletal material at IARAS which is largely comprised of adult skeletons and features few skeletal remains of infants or very young subadults. Deciduous, where available, and permanent first molars were removed from the mandibles of seven adult males, eight adult females, and five subadults of unknown sex. Deciduous first molars were sampled from four individuals of unknown sex, two of whom also had M1s, who died between 3 and 12 years of age. Care was taken to select only unworn teeth, or teeth with very minimal wear, and teeth with carious lesions were avoided completely. Where available rib bones were sampled from each individual to enable comparison between infancy, childhood, and later life. These were compared with bone collagen stable isotope data from an additional 15 individuals.

3.1.2 Comparative skeletal samples

To account for the influence of dietary regime on the isotopic composition of amino acids (Webb et al., 2016), three individuals from two other skeletal collections were included in this study to provide comparative nitrogen isotope data from dentine amino acids. Two adult individuals, SK45 and SK58,with predominantly C_3 diets, were selected from the 18th-19th century St. Barnabus skeletal assemblage (London) (Bleasdale et al., 2019). The names (not given here), biological sex, and age at death were known for these two individuals as they were interred with coffin plates. Another young adult individual, RUS9, with a mixed C_3-C_4 diet, selected from a Russian skeletal assemblage was included opportunistically. This individual had been mistakenly stored with the Ekven assemblage and was initially sampled under the assumption that the skeleton was associated with the Ekven mortuary site. The unexpected isotope results (mean δ^{13}C: –16.0±0.5‰; mean δ^{15}N: +10.9±0.9‰) were inconsistent with the Ekven group (n=35, mean δ^{13}C –11.8±0.4‰; mean δ^{15}N: +20.6±0.7‰) and suggested contributions from a C_4 source of protein which prompted a re-examination of the skeleton. The skull possessed morphological traits that were typical of European ancestry rather than Inuit/Yup'ik ancestry (Dr. M. Dobrovolskaya, personal communication). As the Russian state did not seek to colonize Chukotka until the 17th century, we concluded that the skeleton was at least not contemporaneous with the Ekven individuals and was likely from a western Russian population that had been included by mistake with the Ekven assemblage during its curational history. One permanent mandibular first molar was sampled from each individual, serial sectioned, and prepared for bulk collagen and amino acid specific isotope analysis.

3.1.3 Comparative faunal data

There have been a number of large studies that have examined trophic relationships among marine mammals using stable carbon and nitrogen isotope analysis in the Bering and Chukchi Seas (Clark et al., 2019; McManus-Fry et al., 2018; Szpak et al., 2017; Britton et al., 2013). These data were used to develop a faunal baseline with which to interpret the faunal isotope data. After Bocherens and Drucker (2003) we assumed a consumer-diet shift of 0 to +2‰ for carbon and +3 to +5‰ for nitrogen. To interpret the δ^{15}N values of human amino acids, we measured the δ^{15}N values of bone

collagen amino acids from caribou and a selection of marine mammals from the Yup'ik site of Nunalleq, in southwestern Alaska (Fig. 6.1).

Table 6.2. Biological profile and samples from Ekven, Chukotka, and comparative samples from the UK and Russia. R: Right; L: Left; M1: Permanent first molar; dm1: deciduous first molar; subscript: mandibular tooth; superscript number: maxillary tooth.

Burial #	Culture	Lab ID	Age at death	Sex	Bone sample	Tooth
Ekven, Chukotka						
216	OBS	EKV22	Adult	Male		RM_1
220	OBS	EKV33/12	<12 years	Unknown		Rdm_1, RM_1
276	OBS	EKV11	Adult	Female	Proximal phalanx (hand)	RM_1
277	OBS	EKV29	Adult	Female	Fibula	RM_1
278	Birnik	EKV150	Adult	Unknown	Rib	
279	OBS	EKV34	< 3 years	Unknown	Rib	Ldm_1
280	OBS	EKV16	Subadult	Unknown	Rib	RM_1
281	OBS	EKV01/02/03	<12 years	Unknown	Rib	Ldm_1, LM_1
283A	OBS	EKV137	Adult	Female	Rib	
283B	OBS	EKV127	Adolescent	Unknown	Phalanx (hand)	
284	OBS	EKV20	Adolescent	Female	R ulna	LM_1
285Г	OBS	EKV17	Adolescent	Unknown	Fibula	RM_1
288	OBS	EKV 123	Unknown	Unknown	Rib	
289	OBS	EKV131	Adult	Male	Rib	
290	OBS	EKV145	Adult	Unknown	Rib	
291	OBS	EKV08	Adult	Female	Rib	RM_1
294	OBS	EKV122	Infant	Unknown	Rib	
296	OBS	EKV119	Unknown	Unknown	Rib	

297	OBS	EKV147	Adult	Male	Rib	
298	OBS	EKV35	< 3 years	Unknown	Rib	Rdm_1
299	OBS	EKV140	Unknown	Unknown	Rib	
300	OBS	EKV14	Adult	Male	Rib	LM_1
308	OBS	EKV05	Adolescent	Male	R. humerus	RM_1
309	OBS	EKV134	Adult	Female	Rib	
310	OBS	EKV04	Adult	Male	Rib	RM_1
311	OBS	EKV31	Adult	Male	Rib	LM_1
312	OBS	EKV129	Adult	Female	Rib	
314	OBS	EKV121	Adult	Female	Rib	
318	OBS	EKV10	Adult	Female	Rib	RM_1
320	OBS	EKV07	Adult	Male	Rib	RM_1
321	OBS	EKV27	Adult	Male	Rib	RM_1
322	OBS	EKV146	Infant	Unknown	Rib	
323	OBS	EKV25	Adult	Female	Rib	LM_1
324	OBS	EKV133	Adult	Male	Proximal phalanx (hand)	
325	OBS	EKV21	Adult	Female	Rib	LM_1
326	OBS	EKV23	Adult	Female	Rib	RM_1
327	OBS	EKV18	Adolescent	Unknown	Rib	LM_1
St. Barnabus, London						
45		SK45	29 years	Female		M_1
58		SK58	51 years	Male		M_1
Russia						
		RUS9	Adolescent	Female		LM^1

3.2 Methods

This study conducted bulk collagen and amino acid isotope analysis of dentine incremental samples. The complete methods employed in the study are detailed in Appendix 4. Sample preparation and analysis were conducted at BioArCh, Department of Archaeology, University of York. In brief, permanent mandibular molars and bone samples were demineralised and the teeth were sectioned using method 2 from Beaumont et al. (2013). The dentine sections were gelatinised, lyophilised and bulk carbon and nitrogen isotope ratios were measured in duplicate. Collagen preservation was assessed using atomic C/N ratios, and concentrations of carbon and nitrogen (van Klinken, 1999). Selected faunal bone and human dentine samples were hydrolysed and derivatized using the methods of Corr et al. (2007) as modified by Styring et al. (2015) and Philben et al. (2018). The dentine serial sections were run on the GC-C-IRMS out of sequence to remove any possible instrumental influence on the AA data. The isotopic values from each dental serial section were assigned to a chronological age using the method developed by Beaumont and Montgomery (2015). Collagen was extracted from the bones of 37 individuals using a modification of the Longin (1971) method.

In this study, the introduction of weaning foods and the conclusion of the weaning process were identified from permanent M1s as the point at which infant peak $\delta^{15}N$ values began to decline, and as the point when $\delta^{15}N$ values ceased to decline, respectively (Beaumont et al., 2018). Weaning was deemed to be early if breastfeeding ceased by 2 years of age. As reviewed in Howcroft (2013, p. 23), infants in non-industrial societies were typically breastfed for at least two years. We estimated the rate at which weaning occurred by comparing the length of time that took $\delta^{15}N$ values to stabilise after the initial drop, in other words, how steep was the drop in $\delta^{15}N$ values. We also assessed the possible instances of systemic stress were identified after Beaumont and Montgomery (2016) as infant $\delta^{15}N$ values that exceeded the female bone collagen mean by 2SD or by >3‰.

4 Results

The results are divided into two main sections: the bulk collagen data from bone and dentine increments are presented first, followed by the CSIA data from faunal bone and human dentine amino acids.

4.1 Bulk bone and dentine collagen stable isotope data

Bone collagen was successfully extracted from 35 individuals and dentine collagen was extracted and measured from the teeth of 20 individuals. After the removal of samples with poor atomic C/N ratios and/or samples lost due to analytical issues, 372 incremental samples were included in the final data analysis. The complete data set featuring collagen quality indicators, isotopic values, and age estimations is presented in Appendix 4. A summary of the estimated weaning age ranges with accompanying bone collagen and osteological data is presented in Table 6.3.

Table 6.3 Summary bone collagen and weaning data from 20 individuals from the Siberian site of Ekven.

Burial ID	Sample ID	Sex	Age	Bone $\delta^{13}C$ (‰)	Bone $\delta^{15}N$ (‰)	Magnitude of $\delta^{15}N$ decrease	Timing of $\delta^{15}N$ decrease
308	EKV5	M	Adolescent	–11.4	+21.0	None	No decrease
298	EKV35	?	<3 yrs			None	Minimal decrease antemortem
291	EKV8	F	Adult	–11.5	+20.6	1.1	0.3 - 1 yr
318	EKV10	F	Adult	–11.3	+19.7	1.2	0.3 - 1 yr
321	EKV27	M	Adult	–12.2	+20.4	1.2	0.3 - 1 yr
277	EKV29	F	Adult	–11.6	+19.6	2.8	0.3 - 1.5 yrs
281	EKV1/2/3	?	<12 yrs	–11.4	+20.7	1.9	0.3 - 1.5 yrs
320	EKV7	M	Adult	–11.3	+20.7	1.2	0.3 - 1.5 yrs
300	EKV14	M	Adult	–11.2	+20.2	1.4	0.3 - 1.6 yrs
280	EKV16	?	Subadult	–11.6	+19.4	1.7	0.3 - 2.3 yrs
279	EKV34	?	<3 yrs	–11.5	+22.6	0.9	1.6 – 2.5 yrs
276	EKV11	F	Adult	–12.0	+20.3	1.4	0.3 - 2.5 yrs
284	EKV20	F	Adolescent	–12.0	+20.1	2.3	0.3 - 2.6 yrs
220	EKV12/33	?	<12 yrs			3.0	0.5 - 2.7 yrs
311	EKV31	M	Young adult	–12.0	+20.1	3.6	0.3 - 3 yrs
327	EKV18	?	Adolescent	–12.1	+21.0	4.1	Birth - 3 yrs

285Г	EKV17	?	Adolescent	–11.7	+20.6	2.6	0.3 - 3.5 yrs
326	EKV23	F	Adult	–11.8	+20.7	3.1	Birth - 3.5 yrs
310	EKV4	M	Adult	–11.6	+20.6	1.4	0.3 - 3.5 yrs
323	EKV25	F	Adult	–11.6	+20.3	3.8	0.3 - 3.7 yrs
325	EKV21	F	Adult	–11.9	+20.5	2.7	Birth - 4.5 yrs
216	EKV22	M	Adult			2.2	0.7 - 4.5 yrs

4.1.1 Bone collagen

The mean $\delta^{13}C$ and $\delta^{15}N$ values of all adults and subadults were –11.8 ± 0.4‰ and +20.6 ± 0.7‰, respectively. Adult males and females had identical mean $\delta^{13}C$ values of –11.7‰, and similar $\delta^{15}N$ values of +20.6 ± 0.3‰ (males) and +20.4 ± 0.4‰ (females). The $\delta^{15}N$ values of the humans from Ekven were elevated relative to archaeological marine fauna from sites along the Bering and Chukchi seas (Fig. 6.2).

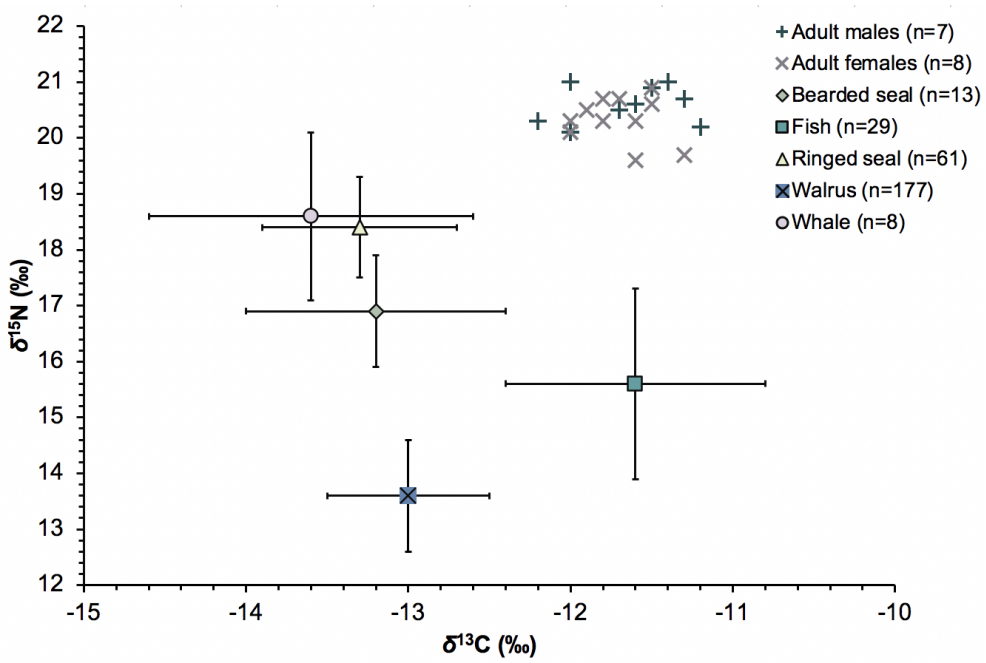

Figure 6.2. Bulk bone collagen stable isotope values from Ekven adult males and females plotted with published data (presented to one SD) from Alaska fauna (Clark et al., 2019; McManus-Fry et al., 2018; Szpak et al., 2017; Britton et al., 2013) and fish from the Aleutian Islands (Byers et al., 2011).

4.1.2 Dentine collagen

4.1.2.1 Timing and rate of weaning

Eight of the Ekven individuals were weaned early, between the ages of one to two years. Three individuals were weaned between the ages of two and three years, consistent with patterns from other non-industrial societies (Howcroft, 2013; Kennedy, 2005; Sellen, 2001). Eight individuals were weaned relatively late, between the ages of three and five years. Weaning foods were introduced to all individuals within the six months of birth, but the individuals who completed the weaning process after the age of three were also weaned more slowly, as indicated by a gradual decline in $\delta^{15}N$ values, than those who were weaned before the age of three years. The rate and completion of the weaning process could not be easily determined for three individuals (burial 308, 284, and 216). Carbon isotope values were, in general, less informative of breastfeeding and weaning practices, in contrast to the findings of Craig-Atkins et al. (2018) which suggested that, for C_3 consumers, dentine $\delta^{13}C$ values may be more sensitive to the introduction of weaning foods than for individuals consuming weaning diets rich in marine proteins and fats. Eleven individuals showed a slight decrease in $\delta^{13}C$ values, however, the decrease only exceeded analytical error (±0.2‰) for three of these. Eight individuals showed an increase in $\delta^{13}C$ values between 0.2 – 0.9‰ with the introduction of weaning foods. No significant differences were found between males (n=7) and females (n=8) with respect to the age at which weaning was completed (Z = –0.237, p = 0.812). The calibrated radiocarbon dates of the early and late weaning groups overlap at two standard deviations so intrapopulation differences in infant feeding practices do not appear to be temporal, but further investigation is warranted.

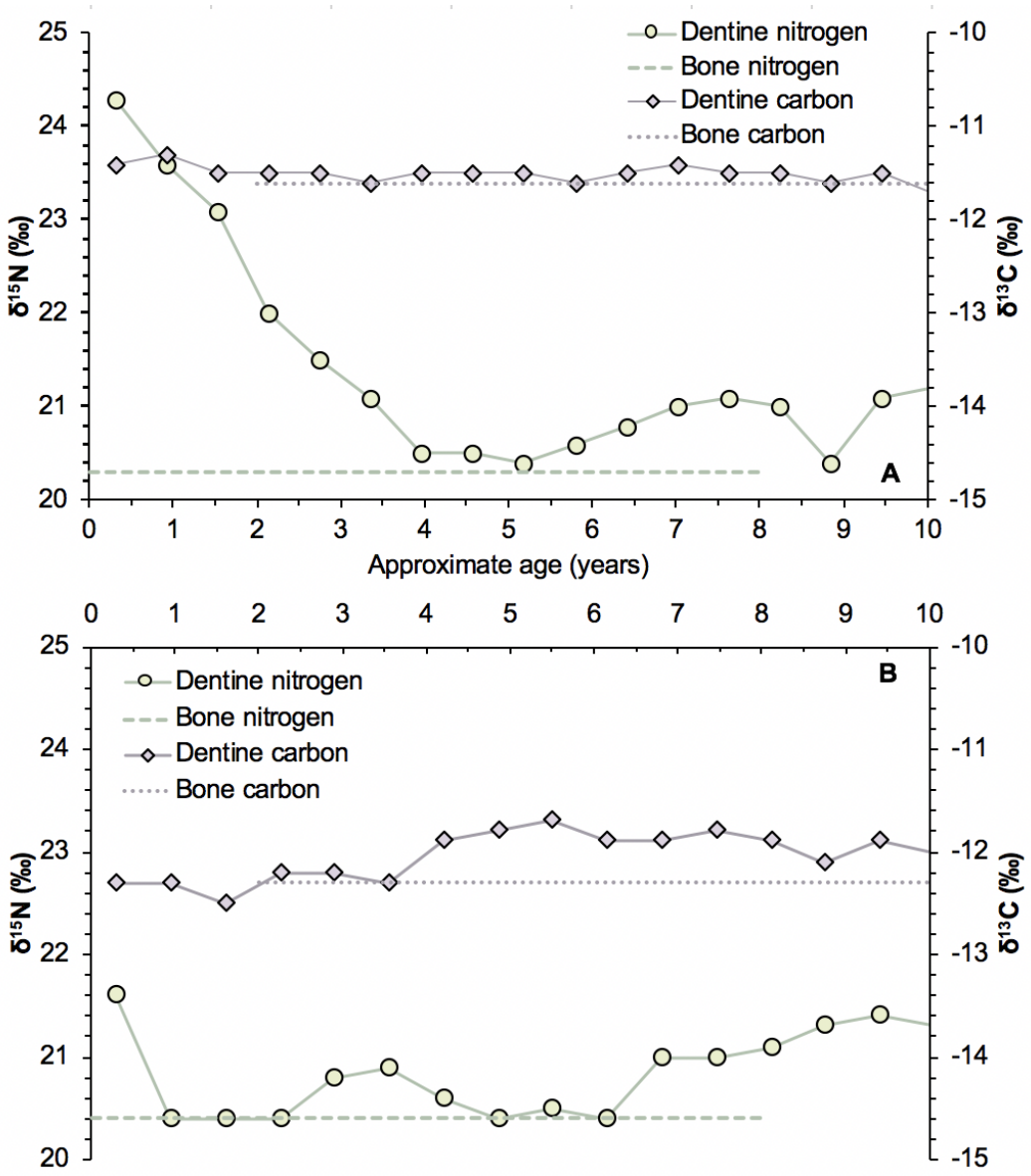

Figure 6.3. Examples of two individuals, burial 323 (top) and burial 318 (bottom) with A) a prolonged decline in δ^{15}N values, suggesting late and gradual weaning; and B) a rapid decline in δ^{15}N values, suggesting an early and abrupt weaning scenario. Bone collagen values represent a long-term average and do not correspond to the x-axis.

4.1.2.2 Deciduous molars

Dentine collagen was extracted from the deciduous first molars of four individuals (Fig. 6.4). Three of the sampled deciduous molars displayed increasing δ^{15}N and δ^{13}C values after birth, consistent with the consumption of breastmilk, but the timing of the increase in δ^{15}N varied between individuals. The highest δ^{15}N values of the subadults from Burials 220 and 298 were attained by approximately six months of age, followed by a gradual decline before stabilising by the age of two or three. The δ^{15}N values of

the subadult from burial 279 began to decline after one and a half years of age, suggesting a late introduction of weaning foods, while the $\delta^{13}C$ values remained relatively stable over the same time period. As this individual died before the tooth finished forming, it is impossible to say whether the weaning process was complete at death. The onset of breastfeeding was not observable in the isotopic profile of Burial 281, as the occlusal surface of the tooth had been worn, however, the $\delta^{15}N$ values began to decline shortly after birth and reached the lowest point by the age of two years.

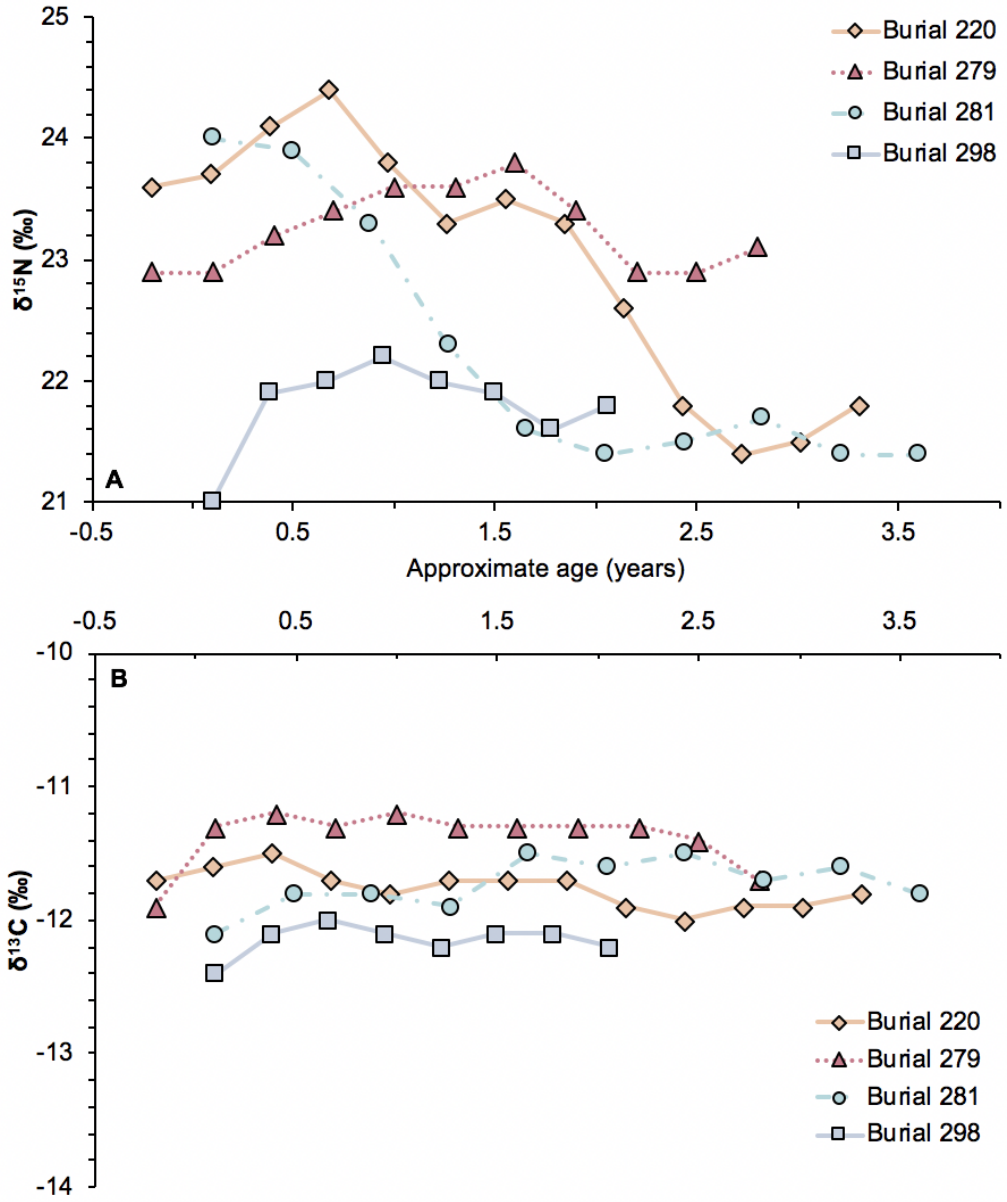

Figure 6.4. Nitrogen (A) and carbon (B) isotope profiles from the deciduous M1s of four subadults.

4.1.2.3 Systemic stress and dentine isotope profiles

It has been suggested that nutritional and/or physiological stress may be identified in dentine isotope profiles by infant $\delta^{15}N$ values that exceed those of adult females by two standard deviations and >+3‰ (Beaumont et al., 2015; Beaumont and Montgomery, 2016). Catabolism of amino acids may cause an increase in tissue $\delta^{15}N$ values (Mekota et al., 2006), while re-use of body lipids for energy may cause a decrease in tissue $\delta^{13}C$ values (Neuberger et al., 2013). The highest dentine $\delta^{15}N$ values (including both permanent and deciduous first molars) of eight individuals exceeded the mean adult female bone collagen $\delta^{15}N$ value (+20.4‰) by +3.4‰ to +4.7‰ (Fig. 6.5). Of the eight, one died before the age of three, two died before the age of 12, one in adolescence, and four survived to adulthood. Two individuals also had negatively covarying $\delta^{13}C$ and $\delta^{15}N$ values, discussed further below, implying periods of nutritional or physiological stress (Beaumont and Montgomery, 2016).

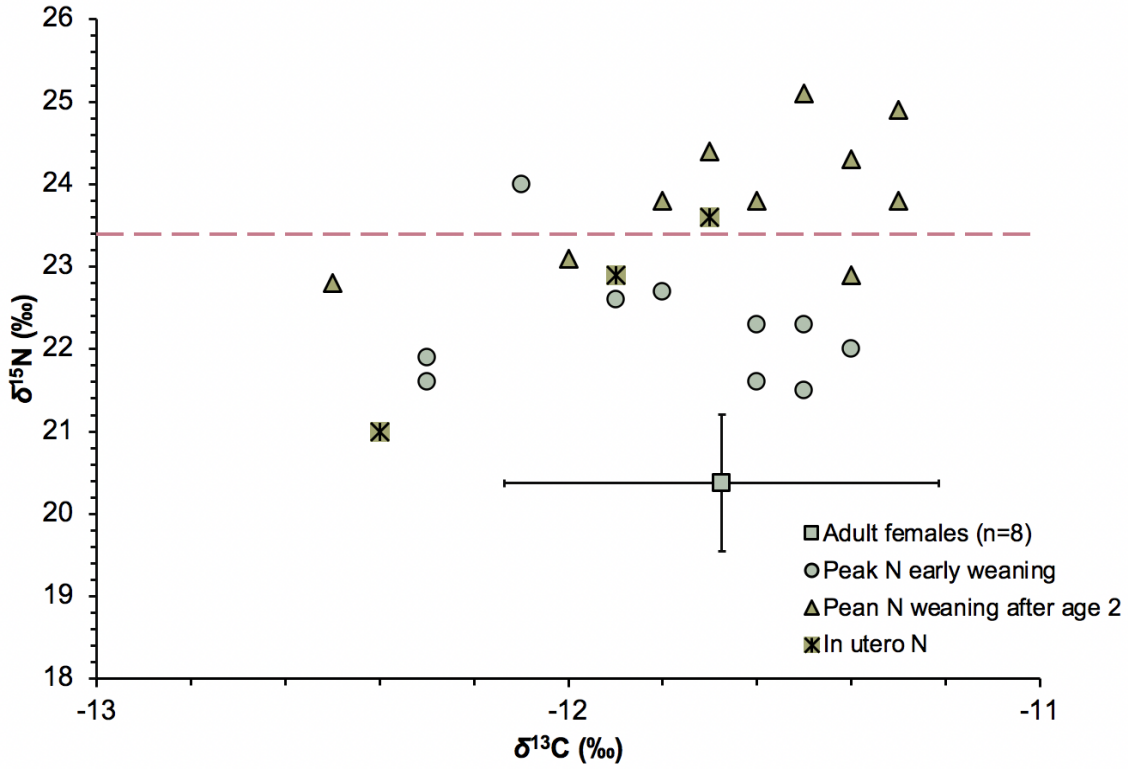

Figure 6.5. Mean (±2SD) $\delta^{15}N$ value of adult females plotted with the peak and in utero (where available) $\delta^{15}N$ values of Ekven infants. The pink dashed line indicates infant samples that are >3‰ higher than the female mean.

Anomalous profiles, including those with negatively co-varying $\delta^{13}C$ and $\delta^{15}N$ values mentioned previously, from the permanent M1s of four individuals are shown in Figure 6.6. Burial 308 (Fig. 6.6A), with an age at death in late adolescence, did not

display the expected drop in $\delta^{15}N$ values associated with the introduction of supplementary foods. Instead, the highest $\delta^{15}N$ and lowest $\delta^{13}C$ values were not reached until the approximate age of 10 years. The individuals from burials 281 and 220 (Fig. 6.6B-C), both of whom died in late childhood, had declining $\delta^{13}C$ values and increasing $\delta^{15}N$ values in the years before death. Over the first five years of life, the $\delta^{13}C$ and $\delta^{15}N$ values of the adolescent biological female from Burial 284 (Fig. 6.6D) negatively covary as each rise in the $\delta^{15}N$ values is associated with a slight decrease in $\delta^{13}C$ values.

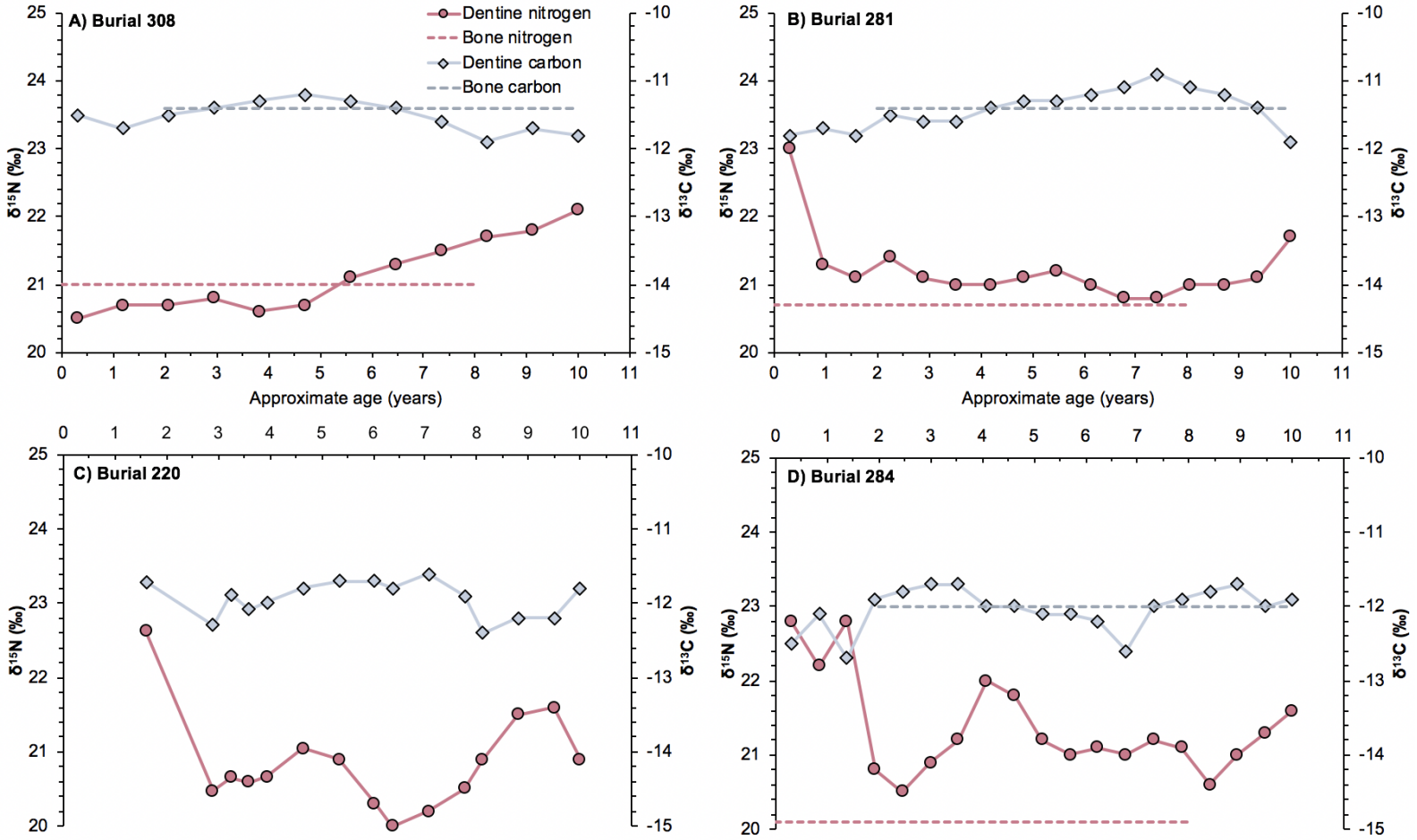

Figure 6.6. Permanent M1 Isotopic profiles featuring negatively co-varying $\delta^{15}N$ and $\delta^{13}C$ values. The legend in plot A applies to all plots. Lines representing bone collagen do not correspond to the x-axis and only serve to show the isotopic values in relation to dentine collagen; bone collagen isotope values were unavailable for burial 220.

4.2 Compound specific nitrogen isotope analysis of amino acids

During acid hydrolysis, glutamate and asparagine are converted to glutamic acid and aspartic acid, respectively, therefore in the following presentation of results the measured $\delta^{15}N$ values are presented as Glx (Glu+Gln) and Asx (Asn + Asp). We achieved baseline separation for Gly, Val, Nle (internal standard), Glx, Pro, Asx, hydroxyproline (Hyp), and Lys. Ser, Thr, and Phe are presented but tended to have high standard deviations due to poor baseline resolution. Leu frequently co-eluted with an unknown peak and is not presented here. As a quality check on the derivatization procedure, we compared the Pro and Hyp $\delta^{15}N$ values of each sample. The post-translational formation of Hyp from Pro does not involve either the breakage or formation of a C-N bond, therefore Hyp and Pro should have very similar $\delta^{15}N$ values (O'Connell and Collins, 2017). Across the 33 samples (analysed in triplicate) in this study, the mean Pro and Hyp were strongly positively correlated with an R^2 value of 0.9893. Bulk dentine $\delta^{15}N$ values were estimated from a mass balance calculation of the measured $\delta^{15}N_{AA}$ values. These were positively correlated with the measured (EA-IRMS) bulk dentine $\delta^{15}N$ values with an R^2 value of 0.9793, and the average offset between the measured and estimated bulk $\delta^{15}N$ values was 0.62 ± 1.04‰.

4.2.1 Faunal samples

The bulk collagen isotope values of the fauna are reported and discussed by Britton et al. (2013) and McManus-Fry et al. (2018). We successfully measured the $\delta^{15}N$ values of amino acids from terrestrial and marine fauna (Fig. 6.7). Due to uncertainty in Glx-Phe trophic discrimination factors between foodwebs (Germain et al., 2013; Kendall et al., 2018) in addition to species-specific patterns of AA isotopic fractionation (McMahon and McCarthy, 2016), we did not attempt to calculate trophic level using the equation developed by Chikaraishi et al. (2009).

Table 6.4. Bulk and AA $\delta^{15}N$ values (±1SD) of comparative archaeological fauna from Nunalleq, Alaska. All AA data are expressed using ‰ units. The bulk collagen data, taken from McManus-Fry et al. (2018), were measured via EA-IRMS.

AA	Caribou	Walrus	Bearded seal	Ringed seal	Beluga whale
N	3	2	2	1	3
Bulk $\delta^{15}N$	+1.7 (0.2)	+14.5 (0.3)	+17.8 (0.0)	+17.2	+20.1 (1.1)
Bulk $\delta^{13}C$	–17.9 (0.4)	–12.4 (0.2)	–12.2 (0.2)	–12.9	–12.9 (0.2)
Ala	+3.0 (0.6)	+19.4 (1.5)	+24.1 (0.5)	+25.5	+27.0 (0.7)
Val	+10.0 (3.4)	+26.9 (0.9)	+27.0 (1.4)	+30.7	+28.4 (1.1)
Glx	+5.5 (0.3)	+21.9 (0.6)	+25.1 (3.2)	+27.5	+29.9 (0.8)
Pro	+4.3 (1.0)	+18.9 (0.3)	+24.1 (0.4)	+23.3	+28.4 (0.9)
Hyp	+5.6 (0.7)	+20.1 (0.7)	+25.6 (0.1)	+24.7	+28.9 (1.7)
Asx	+6.1 (0.7)	+20.1 (0.3)	+24.9 (0.6)	+23.6	+26.5 (0.7)
Gly	–2.1 (0.9)	+8.4 (0.9)	+10.8 (0.1)	+10.9	+12.8 (1.7)
Ser	+0.7 (1.2)	+10.3 (2.0)	+18.2 (1.4)	+14.1	+13.5 (2.1)
Thr	–8.6 (1.1)	–10.4 (0.3)	–11.4 (3.2)	–17.5	–24.3 (1.0)
Phe	+6.6 (0.6)	+12.4 (1.3)	+11.3 (1.6)	+11.7	+10.4 (0.8)
Lys	–0.5 (0.2)	+10.1 (1.1)	+9.7 (1.1)	+8.8	+8.8 (0.8)

The two source AAs, Phe and Lys, distinguished between the marine and terrestrial environments. Among the marine species, $\delta^{15}N_{Phe}$ ranged from 10.2‰ to 13.3‰ and $\delta^{15}N_{Lys}$ ranged from 8.2‰ to 10.9‰. The three Alaskan caribou had much lower mean $\delta^{15}N_{Phe}$ and $\delta^{15}N_{Lys}$ values of 6.6 ± 0.6‰ and –0.5 ± 0.2‰.

The trophic AAs with the highest $\delta^{15}N$ values varied among species. Valine had the highest $\delta^{15}N$ values across the caribou, walrus, bearded and ringed seals, while Glx was the AA most enriched in ^{15}N among the three beluga whales. For all samples, Pro, Ala, and Asx were depleted relative to Glx which aligns with the predicted pattern of isotopic fractionation (Miura and Goto, 2012).

In contrast to patterns of isotope fractionation in collagen of terrestrial ruminants (Kendall et al., 2018) and Arctic orca whales (Matthews and Ferguson, 2014) but similar to the serum of wild-caught and captive harbour seals (e.g. Germain et al., 2013), Gly was depleted in ^{15}N relative to Ser for all samples. Consistent with other studies (e.g. Kendall et al., 2018; Hetherington et al., 2016; Styring et al., 2015; Germain et al., 2013), Thr was the AA most depleted in ^{15}N across all species with the highest and lowest values found in caribou and beluga whale, respectively.

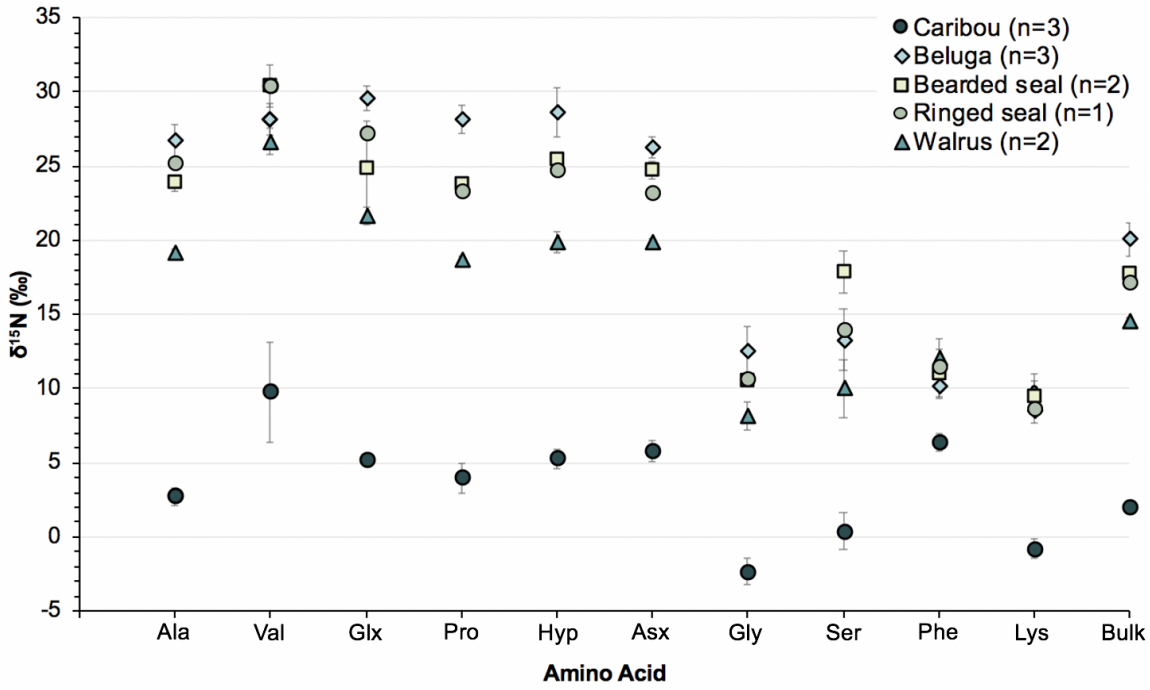

Figure 6.7. $\delta^{15}N$ composition of amino acids isolated from faunal bone collagen. Error bars represent one SD. Threonine values are not included in the figure as they plot far outside the range of data.

4.2.2. Human samples

The results of compound specific isotope analysis of dentine AAs and plots of the incremental bulk collagen isotope values are included in the Supporting Information. Based on the bulk collagen $\delta^{15}N$ values, the first dentine increment from each individual is assumed to correspond to the breastfeeding period. While the absolute values differ by dietary regime, the change in $\delta^{15}N_{AA}$ values with the introduction of weaning foods produces a similar pattern in all sampled individuals (Fig. 6.8).

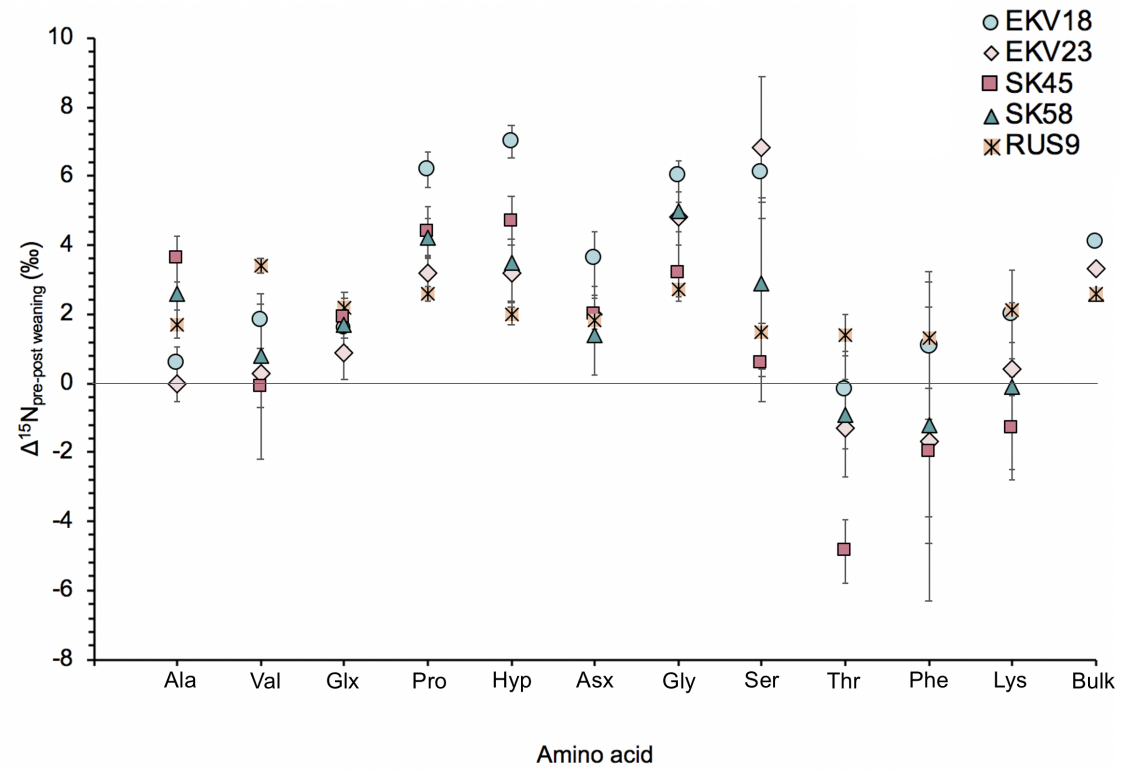

Figure 6.8. The difference in $\delta^{15}N$ values between the first dentine increment, representing the pre-weaning signal, and a post-weaning increment (see SI Table 1) of each individual. EKV 18 represents burial 327 and EKV23 represents burial 326.

The source AAs, Phe and Lys, should undergo minimal isotopic fractionation between trophic levels and thus may be used to trace the source of nitrogen at the base of the foodweb (McClelland and Montoya, 2002). Changes in the $\delta^{15}N$ values of either of these AAs within the incremental samples of an individual should unambiguously signify a change in diet. One limitation of this analysis is that Phe and Lys typically have broad standard deviations due to their late elution and small peak size, however, we were able to achieve acceptable baseline resolution for Lys for most of the samples.

The patterning of $\delta^{15}N_{Lys}$ values is distinct for each of the five individuals (Fig. 6.9). Between the age of 1.5 and 3.4 years, the $\delta^{15}N_{Lys}$ values of EKV18 dropped by 2‰, and a further drop of ~1‰ is observable by 10 years of age. The $\delta^{15}N_{Lys}$ values of EKV23 remained relatively stable over the same age range. The $\delta^{15}N_{Lys}$ values of SK45 increased between the ages of one and four years but stayed within analytical error. Although the standard deviations of the two highest $\delta^{15}N_{Lys}$ values were broad, SK58 showed a significant decrease, exceeding analytical error, in $\delta^{15}N_{Lys}$ between

the ages of 0.3 and 0.8 years of age. As this change is contemporaneous with a decline in bulk collagen $\delta^{15}N$, it plausibly relates to the introduction of weaning foods. The $\delta^{15}N_{Lys}$ of RUS9 declined by 1.7‰ between the ages of 0.9 and 2 years of age, a change that also coincided with a decline in bulk collagen $\delta^{15}N$.

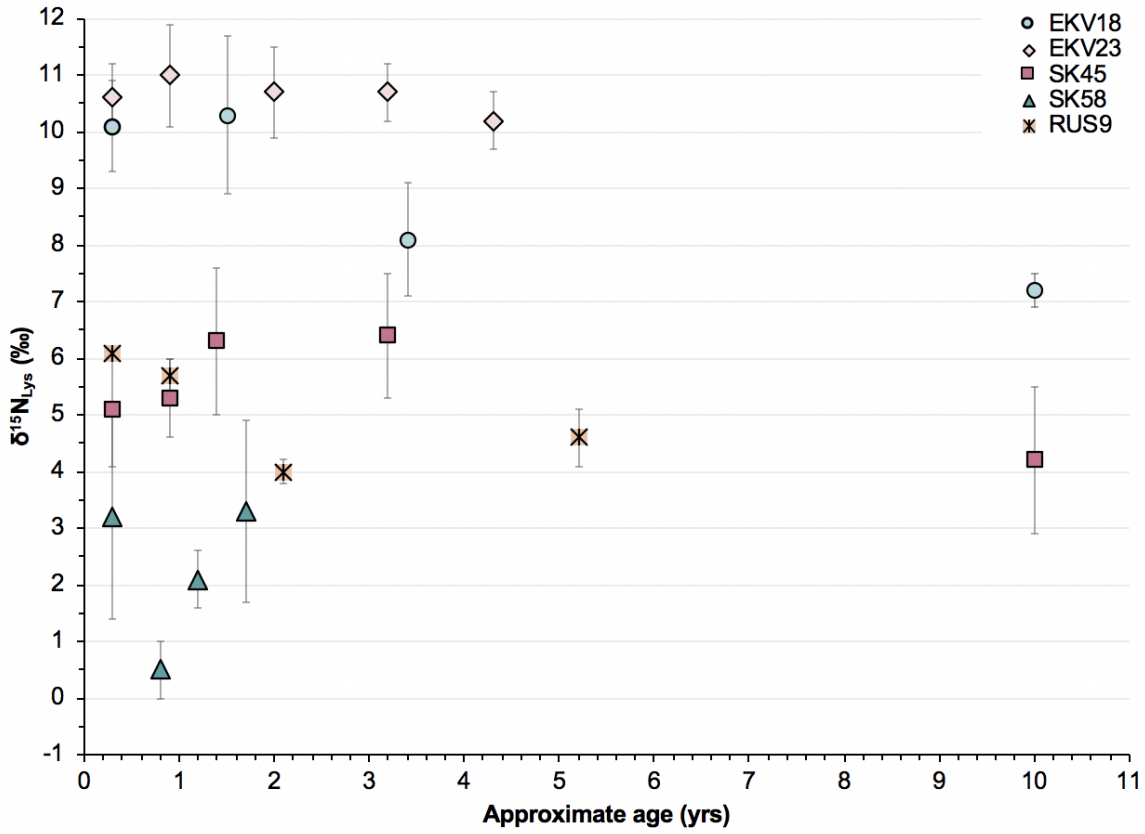

Figure 6.9. Lysine $\delta^{15}N$ values plotted against approximate age of sample formation. EKV 18 represents burial 327 and EKV23 represents burial 326.

The trophic amino acids are those that can exchange nitrogen with glutamic acid and show greater enrichment in ^{15}N due to numerous transamination and deamination reactions (O'Connell, 2017). If the introduction of weaning foods represents a decline in trophic level, then a decline from the peak $\delta^{15}N_{trophic\ AAs}$ can be expected to co-occur with the decline in the $\delta^{15}N$ value of bulk collagen. This study found that with the introduction of weaning foods, the $\delta^{15}N$ values of all trophic AAs declined, regardless of dietary regime. Surprisingly, Glx did not appear to be a sensitive indicator of the introduction of weaning foods, decreasing between 0.9‰ and 2.5‰ over the weaning period.

Proline $\delta^{15}N$ values appeared to track the bulk collagen $\delta^{15}N$ values more so than did Glx (Fig. 6.10). $\delta^{15}N_{Pro}$ declined by 3.2 ‰ and 6.2‰ for EKV 23 and 18,

respectively, by ~4‰ for the two individuals from St. Barnabus, London, and by 2.8‰ for the medieval Russian individual.

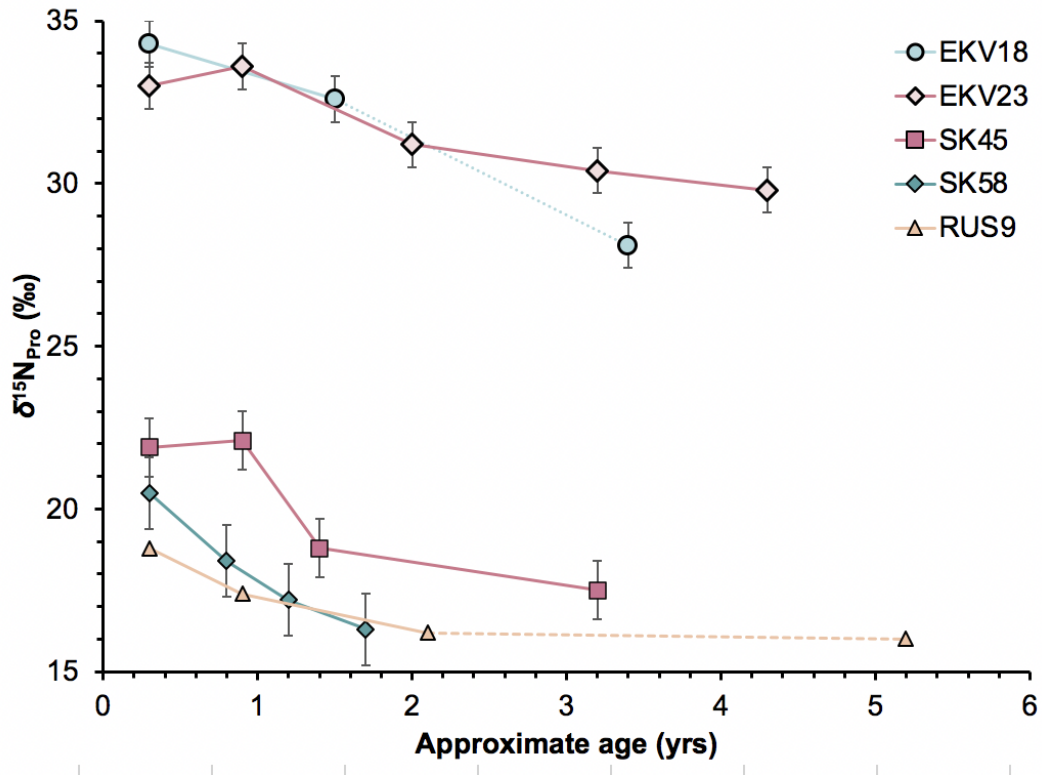

Figure 6.10. $\delta^{15}N_{Pro}$ plotted according to approximate age in years. Error bars represent the propagated analytical error. EKV 18 represents burial 327 and EKV23 represents burial 326.

As with Pro, the $\delta^{15}N_{Gly}$ of all individuals declined by at least 3‰ between the first dentine increment, representing the period of breastfeeding, and later dentine increments representing the consumption of supplementary foods. Threonine $\delta^{15}N$ values were variable across and within individuals. Thr varied with dietary regime as, similar to the Alaskan fauna and to published datasets (e.g. Kendall et al., 2018; Germain et al., 2013), the lowest values were observed among the individuals with marine protein-based diets and higher values among the terrestrial protein consumers. However, the intra-tooth $\delta^{15}N_{Thr}$ values did not appear to correspond to the bulk collagen $\delta^{15}N$ values (Fig. 6.11). The $\delta^{15}N_{Thr}$ values of EKV18 initially fell with the introduction of weaning foods, and then rose again. The $\delta^{15}N_{Thr}$ values of EKV23 and SK45 sharply increased with the introduction of weaning foods, and the $\delta^{15}N_{Thr}$ values of RUS9 fell gradually over the weaning period.

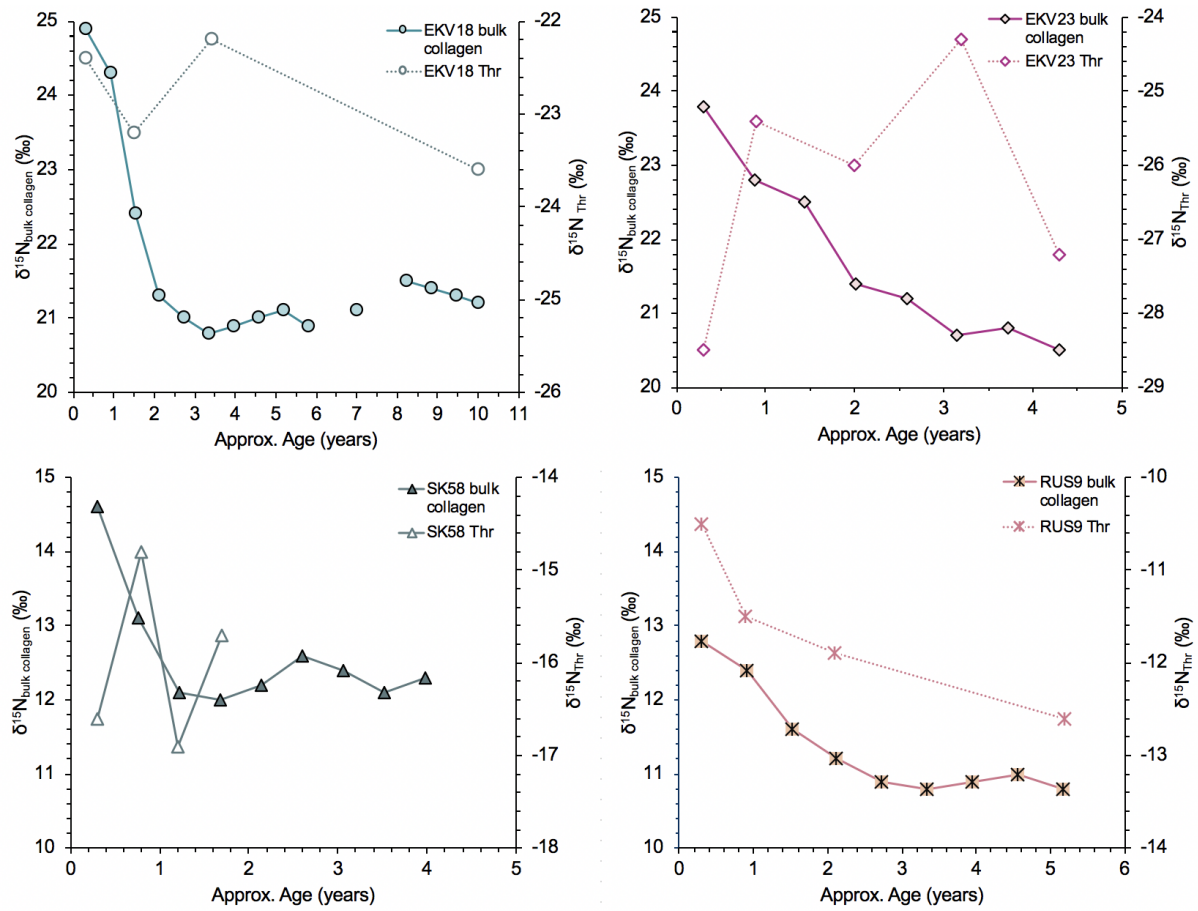

Figure 6.11. Human bulk collagen and Thr δ^{15}N values plotted against age. The secondary y-axis differs between plots. Thr was not measured for SK45. EKV 18 represents burial 327 and EKV23 represents burial 326.

5 Discussion

5.1 Isotopic variation among Ekven infants

Across the sampled individuals, weaning foods were introduced within the first six months of life but the duration of breastfeeding varied. The bulk dentine collagen isotope profiles could be broadly classified into one of two patterns: those who were weaned before the age of two years and those who were weaned later, and often, more gradually.

The individuals with low peak δ^{15}N values also appear to have been fully weaned between the first and second year of life. In Inuit and Yup'ik traditions of the late 19th and early 20th centuries, weaning foods, such as broths or premasticated family meals, could be fed to infants under the age of six months, but complete cessation of

breastfeeding by the age one is inconsistent with ethnographic and nutrition reports (Maynard and Hammes, 1970; Heller et al., 1967), and also with trends in other preindustrial societies (Howcroft, 2013; Kennedy, 2005; Sellen, 2001). It is possible that some of these infants may not have been breastfed at all. Between the ages of 0.3 and 1.0 year, the δ^{15}N values of burial 291 (EKV08), an adult female, only dropped by ~1‰ before stabilizing, and those of burial 318 (EKV10), another adult female, dropped by 1.2‰ over the same period of time. The decline for both individuals is less than the +2-3‰ offset typically observed between lactating females and nursing infants (Howcroft, 2013; Jay, 2009). One possibility is that these individuals were adopted at or shortly after birth. Adoption of newborns and infants was, and continues to be, an important and common cultural practice among Inuit and Yup'ik families that was designed to build and affirm social networks (Billson and Mancini, 2007). Adopted infants were fed meat broths and blubber and although there are accounts of poor health and death afflicting adopted infants, others survived (Rasmussen, 1931).

Just over half of those who were weaned after two years of age had very high peak δ^{15}N values that were suggestive of stress in early life or in utero (Beaumont and Montgomery, 2016). The results should also be considered with respect to osteological markers of stress. A comprehensive osteological analysis of the skeletal assemblage was not available at the time of writing, but one is currently underway. Recent studies conducted by Crowder et al. (2019), King et al. (2018), and Sandberg et al. (2014) examined the relationship between skeletal lesions, dental enamel hypoplasia, and dentine isotope profiles and demonstrated the utility of combining these analyses for characterizing the health status of archaeological populations. It should, however, be noted that the portion of the skeletal assemblage that is curated at the Institute of Archaeology, Moscow, Russia, is biased towards adults and contains few infant and subadult remains which limits the comparisons that can be drawn between survivors and non-survivors among this population.

Seasonal variation in maternal diets, and the influence of high protein diets on trophic level discrimination may also influence the data. The bone collagen isotope data from adult females represent a long-term average of consumed dietary protein. This raises the possibility that seasonal variation, known to occur in the diets of Arctic hunter-gatherers, is obscured by the turnover rate of the analysed tissue. Food storage practices may also attenuate seasonal isotope signals in bone and dentine collagen, or other proteins (Britton et al., 2018). For example, present day Siberian Yupiget

carefully ferment bowhead whale and walrus blubber and meat during the winter so that it will supplement their diet during leaner months (Zdor, 2010; Kozlov et al., 2007). The peak $\delta^{15}N$ values >+23.6‰ may reflect seasonal presence of marine carnivores such as beluga whales or bearded seals in the diets of lactating people. There is also the possibility that the variation in weaning times relates simply to individual circumstances, such as the interval between births and the presence or absence of a sibling.

To the best of our knowledge, there are no comparable incremental isotope datasets from hunter-gatherers with diets composed of such high contributions from marine protein and lipids. High protein diets and marine products will affect the composition of breastmilk (Keikha et al., 2017; Forsum and Lönnerdal, 1980;) and may also influence the magnitude of the trophic discrimination factor (TDF) (Mohan et al., 2016; McMahon et al., 2015). Theoretically, diets high in protein should produce lower TDFs in the trophic AAs of bone and dentine collagen (McMahon and McCarthy, 2016). This may suggest that the very high peak $\delta^{15}N$ values of seven individuals resulted instead from physiological stress. The isotopic data from amino acids, discussed in section 5.2, may help to clarify the issue.

5.2 Amino acid isotope profiles

The source amino acids were indicative of dietary change during infancy and childhood. The results from SK58, an adult male recovered from the 18th century St. Barnabus crypt in London, revealed that source AAs in combination with bulk dentine isotope values, may be used to identify the introduction of weaning foods in archaeological populations. The drop in $\delta^{15}N_{Lys}$ between 0.3 and 0.8 years of age likely indicates the introduction of weaning foods with a different source of nitrogen than the foods consumed by his mother or wet nurse. Similar shifts were not observed in the $\delta^{15}N_{Lys}$ of the two Ekven individuals during weaning, but $\delta^{15}N_{Phe}$ of burial 326 (EKV23) did decline between 0.9 and 3.2 years of age. As with the bulk dentine $\delta^{15}N$ values, interpretation of the source AAs of the Bering Sea hunter-gatherers is complicated by the seasonal dietary variation which is why the source AAs are best considered with respect to the trophic AAs and bulk dentine isotope values.

The source AAs may help to clarify the cause of the very high peak dentine $\delta^{15}N$ value of burial 327 (EKV18). If the high peak dentine $\delta^{15}N$ values resulted from a different source of dietary nitrogen not consumed by other individuals, then this may

be reflected in the $\delta^{15}N$ values of source AAs. The bulk dentine $\delta^{15}N$ values of burial 327 dropped from +24.9‰ to +22.4‰ between 0.3 and 1.5 years of age. Over the same period the $\delta^{15}N_{Lys}$ values of this individual remained stable at approximately +10‰ and were consistent with those of burial 326 who had a lower peak dentine $\delta^{15}N$ value. This suggests that the peak $\delta^{15}N$ value of burial 327 may have resulted from stress, rather than maternal diet. Further osteological analyses of the Ekven skeletal material could determine whether osteological markers of stress are also present.

Across dietary regimes, the introduction of weaning foods appeared to prompt a decline in the $\delta^{15}N$ values of the trophic amino acids; however, the magnitude of the decline differed among these AAs. Regardless of dietary regime, the greatest decrease occurred in the $\delta^{15}N$ values of Pro (mean –4.1‰), while Glx values only varied within 0.9 and 2.5‰ between the period of likely exclusive breastfeeding, represented by peak dentine $\delta^{15}N$ and completion of weaning. Due to its central role in the circulation of nitrogen throughout body tissues, glutamic acid is increasingly used with a source AA, typically Phe, to calculate trophic level. Greater spacing between $\delta^{15}N_{Glx}$ and $\delta^{15}N_{Phe}$ indicates a higher trophic level (Chikaraishi et al., 2009; McClelland and Montoya, 2002). Due to analytical issues with Phe in this study, the $\delta^{15}N_{Lys}$ were used to compare trophic spacing across the humans and wild fauna from the Bering Sea coast (Fig. 6.12). Among the Alaskan animals, greater spacing occurred between $\delta^{15}N_{Glx}$ and $\delta^{15}N_{Lys}$ among the seals (+12.3 to +18.6‰) and beluga (+20.9 to +21.2‰) than among the walrus (+11.4 to +12.2‰) or caribou (+5.8 to +6.2‰) which suggests that within the Bering Sea environment, $\Delta^{15}N_{Glx-Lys}$ is informative of trophic level. This is not the case, however, for the humans. Assuming that exclusive breastfeeding causes a trophic level shift between maternal and infant values, the change in $\Delta^{15}N_{Glx-Lys}$ between the ages of 0.3 and 3.4 years for burial 327 was only +0.4‰, while for burial 326, between the ages of 0.3 and 4.3 years, $\Delta^{15}N_{Glx-Lys}$ changed by –0.5‰. In both cases, the shift was within analytical error.

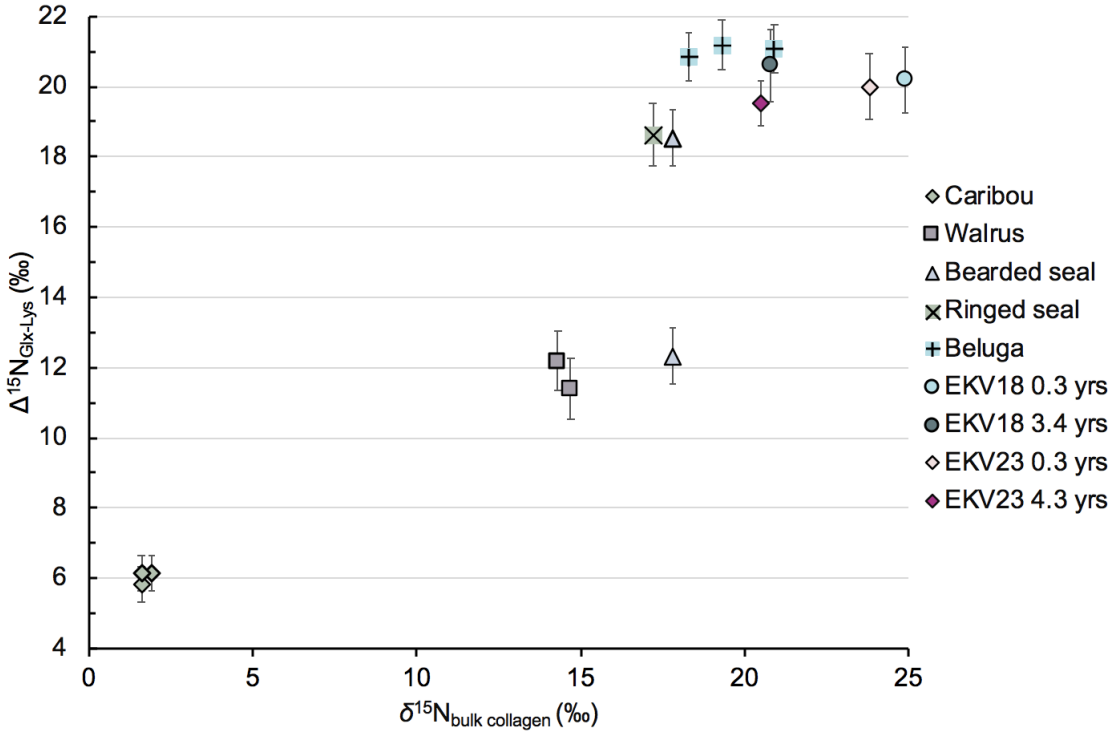

Figure 6.12. Comparison of $\Delta^{15}N_{Glx\text{-}Lys}$ spacing versus bulk collagen $\delta^{15}N$ for wild Alaskan mammals and pre- and post-weaning dentine increments of two individuals, burial 327 (EKV18) and 326 (EKV23) from Ekven.

The high $\delta^{15}N_{Pro}$ values relative to Glx were somewhat unexpected but may be explained by the AA biosynthetic pathways of rapidly growing infants (Fig. 6.13). The low concentration of Arg in breastmilk occurs because Arg is catabolised via arginase to produce Pro in the mammary gland (Wu et al., 2011). The requirement for Arg during infant growth, which functions as a precursor for nitric oxide and polyamines, exceeds the amount of dietary Arg available in milk making *in vivo* synthesis of Arg critical for postnatal development (Tomlinson et al., 2011a; Wu, 1997). In studies of neonatal pigs and healthy preterm human infants, in vivo synthesis of Arg occurs via multiple enzymatic steps in the intestine from a proline precursor (Tomlinson et al., 2011a; Wu, 1997). The synthesis of Arg from Pro would, theoretically, leave the remaining Pro, that subsequently forms the building blocks of bone and dentine collagen, enriched in ^{15}N (Miura and Goto, 2012; Macko et al., 1987). As weaning foods were added to diets of archaeological infants in this study, or as infants aged, several factors, or a combination of factors, may have contributed to the observed decline in $\delta^{15}N_{Pro}$. Weaning foods may have provided a higher concentration of dietary Arg (foods high in Arg include some legumes, poultry, and dairy); the nitrogen source

of Pro changed; or with growth, infants developed the ability to synthesize Arg from Glx, a known pathway of Arg synthesis in adults (Tomlinson et al., 2011b).

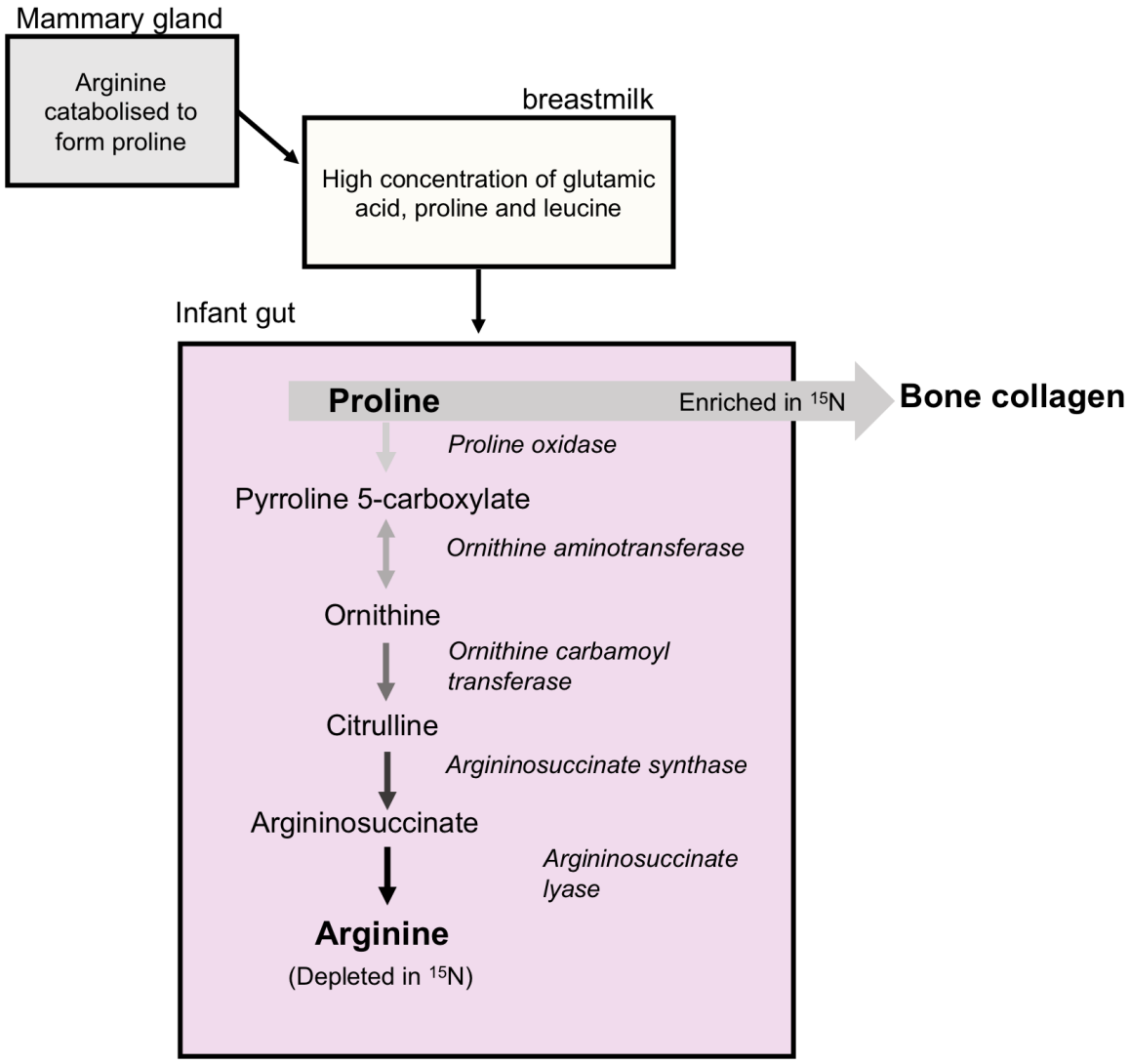

Figure 6.13. Infant pathway of arginine synthesis from proline and subsequent enrichment in ^{15}N of remaining proline used in biosynthesis of bone collagen. Modified from (Tomlinson et al., 2011a).

Gly $\delta^{15}N$ values dropped by an average of –4.7‰ across the five individuals between the dentine increments representing exclusive breastfeeding and increments that formed during, or after, weaning was complete. The demand for Gly is high during the postnatal period as, in addition to composing ~30% of the AA residues in Type I collagen, it is important for the synthesis of creatine and haem (Jackson, 1991). Glycine is present in low concentrations in breastmilk (Tea et al., 2013) therefore a considerable amount must be synthesized de novo by the infant. Glycine can be linked to the body's central nitrogen pool via Ala when it is synthesized from glyoxylate, or

when it is synthesized from serine via serine hydroxymethyltransferase (Wang et al., 2013). Glycine can also be produced from dietary choline which is found in high concentrations in animal products (Friesen et al., 2007). The $\delta^{15}N_{Gly}$ of the dentine increments suggest that Gly was linked to Glx via the central N pool for individuals in this study.

The Thr $\delta^{15}N$ values are difficult to interpret; with the exception of RUS9, in whom the $\delta^{15}N_{Thr}$ values declined over the tooth profile, there was no clear relationship between the introduction of weaning foods and the isotopic composition of Thr. Threonine kinetics are linked to overall protein metabolism. Fuller and Petkze (2017) found a significant difference in the consumer-diet offset of $\delta^{15}N_{Thr}$ among rats fed an adequate protein diet, a medium protein diet, or a high protein diet. Fuller and Petzke (2017) suggested that greater isotopic fractionation occurred as excess Thr was catabolised in the medium- and high-protein diets. Insufficient data is available to interpret the relationship between breastfeeding, weaning, and Thr dynamics, but further research is needed to determine the degree of fluctuation that can be expected in $\delta^{15}N_{Thr}$ within humans during infancy, and during normal life.

6 Conclusion

Inuit and Yup'ik cultures participated in complex social relationships with prey animals and non-human beings and these relationships were maintained through adherence to ritual behaviours and activities, many of which focused on food preparation and consumption and extended to infants. This study analysed the isotopic profile of bulk dentine collagen to reveal diverse infant feeding practices within the ancestral Old Bering Sea culture of Chukotka and St. Lawrence Island, Alaska. Weaning foods were introduced during the first few months of life, but the duration of breastfeeding varied between individuals by one to four years.

This study also pioneered the use of isotopic analysis of single amino acids isolated from incremental dentine samples. In this paper, we demonstrated that it is possible to conduct stable isotope analysis of bulk collagen and amino acids from well preserved incremental (1 mm) dentine samples, however, the addition of CSIA of dentine amino acids is labour intensive and costly, dependent upon skeletal preservation, and should only be undertaken after careful consideration of what new insights can be gained. The source AA lysine showed potential for distinguishing

dietary and physiological influences on infant $\delta^{15}N$ values. Of the trophic AAs, the $\delta^{15}N$ value of proline most closely tracked the cessation of breastfeeding as its role in arginine synthesis led to considerable enrichment in ^{15}N, while $\delta^{15}N_{Glx}$ was not a sensitive indicator of breastfeeding or the weaning process.

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Community Outreach Statement

One of the planned outcomes of this thesis research was to travel to Chukotka in the summer of 2020 to present a summary of the results to local descendent populations of the Old Bering Sea culture. It was hoped that the ArchSci2020 project would be the initial step in a multi-year research programme that would integrate archaeological science and Indigenous research concerns into a holistic approach. These plans were indefinitely disrupted by the global Covid-19 pandemic. However, through continued collaboration with colleagues at the Russian Academy of Sciences and at Stockholm University, we are developing a way to disseminate the results to local communities in advance of publication of the human stable isotope data that forms the basis for this paper.

Supporting Information: Appendix 4

SI File 1 Methods
SI Table 1. Summary data for human AA samples
SI Table 2. Stable isotope values, collagen quality indicators, and estimated age at dentine increment formation for all Ekven samples.
SI Table 3. Stable carbon and nitrogen isotope values of Ekven bone collagen samples
SI Table 4. Amino acid nitrogen isotope values of wild fauna from Nunalleq, Alaska.
SI Figures 1–23

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Chapter 7

Discussion and future directions

This research was designed to address a number of gaps in the bioarchaeological literature of the global Arctic. I sought to examine the performance of maintenance activities, principally the care of infants and domestic animals, among human cultures occupying the North American and Eastern Siberian Arctic between 500 to 1950 CE. This research used a combination of established and novel stable isotope, amino acid, and ancient DNA methods to achieve specific research objectives related to the minimization of destructive sampling protocols, examination of reciprocal dietary relationships between humans and dogs, and the characterization of infant feeding practices of ancient Bering Sea hunter-gatherers. The results of my research will be discussed in the following sections in relation to the research aims of the thesis and with respect to previously published works. While the research presented in this thesis made some significant contributions to Arctic research there remains considerable scope for further research in these areas.

1 Humic acid contamination in archaeological bone collagen

Before the stable isotope data from Arctic archaeological sites could be interpreted, the problem of diagenesis and humic acid contamination had to be contended with. Chapter 2 consisted of a literature review and laboratory experiment comparing the effects of different collagen extraction procedures on the removal of humic acids from Arctic bone collagen samples to answer the following questions:

RQ1 Can a lower concentration of NaOH extract humic acids from bone collagen while simultaneously preserving collagen yields?

The literature review conducted for this study emphasized the importance of tailoring collagen extraction methods to the chemistry of collagen and any contaminating substances. In the archaeological literature, humic acids are removed using strong (0.1 M) NaOH which is far in excess of what is required to solubilise humic acids. Humic acids are theoretically soluble above a pH of 8 (Abate and Masini, 2001), so NaOH solutions at a lower molarity than 0.1 M should be able to remove these substances from archaeological collagen. The experimental research presented in Chapter 3 supported this hypothesis and demonstrated that dilute (0.025 M) NaOH allowed for a greater collagen yield than ultrafiltration, the alternate method employed in the study. The NaOH did cause some collagen hydrolysis, as indicated by racemization of collagen aspartic acid, leucine, serine and valine in the NaOH-treated samples. Despite higher D/L ratios, the AA concentrations of the NaOH-treated collagen were higher than for ultrafiltered collagen, and the differences in AA composition were negligible among the pre-treatments which indicates that the impact of NaOH on collagen AAs should not be a source of concern.

RQ2 Are ultrafilters more or less effective than NaOH at removing humic contaminants from bone collagen?

The use of 30 kDa ultrafilters appeared to skew the $\delta^{13}C$ values of the UF treated collagen lower than NaOH and control collagen samples and had a marked effect on the atomic C/N ratios. These results strongly suggested that ultrafilters were concentrating humic contaminants in the samples. Humic acids will aggregate into larger molecular species below a pH of 4-5 (Abate and Masini, 2003; Kipton et al., 1992), the exact conditions of many gelatinization protocols (Jørkov et al., 2007; Ambrose, 1990; Brown et al., 1988;). Drawing on the results presented in Chapter 2 and building on previous studies (Szpak et al., 2017a; Jørkov et al., 2007), it is becoming clear that the use of ultrafilters to remove humic acids is questionable. However, ultrafiltration may be useful when working with degraded collagen, or when other contaminants are suspected (Fuller et al., 2014).

RQ3 What are the amino acid and isotopic compositions of humic substances extracted from bone?

This study provided the first comprehensive chemical analysis of humic substances extracted from archaeological bone. The humic solids had high atomic C/N ratios and

low $\delta^{13}C$ values that were inconsistent with bone collagen from marine consumers (seals and domestic sled dogs), however, the humics did contain nitrogen that was likely derived from collagen. The humics had much lower AA concentrations than the actual collagen samples, but a broadly similar AA composition. Taken together, the AA results suggest that the humics contained some collagen peptide fragments, the presence of which would explain the high $\delta^{15}N$ values that were measured in the humic solids.

It may be tempting to dismiss the results from Double Mer Point as a worse-case scenario of humic contamination, but in comparison to other bone assemblages from the Subarctic (e.g. Harris et al., 2019), the Double Mer Point bones were well-preserved and the humic acid contamination was manageable. Sample mass was one of the greatest hindrances encountered while conducting the experimental procedures in Chapter 2. The masses of collagen and humic substances obtained from the different pre-treatment methods were insufficient for the number of planned analyses. For example, it would have been ideal to conduct compound specific carbon isotope analysis of collagen treated with ultrafilters and/or NaOH from a representative number of samples, but this was not possible given the initial mass of each bone sample and the loss of collagen that occurred with the use of ultrafilters. While a number of studies have decisively shown the deleterious effects of 0.1 M NaOH on collagen yields, the conclusions of Chapter 2 would have been more robust if the 0.025 M sodium hydroxide treatment was also compared to 0.1 M NaOH.

2 Diets of hunter-fisher-gatherers in the Circumpolar North

Chapter 3 was framed around three research questions:

RQ 4 What is the full range of isotopic variation within and between Arctic populations?

Figure 7.1 compares published $\delta^{13}C$ and $\delta^{15}N$ values of humans from Greenland, Labrador and Nunavut, Canada, north- and southwest Alaska with Ekven, Chukotka. The keratin $\delta^{13}C$ and $\delta^{15}N$ data from Nunalleq (Britton et al., 2013, 2018) have been adjusted by +1.4‰ and +0.9‰ respectively, to bone collagen values for ease of comparison (O'Connell et al. 2001).

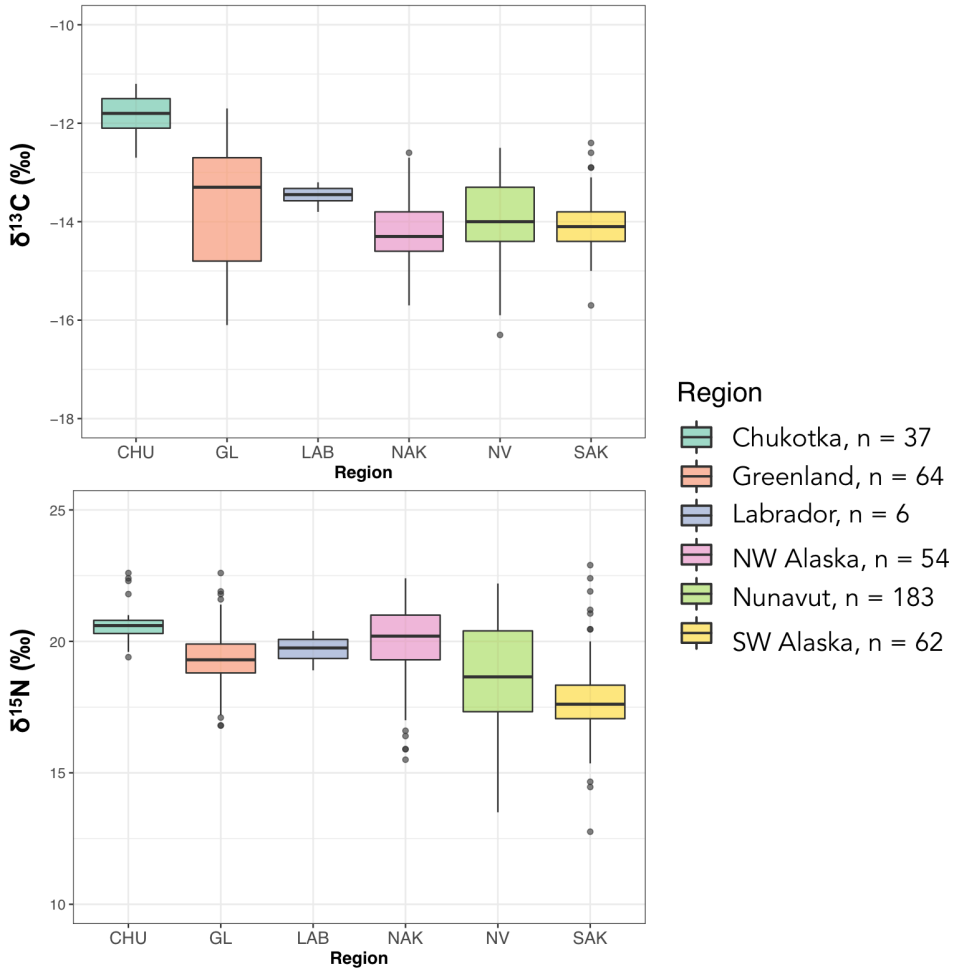

Figure 7.1 A comparison of bone collagen data from Ekven, Chukotka (CHU) with published isotope data Greenland (GL) (Nelson et al., 2012), Hudson Bay (HB) (Coltrain, 2009; Coltrain et al., 2004), Labrador (LAB) (Raghavan et al., 2014), northern (NAK) (Coltrain et al., 2016) and southern (SAK) Alaska (Britton et al., 2018).

The δ^{15}N values have a range of approximately 10‰ with the highest mean values measured in the bone collagen of Ekven OBS adults and the lowest mean values in the corrected hair samples from Nunalleq Yup'ik. This difference aligns with interpreted differences in the subsistence base between regions: salmon were of importance in southern Alaska (Masson-MacLean et al., 2019; Britton et al., 2018; McManus-Fry et al., 2018) while the archaeological evidence collected from coastal Chukotka and St. Lawrence Island suggests that sea mammals, such as walrus, ringed seal and bowhead whale, were predominantly targeted by the OBS culture (Mason and Rasic, 2019; Whitridge, 1999). The individuals from Ekven have the highest δ^{13}C values of any region which suggests a pronounced dietary contribution from walrus, ringed seal, or potential benthic fish, based on published isotopic data

from Bering and Chukchi Sea zooarchaeological assemblages (Clark et al., 2019; Szpak et al., 2017b; Byers et al., 2011).

RQ 5 What biological factors should be considered in the interpretation of human isotope data from Arctic groups?

Drawing on ecological literature, Chapter 3 raised the issue of the high lipid-content of many northern diets. Isotopic studies of bone collagen can effectively identify general sources of dietary protein, but sources of fat are poorly represented (Fernandes et al., 2012). Previous works have further identified possible interactions between climate change and human subsistence in the archaeological past (e.g. Coltrain et al., 2004), a line of questioning that is under investigation in regions of the Canadian Arctic Archipelago and Alaska (Szpak et al., 2019; Szpak et al., 2017b)

RQ 6 How might food preparation and storage influence human stable isotope data?

Previous research programmes have focussed on generating diachronic analyses of human subsistence practices and have examined the intersection of food cultures and social organization. These works have produced complementary datasets showing distinct culture differences in the dietary practices of Inuit and Yup'ik groups across the Arctic (e.g. Britton et al., 2018, 2013). Stable isotope studies have found evidence for a relationship between resource use and residential mobility in Greenland and Alaska (Britton et al., 2018; Nelson, Lynnerup, et al., 2012). Past bioarchaeological research has also made significant contributions to our collective understanding of the relationship between zooarchaeological assemblages, taphonomic bias, and stable isotope data from human skeletal remains (e.g. Coltrain et al., 2004), and shown that the food storage and preservation practices of arctic peoples may attenuate seasonal dietary isotope signals (Britton et al., 2018) in human biological remains.

3 Reciprocal dietary relationships of humans and dogs

Stable isotope studies of Arctic populations have, logically, tended to focus on subsistence-based questions. However, recent calls in anthropological literature have urged alternative approaches to the study of human-animal relationships in the Arctic (see Whitridge, 2018; Hill, 2011). Chapters 4 and 5 investigated the diets of Arctic and

Subarctic sled and herding dogs between the 15th and mid-20th century to ask a central question:

RQ 7 How do dog diets vary geographically across the Arctic and in relation to their social and economic roles in Arctic societies?

Chapters 4 and 5 used a stable isotope-based approach to examine human-dog dietary relationships in the North American and Siberian Arctic. Chapter 4 presented the results of a stable isotope study of the bone collagen of sled dogs from Labrador, Canada, to determine if there were differences in the diets of sled dogs from different geographic regions in Labrador, Canada. Chapter 5 presented ancient DNA and stable isotope analysis of dog and wild animal furs, collected in the late 19th and early 20th centuries, that were used in the fabrication of Arctic clothing. Together, these studies presented a picture of dog provisioning that spanned Greenland westward to the Polar Urals. Across the Arctic, the stable isotope data provided evidence that dog provisioning was largely dependent on locally available resources. In the North American Arctic, dogs were predominantly fed with marine resources, but there were inter-regional differences in the types of marine resources fed to dogs. In Greenland and much of Labrador, marine mammals were the predominant food source, while in Alaska and northern Canada, dogs consumed mixed marine and terrestrial diets. Siberian dogs of Nenet and Khanty reindeer herders consumed terrestrial diets, as did those in Kamchatka Krai. The latter result was surprising as salmon is known ethnographically to be an important food resource for dogs (Strecker, 2018).

Common to all regions was the amount of human labour and energy required to feed and meet the physiological needs of working dogs in cold environments. Among Arctic communities of the North American Arctic, feeding and caring for dogs was a task that fell to both men and women (Braymer-Hayes et al., 2020). This activity required cooperation between dogs and humans: hunting implements had to be manufactured, seal breathing holes scented, seal carcasses transported, butchered and shared between families and with dogs. Among the Nenets of the Siberian Arctic, dogs and humans shared a hearth; women were responsible for feeding herding dogs and did so by cooking soups (Tuisku, 2001). Dogs working in cold environments require at least 50% of their energy from fat (Loftus et al., 2014; Case et al., 2000). In the Eastern Arctic, this dietary requirement was met by feeding dogs the flesh of marine mammals; in Alaska, dogs were fed salmon and marine mammals (McManus-

Fry et al., 2018). Siberian dogs were fed terrestrial sources of protein which tend to be leaner than marine mammals (Hassan et al., 2012; Kuhnlein et al., 1991), but by making a soup, fats from bone marrow could have been liberated which would have provided the dogs with an extra source of fat.

Among mobile societies occupying high latitude environments, dog provisioning tasks would have to be modified to cope with seasonal and regional fluctuations in food resources and raw materials. The two Inuit sites of Nachvak Village and Kongu on the shore of Nachvak Fiord in northern Labrador provide a fascinating glimpse of how dog provisioning changed with locale. Elliott (2017) has proposed that the families who occupied Nachvak Village moved down the fiord in the late 17th century and established a community at Kongu. If so, the sites allow us to track dog provisioning practices at the community level. Nachvak Village, the older of the sites, is located close to a river where Arctic char could be caught and is also near to migrating herds of caribou (Elliott, 2017). In comparison to Kongu, the artefact assemblage featured more caribou bone and fewer seals and supports a more substantial role for caribou as a source of dietary protein and raw material for early Inuit inhabitants of Nachvak (Swinarton, 2008). The stable isotope data from dogs from both sites also show a difference in the proportions of terrestrial versus marine mammal protein consumed by dogs (Fig. 7.2). Fishing, hunting caribou, and hunting seals require the performance of different sets of activities at different times of the year. Amending the types of food preparation actions from Sánchez-Romero and Aranda (2008), these could include: the division of tasks within the family; raw material processing (butchering an animal to feed humans and dependent dogs, drying meat and fish); the maintenance of structures (kayak and/or umiak for sealing, fish nets, meat cache structures, sleds and sledding components), and making and maintaining hunting and food processing implements. The change in dog diets between Nachvak Village and Kongu indicate a shift in the types of day-to-day activities that would have been performed as well.

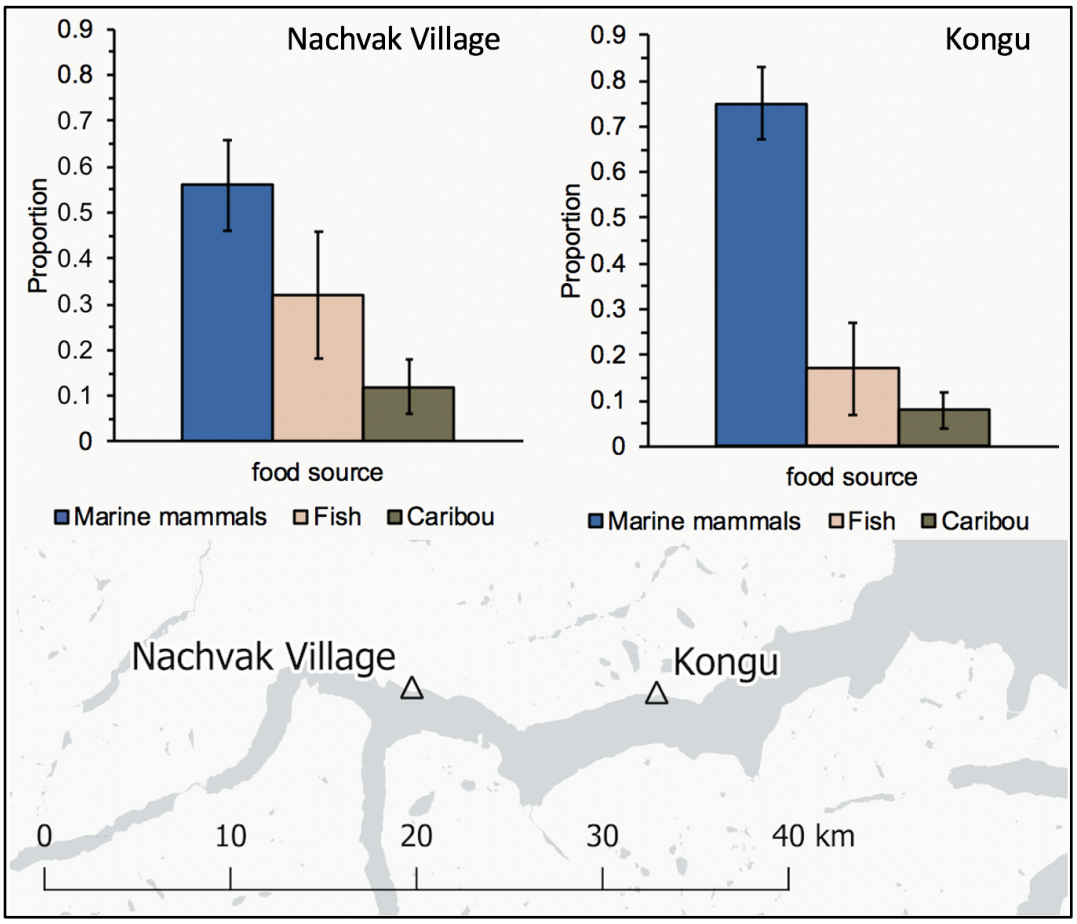

Figure 7.2 Estimated dietary composition of domestic sled dogs recovered from the Inuit sites, Nachvak Village and Kongu, in northern Labrador.

4 Infant feeding practices in Arctic cultures

Stable nitrogen and carbon isotope ratio analysis has been used since the late 20th century to investigate infant feeding practices among archaeological populations and is becoming more popular with recent developments in incremental sampling of archaeological proteins, most commonly dentine. Over the late 20th century and the first decade of the 21st, infant feeding studies were primarily focused on comparisons of the δ^{15}N values of bones from different age cohorts within a skeletal assemblage to determine the approximate age at which breastfeeding ceased. These studies sought to examine past fertility and population demographics, the role of infant feeding in hominid evolution, and the relationship between infant and child mortality with diet (Jay, 2009). Recent advances in skeletal and dental sampling have broadened the range of questions that can be addressed with stable isotope analysis. Deciduous molars, which begin to form during the last trimester before birth, record maternal

dietary and physiological inputs and are now used to investigate maternal and fetal incidents of stress (Beaumont et al., 2018; King et al., 2018; Beaumont et al., 2015).

The roles of infant diet and breastfeeding duration as determinants of long-term infant and maternal health have prompted ethnographic investigations of these practices in urbanized Western contexts, small-scale societies, and in the archaeological past. Ethnographic and anthropological research in a range of global contexts has shown that the types of weaning foods provided to infants depend upon the established cultural beliefs regarding childcare and the female body, economic and social status, access to postnatal care, and on the types of foods available locally (Pak-Gorstein et al., 2009; Lindsay et al., 2008; Kruger and Gericke, 2003; Gebriel, 2000). Prior to the present work, very little was known about Arctic infant feeding practices in the archaeological past. Isotopic breastfeeding studies of high latitude populations were limited to Scandinavia (Howcroft et al., 2014, 2012; Eriksson and Lidén, 2013;) and Lake Baikal in Siberia (Scharlotta et al., 2018). What was known about infant feeding among Inuit and Yup'ik populations came from recorded recollections of elders that may date to as early as the late 19th century (Heller et al., 1967; Rasmussen, 1929, 1931). Among modern Inuit and Yup'ik communities, the choice of weaning foods and the timing of their introduction to infant diets have been of particular concern due to high rates of anaemia and bacterial infections among infants (Christofides et al., 2005; Maynard and Hammes, 1970). As a result, the body of available literature regarding infant feeding in the North American Arctic is growing and it is now possible to discern some regional commonalities. Among present-day communities, while exclusive breastfeeding rates are lower than the national Canadian average, in Nunavut, infants are breastfed until the age of four years (Wielsøe et al., 2016; McIsaac et al., 2014; Christofides et al., 2005). A pattern of long breastfeeding duration appears to be consistent with data collected in Alaska in the mid-20th century as well (Hildes and Schaefer, 1973; Heller et al., 1967;). While present-day Inuit and Yup'ik populations have some access to typical Western foods, such as cereals, infant formula, and animal milks, the types of weaning foods available to prehistoric populations of the Bering Sea coast would have been more limited by western perceptions. It is likely that pre-mastication of family foods would have played an important role in infant feeding (Heller et al., 1967).

RQ 8 How did breastfeeding practices vary among Ekven hunter-gatherers? and *RQ 9 What was the duration of the weaning period?*

Chapter 6 presented the results of stable carbon and nitrogen isotope analysis of bulk collagen and AAs from incrementally sampled dentine. The isotope profiles were assessed with respect to the duration of exclusive breastfeeding, the timing of the introduction of weaning foods, and the amount of time that the weaning process took. The results of this study suggested that weaning foods were introduced to infant diets within the first six months of life, but the cessation of breastfeeding was not associated with a fixed period of time. Half of the individuals included in the study were weaned early, between the ages of one and two years; 40% breastfed until the age of three to five years. Those who were weaned early also tended to be weaned more abruptly than those who were weaned late.

These results are slightly dissimilar to those from the site of Shamanka II in the Cis-Baikal region of Siberia. Scharlotta et al. (2018) found that over 60% of the individuals from Shamanka, shown by incremental dentine analysis of permanent first molars, were weaned quickly before the age of two years, while only 20% were weaned between the ages of four and five years. Scharlotta and colleagues interpret the difference in weaning ages in relation to the perception of extrinsic risk and degree of parental investment. Individuals who were breastfed for a longer period of time received greater parental investment in response to maternal perception of extrinsic risks in the environment (e.g. pathogens) (Scharlotta et al., 2018, p. 593). This is an intriguing interpretation, but some additional biological and cultural factors associated with breastfeeding should also be considered. Among modern Western women, early termination of breastfeeding is associated with nipple pain or mastitis, economic roles, or concerns that the quantity of milk expressed is insufficient to be the needs of the infant (Schwartz et al., 2002). Across human societies, breastfeeding practices and the choice of weaning foods are also strongly influenced by knowledge transmission (Wells, 2006). While a natural capability of most female bodies, breastfeeding is a learned behaviour which is one of the reasons why pronounced cultural variability is observed in infant feeding practices in the archaeological past, among present-day human groups, and even within families (Dettwyler, 2004). Similarly, food has a strong cultural significance among Yup'ik and Inuit societies and represents social relationships within and between families, and between humans and non-human beings (Hill, 2011; Whitridge, 2000; Bodenhorn, 1990). While the same cultural

connotations should not be uncritically assumed for the Old Bering Sea culture, many archaeological similarities have been noted between the OBS and descendent Inuit and Yup'ik groups (Hill, 2011; Whitridge, 1999). The Ekven study is preliminary, and at this point in time it is not possible to state with certainty why there is variation in weaning times, but based on the ethnographic literature, factors such as adoption at, or shortly after, birth; season of birth and seasonality of maternal diet; birth spacing; and other factors relating to food culture and the agency of individuals should be considered.

RQ 10 Can the sources of nitrogen isotope variation in infant collagen be better characterised using nitrogen isotope analysis of dentine amino acids?

This question was addressed in a pilot study that formed a component of Chapter 6. The $\delta^{15}N$ values of AAs extracted from incremental dentine samples of Ekven humans were measured and compared to AA $\delta^{15}N$ values of archaeological fauna from the Alaskan Yup'ik site of Nunalleq. The AA data from the Ekven humans were further contextualised through comparison with AA isotope profiles from two British individuals, and one medieval Russian individual, all of whom had different dietary regimes. The results were intriguing and somewhat unexpected.

As reviewed in Chapter 6, bone and dentine collagen AAs can be categorized as either trophic or source AAs depending on whether the biosynthetic pathway of the AA includes a transamination or deamination reaction (O'Connell, 2017; McClelland and Montoya, 2002). The trophic AAs of the terrestrial Alaskan herbivores were much lower than those of the marine mammals, represented by bearded and ringed seals, beluga, and walrus. Within the marine mammal group, there was further separation between beluga whales, which feed heavily on Polar cod (*Boreogadus saida*), and the walrus, which generally consume shellfish (Quakenbush et al., 2015; Sheffield and Grebmeier, 2009). The $\delta^{15}N$ values of Gly were below 0‰ for the caribou, and below +15‰ for the marine mammals. The two source AAs, Lys and Phe, effectively distinguished marine and terrestrial animals, but there was little separation of $\delta^{15}N_{Lys}$ or $\delta^{15}N_{Phe}$ in the marine mammal group that could help to distinguish the relative contributions of these taxa to human diets.

Although glutamic acid is most commonly used as the canonical trophic amino acid, the results of this study showed that the $\delta^{15}N$ value of Glx did not change substantially over the periods of breastfeeding and weaning. In contrast, proline and glycine appeared to be more sensitive indicators of the weaning process for all individuals,

as a marked decrease in $\delta^{15}N$ values was observed for these two AAs between dentine samples that formed during the exclusive breastfeeding period and those that formed after breastfeeding ceased. The $\delta^{15}N$ values of source AAs varied among the individuals. The lysine $\delta^{15}N$ values of one British individual (SK45) and the individual from Russia (RUS9) dropped in tandem with the bulk collagen $\delta^{15}N$ values, while those of the other British individual (SK58) remained stable throughout infancy. The source AAs may hold some potential for distinguishing the influence of physiological or nutritional stress from diet on infant $\delta^{15}N$ values. One of the Ekven individuals, burial 327 (EKV18) had a very high $\delta^{15}N$ value of the first dentine increment that corresponded to the exclusive breastfeeding period. By relying solely on the bulk dentine $\delta^{15}N$ and $\delta^{13}C$ values, it was not possible to determine if this was due to systemic stress or to seasonality of maternal diet. The trophic AAs of this individual were also elevated in the first dentine increment and dropped by >5‰ with weaning, but the source AAs remained stable throughout this period and were consistent with those of burial 326 (EKV23). This suggests that the high trophic AAs and bulk dentine $\delta^{15}N$ value were due to a physiological or metabolic factor rather than a dietary factor. The latter would have, presumable, also caused a change in the source AA $\delta^{15}N$ values. These results are promising, but preliminary, and further research combining CSIA with osteological analysis is required to better assess the relationship among AA synthesis, growth, stress, diet and the stable isotope values of infant collagen.

5 Future directions

This doctoral research revealed a number of important insights into laboratory methods, human-animal relationships in the Arctic, and infant feeding practices, but this research was also limited by the academic context in which the research took place, and by the choice of primary analyte (collagen) so that in many respects, the work presented here is only a starting point for further research. Some possible avenues of future inquiry are presented in the following sections.

5.1 Indigenous perspectives and ethnographic research

The research presented in Chapters 4-6 produced important and interesting results, but would have benefited immensely from Indigenous collaboration and input into the research design and questions. There are several excellent examples of community led, collaborative research that have, or are currently, taking place in the North American Arctic. Several of these were touched upon in Chapter 3, but there is one in particular that would serve as a fitting model for further research on human-dog relationships, and for future studies of infant feeding and the experience of gender in the Arctic. The Iqaluktuuk Project in Nunavut, Canada, combined archaeological excavation with on-site interviews with community elders. The archaeologists were able to draw upon the recollections of elders and their descriptions of hunting and collection methods at particular locations on the landscape to interpret formation and depositional processes and compare and contrast 20th century subsistence practices

with those of early Inuit settlements and even older Palaeo-Inuit archaeological remains (Friesen, 2002). A similar approach that combined interviews with bioarchaeological research would lend itself to the study of both infant feeding practices and sled dog provisioning. Such an approach could also draw on methods used in public health; focus group discussions have been conducted in Brazil to investigate the relationship among personal beliefs, cultural standards, and weaning practices (Lindsay et al., 2008).

5.2 Archaeological and osteological research

A common impediment to each of the archaeological case studies in this thesis was a relative lack of contextual data to anchor the isotopic research and provide more nuance to the interpretation. The analysis of sled dog bones would have benefited from a comprehensive zooarchaeological analysis. Archaeological research in Labrador is at the forefront of community-led research in Canada, but the history of the discipline in the region is shallow relative to work conducted on the west coast of the country and is in its infancy when compared to the United Kingdom and continental Europe. To the best of my knowledge, the only zooarchaeological analysis of sled dogs in Labrador was conducted by Dr. James Woollett as a component of his PhD research (Woollett, 2003). This research focused on the relationship of dog mortality curves with human responses to 18th-19th century climate variability, and not on the experiences of dogs within that particular context. This is not a critique of Woollett's research, but rather serves to demonstrate the scope of possible research questions that could be asked in the future. For example, the creation of osteobiographies of individual animals is one way of centring the experiences of animals and creating important alternative narratives of the past (Haruda et al., 2020; Hull, 2020; Tourigny et al., 2016).

A valid critique of the work presented in Chapter 6 is the lack of contextual osteological and archaeological data. The addition of an analysis of osteological non-specific stress markers would have provided further insight into the health of the Ekven population. Fortunately, this research is currently being conducted by an ArchSci2020 colleague and the forthcoming results will provide a useful grounding for the isotopic data. Likewise, ongoing chronological research at Ekven stands to refine the

radiocarbon calibrations (Dury et al., in prep). This is anticipated to bring some temporal constraints to the weaning data.

5.3 Methodological developments

This research employed a range of analytical methods including bulk $\delta^{15}N$ and $\delta^{13}C$ analysis, AA composition and racemization, and very limited compound specific isotope analysis of AAs. There are interesting developments in soil geochemistry that could be of use to further our understanding of humic-bone interactions in post-depositional contexts, namely electrospray ionization Fourier transform ion cyclotron resonance mass spectrometry. FT-ICR-MS has been used to characterize humic acids by generating elemental data (H, C, O) in humic substances extracted from soils. When the ratios of H/C and O/C are plotted in a van Krevelen diagram (Fig. 7.3) it may be possible to pinpoint the origin of humic substances extracted from archaeological bone.

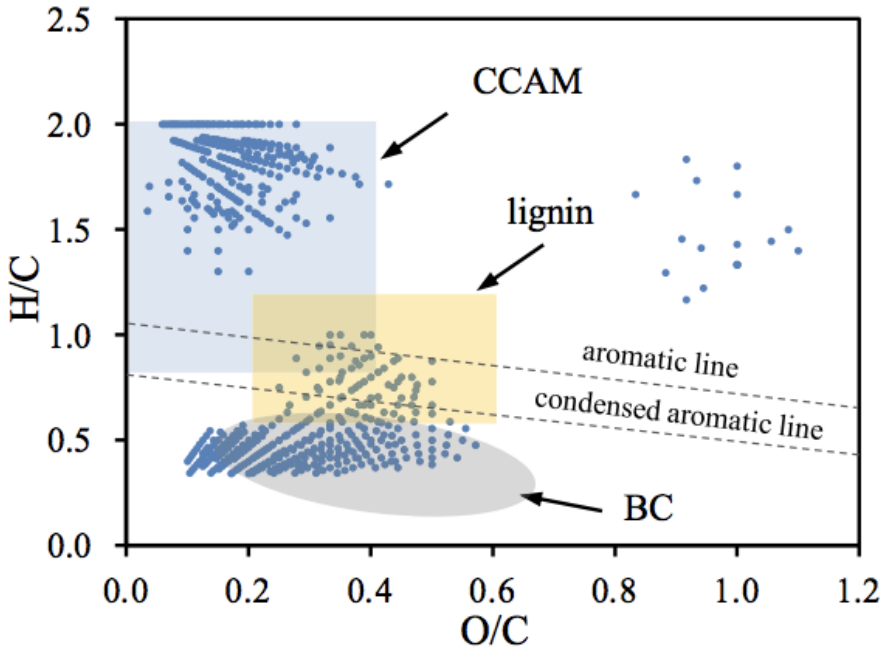

Figure 7.3 Van Krevelen diagram plotting H/C and O/C ratios of humic substances extracted from grassland soil. Shaded boxes represent regions for carboxyl containing aliphatic molecules (CCAM), lignin-like substances, and black carbon-like substances (BC). Image from DiDonato et al., (2016) with data from Ohno et al., (2010).

The ancient DNA analysis of arctic fur clothing, in Chapter 5, revealed that macroscopic analysis had misidentified approximately 30% of the samples. This

finding has relevance for museum collections around the world, especially given the increasing interest in the analysis of museum collections (Ameen et al., 2019; Bro-Jørgensen et al., 2018; Teasdale et al., 2017). A further, controlled study comparing the outcome of DNA and macroscopic methods is warranted.

Isotopic analyses of collagen are limited by the nature of the protein. Collagen largely incorporates isotopic signals from the protein component of diet; bone collagen has a slow turnover rate which produces an averaging effect that obscures short-term changes in diet; and finally, the interpretation of isotopic analyses of bulk collagen are limited by the problem of equifinality. Compound specific isotope analysis provides one means of circumventing equifinality and potentially elucidating isotopic contributions from non-protein sources, discussed in Chapter 3, but the method is still stymied by collagen turnover. Any new developments in the analysis of collagen, particularly on the Bering Sea coast, would be best paired with the interdisciplinary archaeological research discussed above. The research presented in Chapter 6 should be replicated with a larger sample size that includes individuals with different dietary regimes. The addition of carbon compound specific isotope analysis of amino acids would provide further information about the conditional essentiality of proline and glycine during infancy. A longitudinal study of incrementally growing tissues of modern, juvenile animals could also help to characterize the relationship between proline and the introduction of non-milk foods.

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Chapter 8

Conclusions

I began this dissertation by asking a series of methodological and theoretical questions that were informed by feminist epistemology. My first three questions dealt with the effects of humic acids – a common contaminant in archaeological bones recovered from Arctic and Subarctic sites – on bone collagen, and how these could best be removed from collagen while limiting the destructive effects of pretreatment protocols. Could a lower concentration of NaOH be used to extract humic acids from bone collagen while simultaneously preserving collagen yields? Are ultrafilters more or less effective than NaOH at removing humic contaminants from bone collagen? What are the amino acid and isotopic composition of humic substances extracted from bone? My results showed that yes, a chilled concentration of 0.025 M NaOH could effectively solubilise humic acids with few detrimental effects on the collagen molecule. Ultrafilters, chosen to isolate peptides larger than 30 kDa, reduced collagen yields and may have actually concentrated humic acids in the collagen samples. The extracted humic substances featured a fraction of protein that may have been derived from collagen, based on the high $\delta^{15}N$ values, and a fraction derived from plant lignin as suggested by very low $\delta^{13}C$ values and high atomic C/N values. Further research is necessary to fully characterize these substances.

Next, I considered the sources of isotopic and dietary variation among Arctic Inuit and Yup'ik populations that could influence the interpretation of palaeodietary evidence. What is the full range of isotopic variation within and between Arctic populations? Hundreds of stable isotope measurements have been published from archaeological populations in the Canadian Arctic, Alaska, and Greenland and a review of these revealed that there was considerable variation within and among Inuit and Yup'ik communities. While marine foods strongly influenced human isotope values, the primary economic resources differed substantially between regions. Should biological or physiological factors be considered in the interpretation of existing and forthcoming isotope data sets? The quantity and quality of consumed protein have

been linked to trophic effects for both carbon and nitrogen in laboratory settings. The high marine protein diets of Arctic peoples may decrease the diet-collagen $\delta^{15}N$ offsets and render commonly used trophic discrimination factors inappropriate for this context while high contributions from dietary lipids, such as whale (*muktuk*) and seal (*nuktuk*) blubber, may influence collagen $\delta^{13}C$ values to a greater degree than is commonly observed among lower latitude archaeological populations. Could food preparation and storage also influence human stable isotope data? The practice of cold storing and fermenting foods in meat caches that was common across the Arctic likely had little influence on the isotopic composition of the food but may have had the effect of attenuating seasonal dietary signal in sequentially sampled archaeological proteins.

Having determined the best way to proceed with sampling collagen (for my purposes) from Arctic archaeological samples, I proceeded to conduct three archaeological case studies. Human subsistence practices were variable across the Arctic, but what about those of dogs? Chapters 4 and 5 used stable carbon and nitrogen isotope analysis of dog bones and genetically identified fur to ask, how did dog diets vary geographically across the Arctic and in relation to their social and economic roles in Arctic societies? Dog diets corresponded closely to the dominant human subsistence patterns in each region. Marine hunter-gatherers fed their dogs marine foods, and herders fed their dogs terrestrial proteins, perhaps supplemented with anadromous or freshwater fish. The tasks involved in provisioning dogs were labour-intensive and would have occupied a significant amount of time. The labour that would have been invested in feeding dogs suggest that dogs were important members of Arctic societies and fulfilled crucial roles.

Lastly, I asked how about the duration of exclusive breastfeeding and the weaning process among hunter-gatherers affiliated with the Old Bering Sea culture of Chukotka. Very little has been written about the infant feeding practices of hunter gatherers in the Arctic, but 20th century ethnographic research and nutritional surveys of present-day Inuit women suggest that infants experienced prolonged breastfeeding, upwards of three years. In Chapter 6, I took incremental samples of permanent first molar dentine collagen. The results showed that the time at which weaning foods were introduced generally occurred relatively early, within the first six to nine months of life, but the duration of the weaning process varied among individuals. Some individuals were weaned quickly, by the end of the first or second year of life, while others continued to breastfeed until they were three or four years of age. This suggests that

individual choice was likely as important a factor as cultural factors in dictating the age at which breastfeeding ceased. A number of dentine isotopic profiles showed evidence of systemic stress events that may have occurred during late pregnancy and/or during infancy. The health status of lactating people may have also affected the length of time that an infant was breastfed. Chapter 6 also presented the novel results of the isotopic analysis of amino acids from incremental dentine samples. This method showed promise for distinguishing incidences of systemic stress from dietary variation. Infant amino acid profiles may have also evidenced age-specific amino acid metabolism. Contrary to much of the published data, glutamic acid was not a sensitive indicator of trophic level in infants, but the nitrogen isotope value of proline did drop with age. The effect on proline may relate to its role in arginine synthesis in young infants.

To date, the archaeology of maintenance activities has rarely been employed as a theoretical framework outside of Europe. Feminist analyses are rare in Arctic archaeology, but the field lacks the historical depth that characterizes research in the United Kingdom or Europe, and an increasing number of researchers are considering gender as an analytical category. Alternative perspectives are critical in archaeology as they may help to avoid the projection of western cultural norms on the past. Knowledge claims are historically and culturally constituted; feminist research can prompt us to think through unspoken assumptions and reconsider how past societies are being represented, and whose perspectives are prioritized. In this dissertation, I attempted to approach the archaeological record of the Arctic using the principles of feminist archaeology. By analysing the lives of women, children, and non-human persons, I was able to develop new insights into the day-to-day activities that sustained life in the Arctic. I recognize that as a cultural outsider, my perspective on the research topic is partial, but science is successful precisely because it is an iterative process, and it is my hope that future researchers from Arctic communities can build on my results. Biomolecular archaeology is under constant and rapid development. The ArchSci2020 project, comprising stable isotope analysis, ancient DNA and proteomics, bioinformatics, radiocarbon dating, osteology, and residue analysis, is a prime example of how cutting-edge scientific methods can be brought to bear on the unique questions arising in the archaeological record of the Circumpolar North. These developments are exciting, and when they are combined with ethnography, archaeology, and traditional Indigenous ways of knowing, they have the potential to energize and increase the social relevance of archaeological research.

Appendix 1

This appendix includes SI file 1, Methods, and Supporting Tables 1 through 5.

Supporting file 1, Methods

Bone collagen extraction

Chunks of bone (~500 mg) were cut from mammalian skeletal elements using a handheld Dremel tool and the surfaces were mechanically abraded using a stainless-steel burr attachment. The bone samples were manually crushed into smaller pieces, divided into four subsamples and demineralised in ~10 mL of 0.5 M hydrochloric acid at 4℃. These were submitted to one of four pre-treatment procedures, detailed below.

Procedure 1, Control

The samples were gelatinised (70°C, 48 hours), filtered with Ezee filters (40-90 μm pore size, Elkay, UK), frozen and lyophilised (after Honch et al., 2006).

Procedure 2, NaOH

The samples were immersed in 5 ml of chilled 0.025 M NaOH (pH 12.4) in an ultrasonic bath of ice water. The NaOH solution was refreshed every 10 minutes until the solution remained clear and colourless. The bone samples were rinsed with 0.1 M HCl, then rinsed to neutrality with deionized water. The samples were gelatinised, filtered and dried as above.

Procedure 3, UF

The samples were gelatinized and filtered as in the control procedure, followed by ultrafiltration (30 kDa, Amicon, Merck Millipore, Cork). The ultrafilters were filled with deionised water and centrifuged three times (3000 rpm, 15 min) prior to use. Following ultrafiltration, the retentates were pipetted to clean 2 ml microcentrifuge tubes, frozen, and lyophilised.

Procedure 4, NaOH/UF

The samples were treated with NaOH, as in procedure 2, and the waste NaOH was transferred to clean test-tubes. The samples were gelatinised and ultrafiltered as in procedure 3, frozen, and lyophilised.

Humic acid extraction

Humic solids were extracted from the retained waste NaOH solutions through the dropwise addition of approximately 200 µl of 6 M HCl. The solutions were mixed by gentle agitation. Over the next 30 minutes, a brown precipitate formed. The samples were centrifuged, and the supernatant removed. The precipitates were rinsed with deionized water, and left suspended in approximately 250 µl of water, then frozen and lyophilized. Only six of the waste NaOH solutions, all from the bones of marine consumers, produced sufficient humic solids for analysis.

Stable isotope analysis of bulk collagen and humic solids

Stable isotopes of carbon and nitrogen were measured in the collagen samples at BioArCh at the University of York. The samples (1 mg) were weighed in duplicate into tin capsules (4×3.2 mm, OEA labs, Cornwall) and combusted in a Sercon GSL Elemental Analyser coupled to a Sercon mass spectrometre. The raw isotope values were calibrated to the VPDB and AIR scales using international standards (Caffeine [IAEA 600] δ^{13}C: –27.8±0.1‰, δ^{15}N: +1.0±0.1‰; Cane sugar [IA-R006] δ^{13}C: –11.6±0.1‰; and IAEA-N-2 δ^{15}N: +20.3±0.2‰). Replicates of an internal fish gelatin standard (δ^{13}C: –15.2±0.1‰, δ^{15}N: +15.3±0.2‰) were run between every six samples to correct for instrumental drift. Three additional fish gelatin standards were used as check standards. The precision on replicate analyses of the samples was ±0.2‰ or better for δ^{13}C and δ^{15}N.

The humic solids were measured in the Stable Isotope Laboratory of the Department of Geological Sciences, Stockholm University. The samples (0.5 mg) were weighed in duplicate into tin capsules and combusted in a Carlo Erba NC2500 Elemental Analyser interfaced via ConFloIV to a Finnegan Delta V Advantage Mass Spectrometer. The raw isotope data were converted to the V-PDB (carbon) and AIR (nitrogen) scales using in-house calibration standards (Acetilimide 3 δ^{13}C: –27.1±0.1‰, δ^{15}N: +1.0±0.1‰; and Methionine δ^{13}C: –26.2±0.1‰, δ^{15}N: –2.2

±0.1‰;). Precision on duplicate analyses of the samples was ±0.1‰ for $\delta^{13}C$ and $\delta^{15}N$.

Amino acid concentrations and racemization

Chiral amino acid analyses were undertaken following the methods of High et al. (2015). Subsamples (1 mg) of collagen and humic substances extracted from the bone of a domestic sled dog were hydrolysed in 100 µL of 6 M HCl (110°C, 24 hrs), and analysed using a modified method of Kaufman and Manley (1998).

Compound specific carbon isotope analysis of collagen amino acids

Collagen hydrolysis

Collagen samples (1-2 mg) were hydrolysed (110°C, 24 h) in 200 µl of 6 M HCl with 50 µl of Norleucine (Sigma Aldrich). The hydrolysates were cooled to room temperature and filtered with Nanosep® filters (Pall, 0.45 µm) to remove contaminants. The filtrates were transferred to sterile vials and treated with a 3:2 mixture of *n*-hexane and dichloromethane (1 ml x 3) to remove lipids. The samples were dried under a gentle stream of N_2 at room temperature and stored at –18°C until required for derivatization.

Amino acid derivatisation for CSIA

Collagen amino acids were derivatised using the methods of Corr et al. (2007) as modified by Styring et al. (2015) and Philben et al. (2018). The hydrolysates were dissolved in ~100 µl of 0.1 M HCl, vortexed and transferred to a 15 ml Hach tube. The procedure was repeated two times to maximize the recovery of amino acids. The samples were dried under a gentle stream of N_2 at room temperature. Amino acids were esterified by heating (100°C, 60 min) with 1 ml of an acidified 2-propanol solution (4:1 2-propanol: acetyl chloride). The reaction was quenched at –18°C, then the reagent removed under a stream of N_2. The amino acid esters were redissolved twice in 300 µl of dichloromethane (DCM) to ensure removal of the derivatising reagents. The DCM was removed under a stream of N_2 at room temperature. The samples were then acetylated by heating (60°C, 10 min) with 1 ml of a solution of HPLC grade acetone, triethylamine, and acetic anhydride (5:2:1 v/v/v). The reaction was quenched at –18°C and the reagents removed under a stream of N_2. Phase separation was

achieved through the addition of 2 ml of ethyl acetate and 1 ml of a saturated salt solution to each sample. The samples were vortexed, and the organic phase transferred to a clean Hach tube. The procedure was repeated with 1 ml of ethyl acetate. Trace water was removed from each sample with molecular sieves (0.3 nm, Merck, Darmstadt, Germany). The samples were transferred to sterile 2 ml GC vials, and blown to dryness. The amino acid derivatives were dried with two successive additions of 1 ml of DCM. The samples were redissolved in ethyl acetate and aliquoted to sterile GC vials with fixed glass inserts. Samples were stored at –18°C until analysis. Each batch of derivatised samples included one mixture of international amino acid standards purchased from the University of Indiana and SHOKO Science, Japan (50 µl each of Glu, Asp, Hyp, Leu, Val, Gly, Phe, Ala, Nle), one blank containing 50 µl of Nle, and one in house mixture of amino acid standards purchased from Sigma Aldrich (Gillingham, UK) (50 µl each of Glu, Asp, Hyp, Leu, Ile, Val, Gly, Phe, Lys, Pro, Ser, Thr, Tyr, and Arg) that was used to calculate kinetic isotope effect correction factors.

GC-C-IRMS analysis

GC-C-IRMS measurements of the amino acids were conducted using a Delta V Plus isotope ratio mass spectrometer (Thermo Fisher, Bremen, Germany) linked to a Trace Ultra gas chromatograph (Thermo Fisher, Bremen, Germany) with a GC Isolink II interface fitted with a Cu/Ni combustion reactor maintained at 1000°C. Ultra-high-purity-grade helium with a flow rate of 1.4 mL min^{-1} was used as the carrier gas, and parallel acquisition of Flame Ionisation data was achieved by diverting a small part of the flow to an integrated FID (Thermo Fisher). Ethyl acetate was used to dilute the samples, and 1 µL of each sample and 2 µL of each standard were injected at 240°C with a 3.5 second pre-injection dwell time, onto two connected custom DB-35 fused-silica column (30 m × 0.32 mm × 0.50 µm; Agilent J&W Scientific technologies, Folsom, CA, USA). All samples were injected in triplicate. The oven temperature programme used for samples and standards was as follows: 40°C (hold 5 min) then increasing by 15ºC min^{-1} up to 120°C, then by 3°C min^{-1} up to 180°C, then by 1.5°C min^{-1} up to 210°C, then by 5°C min^{-1} up to 280°C (hold 8 min).

The eluted products were combusted to CO_2 and ionized in the mass spectrometer by electron impact. Ion intensities of *m/z* 44, 45, and 46 were monitored in order to automatically compute the $^{13}C/^{12}C$ ratio of each peak in the samples. Computations were made with Isodat (version 3.0; Thermo Fisher) and were based

on comparisons with a repeatedly measured high purity standard CO_2. The results from the analysis are reported in parts per mil (‰) relative to an international standard.

The amino acids were identified by the time at which each eluted from the column. Each run included a mixture of international AA standards and a mixture of inhouse AA standards, both with known isotopic values. The AA mixtures were first analysed alone to identify the peaks (Corr et al., 2007a). In runs that included samples, the AA mixtures bracketed the samples and were used to determine the kinetic isotope effect.

Kinetic Isotope Effect

The N-acetyl-i-propyl derivatization method is associated with a kinetic isotope effect (KIE); isotopically light carbon atoms from the derivatizing agents react non-quantitatively with collagen amino acids to alter the biogenic amino acid $\delta^{13}C$ value (Docherty et al., 2001). The KIE is consistent within a single batch of amino acid derivatives, therefore it is possible to calculate a correction factor for each amino acid using a mixture of amino acid standards with known isotopic values (Docherty et al., 2001). We calculated correction factors for each amino acid after Corr et al. (2007b) and Docherty et al. (2001) using a mixture of in-house amino acid standards (Sigma Aldrich). Each amino acid standard was measured offline using an EA-IRMS (BioArCh and SU) and then derivatized and measured using the GC-C-IRMS. We calculated the $\delta^{13}C$ value of the derivatizing agents using the equation:

$$n_d\delta^{13}C_d = n_{cd}\delta^{13}C_{cd} - n_c\delta^{13}C_c$$

Where n_d is the number of moles of carbon in the derivatizing agent, $\delta^{13}C_d$ is the $\delta^{13}C$ value of the derivatizing agent, n_{cd} is the number of moles of carbon in the derivatized amino acid, $\delta^{13}C_{cd}$ is the $\delta^{13}C$ value of the derivatized amino acid, n_c is the number of moles of carbon in the underivatized amino acid and $\delta^{13}C_c$ is the $\delta^{13}C$ value of the underivatized amino acid (measured offline).

Table 1 Sigma Aldrich amino acid mixture used as in-house standard for the calculation of $\delta^{13}C$ values of amino acid derivatives. EA-IRMS measurements undertaken at BioArCh (UY) and at the Geology Department of SU.

Amino acid	EA-IRMS $\delta^{13}C$ (‰)	SD	Correction factor	GC-C-IRMS $\delta^{13}C$ (‰)	SD
Ala	–19.3	0.02	–41.41	0.11	
Asp	–27.5	0.12	–38.23	0.16	
Glu	–28.6	0.09	–38.03	0.18	
Gly	–33.3	0.02	–40.57	0.19	
Hyp	–12.5	0.03	–48.73	0.23	
Ile	–24.9	0.07	–47.27	0.27	
Leu	–13.8	0.06	–52.00	0.13	
Lys	–13.7	0.11	–49.54	0.38	
Met	–29.9	0.14	–43.58	0.28	
Nle	–27.5	0.02	–44.67	0.19	
Phe	–11.5	0.05	–47.64	0.32	
Pro	–12.3	0.02	–43.16	0.19	
Ser	–12.5	0.09	–47.58	0.28	
Thr	–10.5	0.01	–49.00	0.19	
Tyr	–24.9	0.02	–50.39	0.24	
Val	–10.9	0.02	–46.76	0.15	

Analytical Error

The analytical error on carbon isotope ratio measurements of derivatized amino acids is considerably higher than measurements of underivatized compounds due to the numerous sources of uncertainty which must be quantified. We calculated analytical error on the GC-C-IRMS isotope ratio measurements by propagating the error across each step of the analytical procedure. This included the error on the EA-IRMS measurements of the in-house standards and the error on the GC-C-IRMS measurements of standards (Table 1) and samples.

Statistical analysis

All statistical analyses were conducted using SPSS v. 23 with the level of significance set to 0.05. Due to the small sample size and non-normal distribution of the data, the elemental and isotopic results of each pre-treatment were compared to the control using nonparametric Wilcoxon Signed Rank tests. The relationship of carbon and nitrogen concentrations produced by the control and each pre-treatment were evaluated using Spearman's Rho coefficient. The results were determined to be significant if the p-value was less than 0.05.

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SI Table 1. Stable isotope values and collagen quality indicators of experimental collagen samples

Lab ID	Species	Material	Procedure	% Collagen	%C	%N	C/N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
DMP33	*Pusa hispida*	Whole bone			9.9	2.3	5.08		
DMP33_1	*P. hispida*	Collagen	1	6.9	40.8	15.0	3.17	–13.1	+15.5
DMP33_2	*P. hispida*	Collagen	2	12.4	42.6	16.1	3.09	–13.4	+16.0
DMP33_3	*P. hispida*	Collagen	3	5.0	42.8	15.7	3.17	–13.2	+15.6
DMP33_4	*P. hispida*	Collagen	4	3.9	44.1	16.4	3.14	–13.3	+15.4
DMP29	*Rangifer tarandus*	Whole bone			12.0	2.5	5.62		
DMP29_1	*R. tarandus*	Collagen	1	16.7	44.4	15.8	3.27	–18.5	+2.9
DMP29_2	*R. tarandus*	Collagen	2	2.3	43.5	15.3	3.32	–18.7	+3.3
DMP29_3	*R. tarandus*	Collagen	3	6.2	43.5	15.8	3.21	–18.4	+2.9
DMP29_4	*R. tarandus*	Collagen	4	4.4	43.1	15.8	3.19	–18.2	+3.0
DMP29_8	*R. tarandus*	Humic solids	N/A		44.7	7.2	7.26	–22.3	+6.1
DMP32	*Pagophilus groenlandicus*	Whole bone			9.7	2.4	4.76		
DMP32_1	*P. groenlandicus*	Collagen	1	5.6	42.3	15.2	3.26	–14.2	+15.1
DMP32_2	*P. groenlandicus*	Collagen	2	3.3	38.4	14.4	3.11	–14.2	+15.2
DMP32_3	*P. groenlandicus*	Collagen	3	0.8	42.8	14.7	3.39	–14.5	+15.1
DMP32_4	*P. groenlandicus*	Collagen	4	1.1	39.3	14.3	3.21	–14.1	+14.9

DMP28	*R. tarandus*	Whole bone			17.9	4.3	4.96		
DMP28_1	*R. tarandus*	Collagen	1	6.3	42.9	15.6	3.20	–18.0	+2.1
DMP28_2	*R. tarandus*	Collagen	2	7.6	41.5	15.7	3.08	–17.8	+2.1
DMP28_3	*R. tarandus*	Collagen	3	3.7	43.8	16.0	3.20	–18.0	+2.1
DMP28_4	*R. tarandus*	Collagen	4	1.8	43.2	16.0	3.15	–17.7	+2.3
DMP21	*Canis familiaris*	Whole bone			17.6	3.8	5.41		
DMP21_1	*C. familiaris*	Collagen	1	5.7	41.0	14.1	3.40	–14.3	+18.1
DMP21_2	*C. familiaris*	Collagen	2	5.2	41.9	15.7	3.12	–13.6	+16.1
DMP21_3	*C. familiaris*	Collagen	3	0.7	44.0	13.9	3.70	–15.4	+18.0
DMP21_4	*C. familiaris*	Collagen	4	1.1	42.0	14.8	3.30	–13.8	+18.1
DMP21_5	*C. familiaris*	Humic solid			42.4	5.7	8.70	– 23.1	+20.1
DMP35	*P. hispida*	Whole bone			11.0	2.0	6.40		
DMP35_1	*P. hispida*	Collagen	1	3.5	38.4	13.5	3.31	–14.6	+15.4
DMP35_2	*P. hispida*	Collagen	2	5.1	40.1	14.8	3.16	–14.4	+15.8
DMP35_3	*P. hispida*	Collagen	3	1.7	41.7	13.9	3.51	–15.2	+15.5
DMP35_4	*P. hispida*	Collagen	4	2.2	42.3	15.4	3.21	–14.1	+15.5
DMP35_5	*P. hispida*	Humic solid			40.1	7.9	5.92	–19.4	+17.2
DMP35_9	*P. hispida*	Humic solid			40.1	8.0	5.90	–19.2	+17.6
DMP27	*R. tarandus*	Whole bone			15.8	4.1	4.54		
DMP27_1	*R. tarandus*	Collagen	1	12.0	43.9	16.1	3.18	–18.3	+3.3
DMP27_2	*R. tarandus*	Collagen	2	5.9	42.2	16.0	3.08	–18.5	+3.3

DMP27_3	*R. tarandus*	Collagen	3	9.5	44.7	16.3	3.20	–18.3	+3.4
DMP27_4	*R. tarandus*	Collagen	4	5.0	44.7	16.5	3.17	–18.5	+3.4
DMP38	*Erignathus barbatus*	Whole bone			15.0	3.3	5.33		
DMP38_1	*E. barbatus*	Collagen	1	7.5	43.6	15.4	3.29	–13.9	+14.7
DMP38_2	*E. barbatus*	Collagen	2	9.3	40.2	15.0	3.13	–13.5	+14.6
DMP38_3	*E. barbatus*	Collagen	3	0.8	44.0	12.9	3.97	–15.8	+15.0
DMP38_4	*E. barbatus*	Collagen	4	1.7	39.6	13.7	3.37	–13.9	+14.7
DMP38_5	*E.barbatus*	Humic solid			42.6	6.8	7.30	–20.4	+17.6
DMP17	*C. familiaris*	Whole bone			14.3	3.3	5.12		
DMP17_1	*C. familiaris*	Collagen	1	3.6	38.9	13.3	3.42	–14.4	+18.8
DMP17_2	*C. familiaris*	Collagen	2	2.7	35.1	12.9	3.17	–13.5	+19.1
DMP17_3	*C. familiaris*	Collagen	3	1.1	41.8	13.8	3.54	–14.5	+18.9
DMP17_4	*C. familiaris*	Collagen	4	2.3	40.8	14.9	3.19	–13.3	+18.9
DMP17_5	*C. familiaris*	Humic solid			39.3	6.3	7.26	–20.2	+20.6
DMP48	*P. hispida*	Whole bone			12.6	2.9	5.12		
DMP48_1	*P. hispida*	Collagen	1	3.0	37.7	13.6	3.24	–14.8	+15.4
DMP48_2	*P. hispida*	Collagen	2	7.2	42.8	16.1	3.11	–13.5	+16.0
DMP48_3	*P. hispida*	Collagen	3	1.9	42.6	14.9	3.34	–14.8	+15.5
DMP48_4	*P. hispida*	Collagen	4	0.5	41.5	14.9	3.26	–14.5	+15.5
HI14	*C. familiaris*	Whole bone			10.5	2.6	4.68		

HI14_1	*C. familiaris*	Collagen	1	2.9	37.2	13.0	3.33	–13.6	+19.2
HI14_2	*C. familiaris*	Collagen	2	6.3	37.5	14.1	3.11	–13.6	+19.5
HI14_3	*C. familiaris*	Collagen	3	0.5	41.9	13.9	3.53	–14.1	+19.3
HI14_4	*C. familiaris*	Collagen	4	0.7	No data				
DMP31	*P. groenlandicus*	Whole bone			13.0	3.5	4.33		
DMP31_1	*P.groenlandicus*	Collagen	1	6.5	41.1	15.2	3.15	–14.3	+16.0
DMP31_2	*P. groenlandicus*	Collagen	2	6.0	36.4	13.7	3.11	–14.6	+15.6
DMP31_3	*P. groenlandicus*	Collagen	3	2.6	42.9	15.5	3.23	–14.5	+15.7
DMP31_4	*P. groenlandicus*	Collagen	4	1.8	43.1	15.8	3.18	–14.4	+15.8
DMP31_5	*P. groenlandicus*	Humic solids			40.1	6.6	7.11	–21.1	+19.3

SI Table 2. Amino acid concentrations in three samples of collagen and a humic solid extracted from dog bone.

	DMP17 *Canis familiaris*			
Amino acid (ng/mg)	Control	NaOH	UF	Humic solid
Aspartic acid	357 (19)	476 (47)	361 (54)	162 (7)
Glutamic acid	581 (35)	773 (77)	590 (96)	177 (8)
Serine	250 (4)	315 (29)	240 (28)	89 (5)
L-Threonine	156 (9)	203 (21)	157 (22)	80 (3)
L-Histidine	43 (5)	41 (5)	37 (5)	20 (0)
Glycine	2751 (283)	2772 (9)	2228 (164)	576 (34)
L-Arginine	327 (36)	460 (54)	343 (68)	82 (1)
Alanine	875 (15)	1106 (105)	843 (92)	240 (12)
Tyrosine	14 (1)	14 (2)	11 (3)	14 (1)
Valine	186 (17)	249 (27)	188 (32)	98 (6)
Phenylalanine	104 (15)	146 (9)	107 (22)	49 (0)
Leucine	206 (16)	281 (30)	207 (34)	101 (3)
Isoleucine	94 (10)	132 (14)	98 (18)	53 (1)

SI Table 3. Amino acid composition of three samples of and humic solids extracted from dog bone.

	DMP17 *Canis familiaris*			
Amino aicd (%)	Control	NaOH	UF	Humic solid
Aspartic acid	6	7	7	9
Glutamic acid	10	11	11	10
Serine	4	5	4	5
Threonine	3	3	3	5
Histidine	1	1	1	1
Glycine	45	40	41	33
Arginine	6	7	6	5
Alanine	15	16	16	14
Tyrosine	0	0	0	1

Valine	3	4	3	6
Phenylalanine	2	2	2	3
Leucine	4	4	4	6
Isoleucine	2	2	2	3

SI Table 4. Amino acid D/L ratios in three samples of collagen and a humic solid extracted from dog bone.

	DMP17 *Canis familiaris*			
Amino acid D/L	Control	NaOH	UF	Humic solid
Aspartic acid	0.09	0.13	0.10	0.08
Glutamic acid	0.03	0.03	0.03	0.05
Serine	0.00	0.02	0.00	0.02
Alanine	0.02	0.02	0.02	0.05
Valine	0.02	0.03	0.02	0.02
Tyrosine	0.01	0.00	0.03	0.13
Phenylalanine	0.02	0.02	0.02	0.04
Leucine	0.02	0.02	0.01	0.00
Isoleucine	0.00	0.01	0.01	0.03

SI Table 5. Amino acid carbon isotope values from a samples of bearded seal collagen processed using 0.025 M NaOH.

	DMP38 Erignathus barbatus			
Amino acid	1	2	3	Average (analytical error)
Alanine	–14.33	–14.68	–14.99	–14.67 (0.44)
Glycine	+2.18	+1.65	+2.04	+1.96 (0.73)
Valine	–19.04	–19.16	–19.67	–19.29 (0.47)
Leucine	–18.34	–18.50	–18.69	–18.51 (0.32)
Isoleucine	–16.22	–15.49	–15.78	–15.83 (0.62)
Norleucine	–27.58	–27.43	–27.49	–27.50 (0.36)
Threonine	–8.27	–7.92	–8.21	–8.13 (0.57)
Serine	–3.34	–3.66	–3.11	–3.37 (0.98)
Proline	–13.96	–14.50	–14.57	–14.34 (0.52)

Aspartic acid	–15.69	–16.64	–16.29	–16.21 (0.68)
Glutamic acid	–13.75	–13.67	–14.38	–13.93 (0.61)
Hydroxyproline	–15.53	–15.68	–15.38	–15.53 (0.59)
Phenylalanine	–25.19	–25.08	–25.67	–25.31 (0.61)
Lysine	–13.65	–12.81	–12.43	–12.96 (1.05)
Mass balance	–11.0	–11.0	–11.1	–11.0 (0.1)
Measured Control				–13.9
Measured NaOH				–13.5
Measured UF				–15.8
Measured NaOH/UF				–13.9

Appendix 2

This file includes:
Supporting information file 1
Supporting information file 2
Supporting information file 3
Supporting tables 1 - 8

Supporting Information File 1: Site contexts and samples

The following document details the site contexts (1-4) and sampled skeletal elements (Table 1). Where possible, we sampled the same element to ensure that no dogs were sampled twice, but we also relied on element size and isotope values (SI Table 5) to distinguish individuals.

1. Double Mer Point

We sampled 22 dog and 25 wild animal skeletal elements from Houses 2 and 3, and the barrier between Houses 1 and 2 from Double Mer Point (GbBo-02). Eleven of the 22 samples were sufficiently well-preserved to observe tooth wear. Of the eleven, two dogs (DMP9 and DMP19), had teeth that were still in the process of erupting, while the root of the mandibular canine of another (DMP17) had not closed, placing age at death around the age of six months (Shabestari et al., 1967). Five other dogs had very minimal tooth wear, and the teeth of three others were sufficiently worn to expose the pulp chamber. If a relationship between age and dental attrition exists for sled dogs, as it does among grey wolves (Gipson et al., 2000), then over a third of the dogs likely died as juveniles. These findings are consistent with those of Woollett (2003), who observed a bimodal mortality curve among sled dogs at the Northern Labrador site of Uivak Point 1. Most sled dogs were either killed before the age of 18 months, or after they had reached the end of their working life, at five or six years of age (Woollett, 2003).

2. North Coast sites

Nachvak Village (IgCx-03) was an Inuit winter settlement occupied between the 15th and 17th centuries (Swinarton, 2008). The site lies 30km from the mouth of Nachvak Fiord, adjacent to a polynya that would have provided hunting access to seals during the winter (Swinarton, 2008; Whitridge, 2006). The remains of four of the approximately 14 sod, stone, and whale bone houses were excavated between 2003 and 2006. Few European artefacts were recovered during the excavation, suggesting that the site was primarily occupied during the precontact period (Whitridge, 2005). We sampled the long bones (predominantly humeri) of six dogs, and 16 skeletal elements from wild fauna from House 6, thought to be one of the earliest houses at the site, and from House 12, which may date to the 17th century (Swinarton, 2008).

Kongu, another winter village site, approximately 15km from Nachvak Village and closer to the mouth of the fiord, was occupied between the 18th century and mid-19th century (Whitridge, 2005; Swinarton, 2008). We obtained nine faunal, five domestic dog, and one dog/wolf samples (long bones and mandibles) from the East and West trenches which were excavated through the middens associated with three communal houses, and from the Centre trench, which was associated with the midden of a smaller featurethat may predate the construction of the communal houses (Elliott, 2017). While the faunal assemblages from Nachvak Village and Kongu were both dominated by marine mammal remains, a greater amount of fish and bird remains were recovered at Kongu, and a higher percentage of caribou bone was identified at Nachvak (Elliott, 2017; Swinarton, 2008).

Khernertok, or Black Island, is the location of two Inuit winter houses occupied during the 18th century. We sampled the long bones and cranial fragments of four dogs, 2 dog/wolves and nine faunal remains from the larger and earlier of the two houses, House 2, which is reported to have been occupied during the 1770s by the Inuit trader Mikak, and her husband Pualo (Fay, 2015). House 2 was first investigated by Taylor (1974), but not excavated until the summers of 2010 and 2011 (Fay, 2015). Ringed and harp seal composed the bulk of the recovered faunal remains, with smaller amounts of caribou, fox, domestic dog, and fish species (Swinarton, 2012).

3. South Coast sites

We obtained dog and faunal samples from two communal houses in Sandwich Bay: Huntingdon Island 5 (FkBg-3), and Pigeon Cove (FlBf-6). Huntingdon Island 5 is a winter house site occupied in the first half of the 18th century (Rankin 2015). We obtained one wolf sample from the midden associated with House 2, and 13 dog skeletal elements (mandibles and post-cranial elements) from the exterior middens associated with Houses 3 and 4 (Rankin, 2015). The single communal house at Pigeon Cove was occupied during the latter half of the 18th century and may have been the winter residence of a high-status trader, based on the large number of European artefacts recovered from the site (Rankin, 2015). We sampled eight wild fauna, including three wolves, in addition to four dog elements, and two dog/wolf elements.

4. Red Bay sites

Faunal specimens were selected from archaeological assemblages associated with a pair shipwrecks at Red Bay, believed to the galleon *San Juan* (24M), lost in 1565 (Grenier, 2001) as well as an smaller unnamed support vessel (28M) (Stevens, 1985). We sampled specimens from a variety of marine taxa including nine baleen whales, that were collected during underwater excavations carried out by Parks Canada during the early 1980s (Parks Canada, 1982; Ringer, 1983; Ringer, 1985; Stevens, 1985). These specimens are thought to derive from refuse associated with 16th century Basque whaling activities (Tuck & Grenier, 1981).

Table 1. A list of sampled canid skeletal elements and evidence for dog sledding.

Lab No.	Species	Context	Element	Evidence for dog sledding
Nachvak Village				
MARC 2024	*C. familiaris*	House 12	Innominate	Dog trace parts; sled parts (Elliott, 2017). Ethnographic report of large dog teams from Nachvak Fiord (Taylor, 1974).
MARC 2030	*C. familiaris*	House 12	R humerus	
MARC 2031	*C. familiaris*	House 12	L humerus	
MARC 2032	*C. familiaris*	House 6	L humerus	
MARC 2033	*C. familiaris*	House 6	R humerus	

MARC 2035	*C. familiaris*	House 6	R tibia	
Kongu				
MARC 2014	*C. familiaris*	Centre trench	L tibia	Dog trace parts; sled parts (Elliott, 2017) Ethnographic report of large dog teams from Nachvak Fiord (Taylor, 1974).
MARC 2015	*C. familiaris*	Centre trench	Humerus	
MARC 2010	*C. familiaris*	East trench	Mandible	
MARC 2017	*C. familiaris*	East trench	Mandible	
MARC 2009	*C. familiaris*	West trench	Ulna	
MARC 2008	Dog/wolf	West trench	Mandible	
Khernertok				
MARC 1991	*C. familiaris*	House 2	R tibia	Sled shoes (Fay, 2016)
MARC 2002	*C. familiaris*	House 2	R tibia	
MARC 2004	*C. familiaris*	House 2	L tibia	
MARC 2063	*C. familiaris*	House 2	R tibia	
MARC 1997	Dog/wolf	House 2	Vertebra	
MARC 2000	Dog/wolf	House 2	Cranium	
Pigeon Cove				
MARC 1922	*C. familiaris*	House 1	Femur	Sled shoes (Rankin, 2015)
MARC 1923	*C. familiaris*	House 1	Femur	
MARC 1931	*C. familiaris*	House 1	Humerus	
MARC 1934	*C. familiaris*	House 1	Bone fragment	
MARC 1929	Dog/wolf	House 1	Tibia	
MARC 1930	Dog/wolf	House 1	Tibia	
Double Mer Point				
DMP 01	*C. familiaris*	House 1/2 barrier	R mandible	Sled shoes (Bohms, 2018); trace buckles (Elliott, 2017)
DMP 02	*C. familiaris*	House 1/2 barrier	R mandible	

DMP 02c	*C. familiaris*	House 1/2 barrier	R mandibular canine
DMP 04	*C. familiaris*	House 1/2 barrier	L mandible
DMP 04c	*C. familiaris*	House 1/2 barrier	L mandibular canine
DMP 07	*C. familiaris*	House 2	L mandible
DMP 08	*C. familiaris*	House 2	L mandible
DMP 09	*C. familiaris*	House 2	R mandible
DMP 10	*C. familiaris*	House 2	L mandible
DMP 11	*C. familiaris*	House 2	Mandible
DMP 13	*C. familiaris*	House 2	Mandible
DMP 14	*C. familiaris*	House 2	R mandible
DMP 16	*C. familiaris*	House 2	R mandible
DMP 17	*C. familiaris*	House 3	L mandible
DMP 17c	*C. familiaris*	House 3	L mandibular canine
DMP 18	*C. familiaris*	House 3	Mandible
DMP 19	*C. familiaris*	House 3	L mandible
DMP 20	*C. familiaris*	House 3	L mandible
DMP 21	*C. familiaris*	House 3	R mandible
DMP 22	*C. familiaris*	House 3	R mandible
DMP 23	*C. familiaris*	House 3	Mandible
DMP 24	*C. familiaris*	House 3	R mandible
DMP 24c	*C. familiaris*	House 3	R mandibular canine
DMP 06	Dog/wolf	House 2	Mandible
DMP 12	Dog/wolf	House 2	L mandible
DMP 15	Dog/wolf	House 2	L mandible

Huntingdon Island 5				
HI01	*C. familiaris*	House 3	Vertebra	Dog trace buckles; Sled shoes (Rankin, 2015)
HI03	*C. familiaris*	House 3	L mandible	
HI07	*C. familiaris*	House 4	L mandible	
HI09	*C. familiaris*	House 4	Mandible	
HI10	*C. familiaris*	House 4	L mandible	
HI11	*C. familiaris*	House 4	R mandible	
HI12	*C. familiaris*	House 4	L mandible	
HI13	*C. familiaris*	House 4	L mandible	
HI14	*C. familiaris*	House 4	L mandible	
HI15	*C. familiaris*	House 4	L mandible	
HI16	*C. familiaris*	House 4	L mandible	
HI17	*C. familiaris*	House 4	L mandible	
HI02	Dog/wolf	House 3	Innominate	

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Supporting Information File 2. Standards and Instrumental Analyses

1. Terra Facility, Department of Earth Sciences, Memorial University of Newfoundland
The samples were tightly folded into tin capsules (7x7, Elemental Microanalysis, Southampton, UK) and combusted in a Carlo Erba NA 1500 Series elemental analyser coupled to a Delta V Plus mass spectrometer via a ConFloII interface. The following standards were used to convert the raw isotope measurements to δ values relative to the VPDB and AIR scales: IAEA-N-1, IAEA-N-2, D-Fructose, and MUN-CO-2 were included in the first two analytical sessions, and EDTA#2 was substituted for MUN-CO-2 in the third analytical session (Table 1). Analytical accuracy and precision were monitored with replicate analyses of a casein protein standard (Table 2). Mean calibration and check standard isotope values obtained over three analytical runs are presented in Table 3.

Table 1. Calibration standards included in three analytical runs at the TERRA Facility. EDTA #2 was only included in one run (11/07/2014).

Standard	Material	Accepted $\delta^{13}C$ (‰, VPDB)	Accepted $\delta^{15}N$ (‰, AIR)
IAEA-N-1	Ammonium sulphate		+0.43
IAEA-N-2	Ammonium sulphate		+20.32
D-Fructose	Sugar	–10.53	
MUN-CO-2	Calcium carbonate	–40.11	
EDTA #2	Tetracarboxylic acid	–40.38	–0.79

Table 2 Check standard used to monitor analytical accuracy and precision.

Standard	Material	Mean $\delta^{13}C$ (‰, VPDB)	Mean $\delta^{15}N$ (‰, AIR)
B2155	Casein	–27.03 ± 0.13	+5.97 ± 0.08

Table 3 Mean calibration and check standards as measured over three analytical runs.

Run date	Standard	N	Mean $\delta^{13}C$ (‰, VPDB)	Mean $\delta^{15}N$ (‰, AIR)
17/12/2013	IAEA-N-1	6		±0.13
20/12/2013	IAEA-N-1	6		±0.05

11/07/2014	IAEA-N-1	6		±0.02
17/12/2013	IAEA-N-2	6		±0.03
20/12/2013	IAEA-N-2	6		±0.08
11/07/2014	IAEA-N-2	6		±0.02
17/12/2013	D-Fructose	5	±0.06	
20/12/2013	D-Fructose	5	±0.19	
11/07/2014	D-Fructose	5	±0.05	
17/12/2013	MUN-CO-2	6	±0.05	
20/12/2013	MUN-CO-2	6	±0.15	
11/07/2014	EDTA #2	6	±0.04	
17/12/2013	B2155	4	–27.28 ±0.03	5.89 ±0.09
20/12/2013	B2155	4	–27.24 ±0.12	5.74 ±0.05
11/07/2014	B2155	4	–27.34 ±0.19	5.78 ±0.10

Measurement precision (the pooled standard deviation of all check and calibration standards) was ±0.11‰ for carbon (*df*=36) and ±0.07‰ for nitrogen (*df*=39). Analytical accuracy, using measurements of the check standard, B2155, was ±0.29 for the $\delta^{13}C$ measurements and ±0.20 for $\delta^{15}N$. Analytical uncertainty was not calculated for the samples run at Memorial University as no sample replicates were included in the analyses.

2. BioArCh, Department of Archaeology, University of York

Collagen samples (1 mg) were weighed in duplicate into tin capsules (4 mm x 3.2 mm, OEA labs, Callington, UK) and combusted in a Sercon GSL elemental analyser coupled to a 20-22 Sercon mass spectrometer in continuous flow (Sercon, Crewe, UK). The raw data were converted to the VPDB and AIR scales using an in-house fish gelatin standard, IAEA-N-2, IAEA-600, and Cane sugar (Table 4). Analytical accuracy and precision were monitored using an in-house fish gelatin standard (Table 5). The mean isotope values for check and calibration standards are presented in Table 6.

Table 4 Calibration standards included in one analytical run at BioArCh.

Standard	Material	Accepted $\delta^{13}C$ (‰, VPDB)	Accepted $\delta^{15}N$ (‰, AIR)

IAEA-600	Caffeine	–22.77	+1.00
IAEA-N-2	Ammonium sulphate		+20.30
CANE	Sugar	–11.64	

Table 5 Check standard used to monitor analytical accuracy and precision.

Standard	Material	Mean δ^{13}C (‰, VPDB)	Mean δ^{15}N (‰, AIR)
Fish gel	Fish gelatin	–15.32. ± 0.03	+15.2 ± 0.12

Table 6 Mean calibration and check standards as measured over one analytical run.

Run date	Standard	N	Mean $\delta^{13}C$ (‰, VPDB)	Mean $\delta^{15}N$ (‰, AIR)
14/02/2018	IAEA-600	3	±0.02	±0.08
	IAEA-N-2	3		±0.02
	CANE	3	±0.01	
	Fish gel	3	±0.02	±0.03

Measurement precision (the pooled standard deviation of all check and calibration standards) was ±0.02‰ for carbon (*df*=6) and ±0.06‰ for nitrogen (*df*=4). Analytical accuracy, using measurements of the check standard, Fish gel, was ±0.03 for the $\delta^{13}C$ measurements and ±0.13 for $\delta^{15}N$. Analytical uncertainty was calculated using replicate analyses of the collagen samples and was ±0.07‰ for carbon and ±0.20‰ for nitrogen.

3. Department of Anthropology, University of British Columbia

Collagen samples (0.5 mg) were tightly folded into tin capsules and combusted in an Elementar vario MICRO cube elemental analyser coupled to an Isoprime mass spectrometer in continuous flow mode. The raw data were converted to the VPDB and AIR scales using USGS-40 and USGS 41 (Table 7). Instrumental accuracy and precision were monitored using three in-house standards (Table 8). Mean calibration and check standard isotope values measured over one run are presented in Table 9).

Table 7 Calibration standards included in one analytical run at UBC

Standard	Material	Accepted $\delta^{13}C$ (‰, VPDB)	Accepted $\delta^{15}N$ (‰, AIR)
USGS40	Glutamic Acid	–26.39	–4.52
USGS41	Glutamic Acid	+36.55	+47.55

Table 8 In-house check standards used to monitor accuracy and precision.

Standard	Material	Mean $\delta^{13}C$ (‰, VPDB)	Mean $\delta^{15}N$ (‰, AIR)
MET	Methionine	–28.62	–5.03

SRM-1	Caribou bone collagen	–19.36	+1.81
SRM-2	Walrus bone collagen	–14.76	+15.59

Table 9 Mean calibration and check standards analysed during one run.

Run date	Standard	N	Mean δ^{13}C (‰, VPDB)	Mean δ^{15}N (‰, AIR)
06/08/2017	USGS40	10	±0.05	–4.52 ±0.12
06/08/2017	USGS41	9	±0.08	+47.55 ±0.34
06/08/2017	MET	8	–28.63 ±0.06	–4.95 ±0.05
06/08/2017	SRM-1	8	–19.44 ±0.07	+1.82 ±0.09
06/08/2017	SMR-2	6	–14.83 ±0.07	+15.59 ±0.14

Measurement precision (the pooled standard deviation of all check and calibration standards) was ±0.07‰ for carbon (*df*=36) and ±0.18‰ for nitrogen (*df*=36). Analytical accuracy, using measurements of three internal check standards, was ±0.12 for the δ^{13}C measurements and ±0.13 for δ^{15}N. Analytical uncertainty was calculated using replicate analyses of the collagen samples and was ±0.15‰ for carbon and ±0.23‰ for nitrogen.

4. IsoAnalytical, Crewe, UK

Collagen samples (1 mg) were tightly folded into tin capsules and combusted in a Europa Scientific elemental analyser coupled to a Europa Scientific 20-22 mass spectrometer. The raw isotope data were referenced to the VPDB and AIR scales using IA-R068 (Table 10). Analytical accuracy and precision were monitored using three check standards, IA-R069, IA-R038, and a mixture of IAEA-C7 and IA-R046 (Table 11). Mean calibration and check standards are presented in Table 12.

Table 10 Calibration standards included in one analytical run at IsoAnalytical

Standard	Material	Accepted δ^{13}C (‰, VPDB)	Accepted δ^{15}N (‰, AIR)
IA-R068	Soy protein	–25.22	+0.99

Table 11 In-house check standards used to monitor accuracy and precision.

Standard	Material	Mean $\delta^{13}C$ (‰, VPDB)	Mean $\delta^{15}N$ (‰, AIR)
IA-R069	Tuna protein	–18.88	+11.60
IA-R038	L-alanine	–24.99	–0.65
IA-R046*	Ammonium sulfate		+22.04
IAEA-C7*	Oxalic acid	–14.48	

*Combined

Table 12 Mean calibration and check standards analysed during one run.

Run date	Standard	N	Mean $\delta^{13}C$ (‰, VPDB)	Mean $\delta^{15}N$ (‰, AIR)
11/09/2017	IA-R068	12	±0.04	±0.02
	IA-R069	5	–18.86 ±0.03	+11.78 ±0.05
	IA-R038	5	–25.06 ±0.09	–0.50 ±0.04
	IA-R046/IAEAC7	5	–14.51 ±0.05	+21.88 ±0.07

Measurement precision (the pooled standard deviation of all check and calibration standards) was ±0.05‰ for carbon (*df*=23) and ±0.04‰ for nitrogen (*df*=23). Analytical accuracy and uncertainty were not calculated for the IsoAnalytical samples.

Supporting Information File 3: SIMMR model results

Table 1. Summary output from the SIMMR model featuring the 25% to 97.5% quantiles. Mean (±1SD) and median proportions are in bold.

Site	Food source	2.5%	25%	50%	75%	97.5%	Mean	SD
Nachvak Village	Marine Mammals	0.34	0.48	**0.55**	0.62	0.74	**0.55**	0.10
	Fish	0.07	0.22	**0.34**	0.44	0.61	**0.34**	0.15
	Caribou	0.02	0.07	**0.11**	0.16	0.25	**0.12**	0.06
Kongu	Marine Mammals	0.56	0.69	**0.74**	0.80	0.89	**0.74**	0.08
	Fish	0.03	0.10	**0.17**	0.25	0.39	**0.18**	0.10
	Caribou	0.02	0.05	**0.08**	0.11	0.18	**0.08**	0.04
Khernertok	Marine Mammals	0.48	0.62	**0.70**	0.76	0.86	**0.69**	0.10
	Fish	0.03	0.12	**0.21**	0.30	0.47	**0.22**	0.12
	Caribou	0.02	0.05	**0.08**	0.12	0.19	**0.10**	0.05
Double Mer Point	Marine Mammals	0.73	0.80	**0.83**	0.87	0.92	**0.83**	0.05
	Fish	0.02	0.08	**0.12**	0.17	0.24	**0.13**	0.06
	Caribou	0.01	0.03	**0.04**	0.06	0.09	**0.04**	0.02
Pigeon Cove	Marine Mammals	0.58	0.71	**0.77**	0.82	0.90	**0.76**	0.08
	Fish	0.03	0.09	**0.15**	0.23	0.37	**0.17**	0.09
	Caribou	0.01	0.04	**0.07**	0.10	0.16	**0.07**	0.04
Huntingdon Island 5	Marine Mammals	0.71	0.77	**0.83**	0.87	0.93	**0.83**	0.06
	Fish	0.02	0.07	**0.12**	0.17	0.26	**0.12**	0.07
	Caribou	0.01	0.03	**0.05**	0.07	0.11	**0.05**	0.03

SI Table 1 Calibration and check standards in use at BioArCh

Type of standard	N Calibration	N Calibration2	N Check	C Calibration	C Calibration 2	C Check
Standard name	IAEA 600	IAEA-N-2	Sigma fish gel	IAEA 600	IA CANE	Sigma fish gel
Analytical session	1	1	1	1	1	1
Known delta	1.0	20.3	15.2	-27.77	-11.64	-15.32
SD	0.2	0.2	0.12	0.04	0.03	0.03
Measured mean	0.91	20.49	15.15	-27.59	-11.72	-15.32
Measured SD	0.08	0.02	0.03	0.02	0.01	0.02
N	3	3	3	3	3	3
measured values	0.82	20.46	15.2	-27.61	-11.70	-15.31
	1.02	20.52	15.14	-27.56	-11.73	-15.29
	0.89	20.49	15.12	-27.59	-11.71	-15.34
Standard uncertainty	**0.198**			**0.071**		
Precision	**0.058**			**0.017**		
Accuracy	**0.13**			**0.03**		

SI Table 2 Calibration and check standards used at MUN

Type of standard	N Calib	N Calib 2	N Calib 6	N Calib 3	N Calib 4	N Calib 5	N Check	N Check2	N Check3	C Calib	C Calib2	C Calib3	C Calib4	C Calib5	C Calib6	C Check	C Check 2	C Check 3
Standard name	IAEA N-1	IAEA -N-2	IAEA -N-1	IAEA -N-2	IAEA -N-1	IAEA -N-2	B2155	B2155	B2155	D-Fructose	MUN-CO-2	D-Fructose	MUN-CO-2	D-Fructose	EDTA#2	B2155	B2155	B2155
Analytical session	1	1	2	2	3	3	1	2	3	1	1	2	2	3	3	1	1	1
Known delta	0.43	20.32	0.43	20.32	0.43	20.32	5.97	5.97	5.97	-10.53	-40.11	-10.53	-40.11	-10.53	-40.11	-27.03	-27.03	
SD	0.07	0.09	0.07	0.09	0.07	0.09	0.08	0.08	0.08	0.11	0.15	0.11	-0.15	0.11	-0.15	0.13	0.13	0.13
Measured mean	0.43	20.32	0.43	20.32	0.43	20.32	5.89	5.74	5.78	-10.54	-40.11	-10.55	-40.11	-10.54	-40.38	-27.28	-27.24	-27.34
Measured SD	0.12	0.03	0.05	0.08	0.02	0.02	0.09	0.05	0.1	0.06	0.05	0.19	0.15	0.05	0.04	0.03	0.12	0.19
N	6	6	6	6	6	6	4	4	4	5	6	5	6	5	6	4	4	4
measured values	0.23	20.31	0.36	20.26	0.42	20.33	5.99	5.72	5.86	-10.56	-40.16	-10.58	-40.06	-10.51	-40.4	-27.24	-27.13	-27.32
	0.48	20.34	0.49	20.35	0.46	20.34	5.91	5.81	5.87	-10.53	-40.09	-10.53	-40.15	-10.58	-40.38	-27.3	-27.37	-27.08
	0.61	20.31	0.48	20.27	0.41	20.28	5.78	5.75	5.68	-10.49	-40.07	-10.82	-40.21	-10.46	-40.34	-27.31	-27.32	-27.52

	0.39	20.29	0.42	20.46	0.45	20.34	5.86	5.69	5.69	-10.62	-40.19	-10.29	-39.88	-10.56	-40.37	-27.26	-27.15	-27.42
	0.37	20.38	0.4	20.34	0.44	20.32				-10.48	-40.08	-10.54	-40.31	-10.57	-40.45			
	0.5	20.29	0.44	20.25	0.41	20.31					-40.07		-40.05		-40.35			
Standard uncertainty																		
Precision	**0.058**									**0.11**								
Accuracy	**0.13**									**0.29**								

SI Table 3 Check and calibration standards used at UBC

Type of standard	N Calibration	N Calibration2	N Check	N Check2	N Check3	C Calibration	C Calibration2	C Check	C Check 2	C Check 3
Standard name	USGS40	USGS41a	MET	SRM-1	SRM-2	USGS40	USGS41a	MET	SRM-1	SRM-2
Analytical session	CN17-08	CN17-08	CN17-08	CN17-08	CN17-08	CN17-08	CN17-08	CN17-08	CN17-08	CN17-08
Known delta	-4.52	47.55	-5.03	1.81	15.59	-26.39	36.55	-28.62	-19.36	-14.76
SD	0.06	0.06	0.12	0.12	0.12	0.04	0.08	0.10	0.11	0.12
Measured mean	-4.52	47.55	-4.95	1.82	15.59	-26.39	36.55	-28.63	-19.44	-14.83
Measured SD	0.12	0.34	0.05	0.09	0.14	0.05	0.08	0.06	0.07	0.07
N	10.00	9.00	8	8	6	10.00	9.00	8.00	8.00	6.00
measured values	-4.42	47.98	-4.90	1.90	15.77	-26.35	36.60	-28.67	-19.50	-14.83
	-4.40	47.93	-4.87	1.89	15.68	-26.39	36.52	-28.59	-19.39	-14.77
	-4.46	47.33	-4.93	1.86	15.65	-26.35	36.49	-28.71	-19.38	-14.75
	-4.42	47.71	-4.96	1.89	15.50	-26.34	36.64	-28.58	-19.37	-14.83
	-4.48	47.44	-4.95	1.66	15.39	-26.35	36.66	-28.55	-19.38	-14.83
	-4.67	47.87	-4.99	1.83	15.55	-26.38	36.58	-28.57	-19.41	-14.95
	-4.49	47.49	-5.02	1.85		-26.39	36.56	-28.65	-19.52	
	-4.79	47.06	-4.94	1.71		-26.40	36.50	-28.70	-19.56	
	-4.58	47.14				-26.44	36.40			
	-4.48					-26.52				
Standard uncertainty	**0.228**									
Precision	**0.184**									
Accuracy	**0.131**									

SI Table 4 Check and calibration standards used at IsoAnalytical

Type of standard	**N Calibration**	**N Check**	**N Check2**	**N Check3**	**C Calibration 2**	**C Check**	**C Check2**	**C Check3**
Standard name	IA-R068	IA-R038	IA-R069	IA-R046/IAEA-C7	IA-R068	IA-R038	IA-R069	IA-R046/IAEA-C7
Analytical session	1	1	1	1	1	1	1	1
Known delta	0.99	-0.65	11.6	22.04	-25.22	-24.99	-18.88	-14.48
SD								
Measured mean	0.99	-0.5	11.78	21.88	-25.23	-25.06	-18.86	-14.51
Measured SD	0.02	0.04	0.05	0.07	0.04	0.09	0.03	0.05
N	12	5	5	5	12	5	5	5
measured values	1.00	-0.53	11.83	21.88	-25.26	-24.92	-18.87	-14.50
	0.97	-0.47	11.74	22.01	-25.26	-25.12	-18.83	-14.45
	1.00	-0.46	11.74	21.86	-25.18	-25.08	-18.85	-14.49
	0.99	-0.49	11.75	21.84	-25.28	-25.15	-18.84	-14.57
	1.02	-0.54	11.82	21.82	-25.20	-25.03	-18.91	-14.56
	1.00				-25.22			
	0.97				-25.29			
	0.99				-25.18			
	1.02				-25.18			
	0.98				-25.24			
	0.98				-25.19			
	0.97				-25.23			
Standard uncertainty								

Precision	**0.042**		**0.047**
Accuracy			

SI Table 5 BioArCh sample replicates

Sample replicates	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
AH_Bov_Coll	6.59	-23.03
	6.53	-22.99
Mean	6.57	-23.12
SD	0.17	0.04
Dog1	19.57	-13.11
	19.56	-13.07
Mean	19.39	-13.04
SD	0.19	0.04
Dog2	20.77	-12.57
	20.88	-12.60
Mean	20.63	-12.52
SD	0.21	0.03
Dog3	19.17	-13.13
	19.17	-13.19
Mean	19	-13.11
SD	0.19	0.04
Dog4	20.96	-13.61
	20.89	-13.71
Mean	20.72	-13.62
SD	0.21	0.06

SI table 6 UBC sample replicates

Sample replicates	**δ15N (‰)**	**δ13C (‰)**
2602	18.09	-13.84
	18.15	-13.77
Mean	18.12	-13.81
SD	0.04	0.05
2614	17.45	-13.50
	17.5	-13.40
Mean	17.48	-13.44
SD	0.04	0.05

SI Table 6 Isoanalytical sample replicates

Sample replicates	δ15N (‰)	δ13C (‰)
DMP 04	19.6327	-12.6373
	19.6441	-12.5085
Mean	19.6384	-12.5729
SD	0.00806102	0.09107535
DMP10	19.4286	-14.5918
	19.3377	-14.6775
Mean	19.38	19.38
SD	0.06	0.06
DMP12	18.99	-13.1218
	18.93	-13.0213
Mean	18.96	-12.52
SD	0.04	0.03
DMP15	17.5825	-13.31
	17.6101	-13.27
Mean	17.6	-13.29
SD	0.02	0.03
DMP20	18.2171	-13.2779
	18.2017	-13.2506
Mean	18.21	-13.26
SD	0.01	0.02
DmP24	18.0386	-13.0845
	18.0055	-13.0913
Mean	18.02	-13.09
SD	0.02	0
DMP30	15.3267	-14.8653
	15.3352	-14.8388
Mean	15.33	-14.85
SD	0.01	0.02
DMP36	15.6833	-13.776
	15.6911	-13.7646

Mean	15.69	-13.77
SD	0.01	0.01
DMP42	17.7464	-13.7455
	17.7784	-13.7574
Mean	17.76	-13.75
SD	0.02	0.01
DMP44	19.6724	-14.3722
	19.7233	-14.2791
Mean	19.7	-14.33
SD	0.04	0.07
DMP47	13.6189	-14.5
	13.7147	-14.5
Mean	13.67	-14.5
SD	0.07	0
DMP52	16.9335	-13.32
	16.8197	-13.31
Mean	16.88	-13.31
SD	0.08	0.01
HI03	14.9729	-16.6279
	15.1784	-16.6044
Mean	15.08	-16.62
SD	0.15	0.02
HI10	19.3651	-12.8547
	19.4185	-12.7544
Mean	19.39	-12.8
SD	0.04	0.07
HI13	18.274	-13.3883
	18.3066	-13.3306
Mean	18.29	-13.36
SD	0.02	0.04
HI16	19.2856	-13.1721
	19.3007	-13.1869
Mean	19.29	-13.18

SD	0.01	0.01

SI Table 7 Stable isotope values and collagen quality indicators of domestic dogs and 'dog/wolves' from Labrador, Canada

Lab ID	Site	Species	Dwelling type	Context	Date	Bone	% collagen	%C	%N	C/N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
MARC_2024	Nachvak Village	*C. familiaris*	Single family house?	House 12	1450 - 1700	Innominate	18.0	44.6	15.5	3.40	-14.6	+14.6
MARC_2030	Nachvak Village	*C. familiaris*	Single family house?	House 12	1450 - 1700	Right Humerus	20.4	45.5	15.8	3.36	-14.2	+16.0
MARC_2031	Nachvak Village	*C. familiaris*	Single family house?	House 12	1450 - 1700	Left Humerus	16.9	42	14.6	3.36	-13.9	+17.3
MARC_2032	Nachvak Village	*C. familiaris*	Single family house?	House 6	1450 - 1700	Left Humerus	12.7	46	16	3.35	-14.1	+17.3
MARC_2033	Nachvak Village	*C. familiaris*	Single family house?	House 6	1450 - 1700	Right Humerus	14.6	44.5	15.6	3.33	-14.1	+17.2
MARC_2035	Nachvak Village	*C. familiaris*	Single family house?	House 6	1450 - 1700	Right Tibia	22.3	43.4	15.3	3.31	-14.3	+16.5
MARC_2014	Kongu	*C. familiaris*	Feature - kashim?	Centre trench	~1700 - mid-1800s	Left Tibia	14.6	47.0	16.3	3.36	-13.9	+17.2
MARC_2015	Kongu	*C. familiaris*	Feature - kashim?	Centre trench	~1700 - mid-1800s	Humerus	17.4	44.7	15.1	3.45	-14.4	+16.6
MARC_2010	Kongu	*C. familiaris*	Communal house	East trench	~1700 - mid-1800s	Mandible	14.3	43.7	15.4	3.31	-13.0	+18.3
MARC_2017	Kongu	*C. familiaris*	Communal house	East trench	~1700 - mid-1800s	Mandible	19.5	44.7	16.2	3.22	-12.7	+18.2
MARC_2009	Kongu	*C. familiaris*	Communal house	West trench	~1700 - mid-1800s	Ulna	18.2	46.5	15.8	3.43	-13.5	+17.3
MARC_2008	Kongu	Dog/wolf	Communal house	East trench	~1700 - mid-1800s	Mandible	16.8	45.8	16.2	3.30	-13.1	+18.6

MARC_1991	Khernertok	*C. familiaris*	Communal house	House 2	Late 1700s	Right Tibia	16.6	45.0	15.9	3.30	-13.7	+16.5
MARC_2002	Khernertok	*C. familiaris*	Communal house	House 2	Late 1700s	Right Tibia	11.7	44.6	15.9	3.27	-13.2	+17.5
MARC_2004	Khernertok	*C. familiaris*	Communal house	House 2	Late 1700s	Left Tibia	16.8	45.7	15.9	3.35	-13.4	+16.7
MARC_2063	Khernertok	*C. familiaris*	Communal house	House 2	Late 1700s	Right Tibia	10.2	44.9	16.1	3.25	-13.4	+16.6
MARC_1997	Khernertok	Dog/wolf	Communal house	House 2	Late 1700s	Vertebra	18.9	47.5	17.1	3.24	-13.1	+18.4
MARC_2000	Khernertok	Dog/wolf	Communal house	House 2	Late 1700s	Cranium	18.5	46.0	16.3	3.29	-19.9	+5.6
MARC_1922	Pigeon Cove	*C. familiaris*	Communal house	House 1	Mid - Late 1700s	Femur	10.1	45.3	15.8	3.34	-13.8	+19.2
MARC_1923	Pigeon Cove	*C. familiaris*	Communal house	House 1	Mid - Late 1700s	Femur	8.2	41.7	14.7	3.31	-13.2	+18.7
MARC_1931	Pigeon Cove	*C. familiaris*	Communal house	House 1	Mid - Late 1700s	Humerus	16.2	46.7	16.7	3.26	-13.1	+18.8
MARC_1934	Pigeon Cove	*C. familiaris*	Communal house	House 1	Mid - Late 1700s	Fragment	10.2	40.6	14.1	3.36	-13.7	+18.3
MARC_1929	Pigeon Cove	Dog/wolf	Communal house	House 1	Mid - Late 1700s	Tibia	13.1	44.9	15.1	3.47	-13.8	+17.5
MARC_1930	Pigeon Cove	Dog/wolf	Communal house	House 1	Mid - Late 1700s	Tibia	11.8	46.3	16.1	3.36	-14.4	+17.6
DMP01	Double Mer	*C. familiaris*	Communal house	House 1/2 barrier	Mid-1700s to early 1800s	Right Mandible	15.6	46.0	16.8	3.20	-13.6	+18.1
DMP02	Double Mer	*C. familiaris*	Communal house	House 1/2 barrier	Mid-1700s to early 1800s	Right Mandible	5.4	43.7	16.3	3.14	-12.4	+20.5

DMP02c	Double Mer	*C. familiaris*	Communal house	House barrier	1/2	Mid-1700s to early 1800s	Right mandibular canine	22.7	44.4	16.2	3.20	-13.1	+19.0
DMP04	Double Mer	*C. familiaris*	Communal house	House barrier	1/2	Mid-1700s to early 1800s	Left Mandible	6.1	43.8	16.5	3.10	-12.6	+19.6
DMP04c	Double Mer	*C. familiaris*	Communal house	House barrier	1/2	Mid-1700s to early 1800s	Left mandibular canine	21.3	42.1	15.4	3.19	-12.5	+20.6
DMP07	Double Mer	*C. familiaris*	Communal house	House 2		Mid-1700s - early 1800s	Left Mandible	3.4	38.1	14.5	3.07	-13.1	+17.9
DMP08	Double Mer	*C. familiaris*	Communal house	House 2		Mid-1700s - early 1800s	Left Mandible	8.5	35.0	13.2	3.10	-13.3	+17.7
DMP09	Double Mer	*C. familiaris*	Communal house	House 2		Mid-1700s - early 1800s	Right Mandible	2.8	40.9	15.2	3.13	-13.0	+19.1
DMP10	Double Mer	*C. familiaris*	Communal house	House 2		Mid-1700s - early 1800s	Left Mandible	2.1	35.1	11.1	3.69	-14.6	+19.4
DMP11	Double Mer	*C. familiaris*	Communal house	House 2		Mid-1700s - early 1800s	Mandible	3.5	39.6	14.5	3.18	-15.6	+14.2
DMP13	Double Mer	*C. familiaris*	Communal house	House 2		Mid-1700s - early 1800s	Mandible	1.3	Not measured				
DMP14	Double Mer	*C. familiaris*	Communal house	House 2		Mid-1700s - early 1800s	Right Mandible	1.1	33.5	12.2	3.21	-13.8	+17.0
DMP16	Double Mer	*C. familiaris*	Communal house	House 2		Mid-1700s - early 1800s	Right Mandible	5.5	39.2	14.9	3.07	-12.7	+18.3
DMP17	Double Mer	*C. familiaris*	Communal house	House 3		Mid-1700s - early 1800s	Left Mandible	2.7	35.1	12.9	3.17	-13.5	+19.1
DMP17c	Double Mer	*C. familiaris*	Communal house	House 3		Mid-1700s - early 1800s	Left mandibular canine	22.5	45.6	16.0	3.33	-13.6	+20.7

DMP18	Double Mer	*C. familiaris*	Communal house	House 3	Mid-1700s - early 1800s	Mandible	7.8	38.9	14.5	3.13	-13.0	+18.7
DMP19	Double Mer	*C. familiaris*	Communal house	House 3	Mid-1700s - early 1800s	Left Mandible	4.4	37.9	12.5	3.55	-14.7	+18.6
DMP20	Double Mer	*C. familiaris*	Communal house	House 3	Mid-1700s - early 1800s	Left Mandible	4.7	40.8	15.3	3.11	-13.3	+18.2
DMP21	Double Mer	*C. familiaris*	Communal house	House 3	Mid-1700s - early 1800s	Right Mandible	5.2	41.9	15.7	3.12	-13.6	+16.1
DMP22	Double Mer	*C. familiaris*	Communal house	House 3	Mid-1700s - early 1800s	Right Mandible	3.4	37.4	13.9	3.14	-13.1	+18.2
DMP23	Double Mer	*C. familiaris*	Communal house	House 3	Mid-1700s - early 1800s	Mandible	4.6	40.3	14.4	3.27	-13.7	+18.4
DMP24	Double Mer	*C. familiaris*	Communal house	House 3	Mid-1700s - early 1800s	Right Mandible	7.0	43.1	16.2	3.10	-13.1	+18.0
DMP24c	Double Mer	*C. familiaris*	Communal house	House 3	Mid-1700s - early 1800s	Right mandibular canine	22.5	41.9	15.4	3.17	-13.0	+19.4
DMP06	Double Mer	Dog/wolf	Communal house	House 2	Mid-1700s - early 1800s	Mandible	2.6	38.8	14.4	3.15	-12.4	+21.3
DMP12	Double Mer	Dog/wolf	Communal house	House 2	Mid-1700s - early 1800s	Left Mandible	3.7	40.7	15.1	3.15	-13.1	+19.0
DMP15	Double Mer	Dog/wolf	Communal house	House 2	Mid-1700s - early 1800s	Left Mandible	15.2	40.1	14.9	3.13	-13.3	+17.6
HI01	Huntingdon Island	*C. familiaris*	Communal house	House 3	Early to mid-1700s	Vertebra	3.6	37.8	12.3	3.58	-16.7	+13.9
HI03	Huntingdon Island	*C. familiaris*	Communal house	House 3	Early to mid-1700s	Left Mandible	1.9	29.8	9.2	3.78	-16.6	+15.1
HI07	Huntingdon Island	*C. familiaris*	Communal house	House 4	Early to mid-1700s	Left Mandible	5.5	42.1	16.7	2.93	-13.2	+18.2

HI09	Huntingdon Island	*C. familiaris*	Communal house	House 4	Early to mid-1700s	Mandible	3.5	40.2	15.6	3.00	-12.9	+17.6
HI10	Huntingdon Island	*C. familiaris*	Communal house	House 4	Early to mid-1700s	Left Mandible	8.8	44.8	17.4	3.00	-12.9	+19.4
HI11	Huntingdon Island	*C. familiaris*	Communal house	House 4	Early to mid-1700s	Right Mandible	3.0	33.8	11.6	3.40	-14.9	+19.3
HI12	Huntingdon Island	*C. familiaris*	Communal house	House 4	Early to mid-1700s	Left Mandible	3.2	42.0	16.7	2.94	-13.2	+19.5
HI13	Huntingdon Island	*C. familiaris*	Communal house	House 4	Early to mid-1700s	Left Mandible	11.0	42.8	17.0	2.94	-13.4	+18.3
HI14	Huntingdon Island	*C. familiaris*	Communal house	House 4	Early to mid-1700s	Left Mandible	6.3	37.5	14.1	3.11	-13.6	+19.5
HI15	Huntingdon Island	*C. familiaris*	Communal house	House 4	Early to mid-1700s	Left Mandible	3.6	42.4	16.4	3.01	-13.6	+17.9
HI16	Huntingdon Island	*C. familiaris*	Communal house	House 4	Early to mid-1700s	Left Mandible	8.7	39.9	15.2	3.07	-13.2	+19.3
HI17	Huntingdon Island	*C. familiaris*	Communal house	House 4	Early to mid-1700s	Left Mandible	2.0	39.0	15.3	2.97	-13.1	+19.4
HI02	Huntingdon Island	Dog/wolf	Communal house	House 3	Early to mid-1700s	Innominate	10.0	42.0	15.2	3.22	-14.0	+19.1

SI Table 8 Stable isotope values and collagen quality indicators of wild Labrador fauna

Lab ID	Site	Species	Common name	Bone	% Collagen	% C	% N	C/N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
MARC_2023	Nachvak Village	*Lagopus* sp.	Ptarmigan sp.	Cranium	17.6	45.7	16.2	3.29	-20.5	+1.2
MARC_2028	Nachvak Village	*Rangifer tarandus*	Caribou	Innominate	18.3	46.6	16.1	3.38	-18.2	+2.0
MARC_2027	Nachvak Village	*Baleinidae* sp.	Bowhead/Atlantic Right whale	Vertebra	18.9	44.6	16.1	3.23	-14.3	+11.9
MARC_2029	Nachvak Village	*Ursus maritimus*	Polar bear	Ulna	21.0	44.7	16.4	3.18	-12.7	+19.7

MARC_2290	Nachvak Village	*Pagophilus groenlandicus*	Harp seal	element not recorded	4.6	38.1	12.4	3.58	-15.3	+16.9
MARC_2301	Nachvak Village	*Pagophilus groenlandicus*	Harp seal	element not recorded	11.3	46.2	16.4	3.29	-14.0	+15.9
MARC_2293	Nachvak Village	*Pusa hispida*	Ringed seal	element not recorded	19.5	46.2	16.4	3.29	-13.6	+13.8
MARC_2297	Nachvak Village	*Pusa hispida*	Ringed seal	element not recorded	16.4	45.5	16.2	3.28	-13.6	+16.6
MARC_2298	Nachvak Village	*Pusa hispida*	Ringed seal	element not recorded	10.8	43.3	15.4	3.28	-14.0	+14.0
MARC_2291	Nachvak Village	*V. vulpes*	Red fox	element not recorded	17.9	45.7	16.2	3.30	-18.8	+6.9
MARC_2292	Nachvak Village	*V. vulpes*	Red fox	element not recorded	11.8	45.8	15.7	3.41	-19.6	+5.9
MARC_2300	Nachvak Village	*V. vulpes*	Red fox	element not recorded	9.6	40.1	13.8	3.39	-17.4	+10.1
MARC_2038	Nachvak Village	*V. vulpes*	Red fox	element not recorded	16.2	44.8	15.6	3.35	-19.4	+6.3
MARC_2034	Nachvak Village	*Vulpes* sp.	Fox sp.	Right Tibia	19.9	45.9	16.6	3.23	-19.7	+5.3
MARC_2037	Nachvak Village	*V. vulpes*	Red fox	Left Mandible	19.2	44.6	16.2	3.21	-18.7	+7.0
MARC_2299	Nachvak Village	*V. lagopus*	Arctic fox	element not recorded	19	45.4	16.4	3.23	-19.8	+4.7
MARC_2007	Kongu	*Odobenus rosmarus*	Walrus	Ulna	21.0	42.7	15.5	3.21	-13.3	+11.2
MARC_2011	Kongu	*Eider* sp.	Eider sp.	Coracoid	12.7	45.7	15.5	3.44	-13.3	+15.8
MARC_2020	Kongu	*Pusa hispida*	Ringed seal	Femur	11.8	44.7	15.0	3.48	-14.4	+14.4
MARC_2294	Kongu	*Pusa hispida*	Ringed seal	auditory bulla	14.8	46.4	15.8	3.43	-14.6	+15.6

MARC_2022	Kongu	*Pagophilus groenlandicus*	Harp seal	Ulna	16.1	43.6	15.1	3.37	-15.0	+16.2
MARC_2295	Kongu	*Pagophilus groenlandicus*	Harp seal	auditory bulla	17.3	47.7	16.9	3.29	-14.1	+17.3
MARC_2060	Kongu	*E. barbatus*	Bearded seal	Femur	13.2	42.1	15.1	3.25	-13.0	+16.0
MARC_2061	Kongu	*Rangifer tarandus*	Caribou	Fragment	16.8	46.5	15.8	3.43	-19.2	+2.3
MARC_2013	Kongu	*Lepus* sp.	Hare sp.	Innominate	24.8	44.0	15.4	3.33	-21.4	+1.3
MARC_1992	Khernertok	*Alle alle*	Dovekie	Scapula	17.1	45.6	15.5	3.43	-17.3	+14.9
MARC_1995	Khernertok	*Alle alle*	Dovekie	Long bone	7.4	43.2	15.0	3.36	-16.6	+14.9
MARC_1994	Khernertok	*Uria aalge*	Murre	Humerus	16.4	46.4	16.5	3.28	-15.5	+16.6
MARC_2001	Khernertok	*Eider* sp.	Eider sp.	Cranium	15.3	45.4	15.6	3.40	-14.5	+15.3
MARC_2006	Khernertok	*Myxocepphallus*	Sculpin sp.	Fragment	12.9	46.0	16.6	3.23	-12.9	+16.6
MARC_2005	Khernertok	*Lepus* sp.	Hare sp.	Femur	12.7	43.9	15.2	3.37	-20.7	+0.9
MARC_1998	Khernertok	*Rangifer tarandus*	Caribou	Rib	22.9	46.9	16.5	3.32	-18.3	+1.6
MARC_1993	Khernertok	*V. lagopus*	Arctic fox	Mandible	17.1	47.5	16.7	3.32	-17.8	+7.8
MARC_2003	Khernertok	*V. vulpes*	Red fox	Tibia	9.6	44.1	15.7	3.28	-19.7	+3.3
MARC_1928	Pigeon Cove	*Erignathus barbatus*	Bearded seal	Humerus	20.2	48.3	17.2	3.28	-13.5	+15.0
MARC_1919	Pigeon Cove	*Gulo gulo*	Wolverine	Mandible	12.9	43.1	15.1	3.33	-18.9	+8.9
MARC_1924	Pigeon Cove	*Branta canadensis*	Canada goose	Humerus	14.3	43.7	15.1	3.38	-14.9	+8.8
MARC_1932	Pigeon Cove	*Rangifer tarandus*	Caribou	Long bone fragment	17.5	45.0	16.0	3.28	-18.2	+2.1
MARC_1918	Pigeon Cove	*C. lupus*	Grey Wolf	Mandible	11.1	46.2	15.5	3.48	-17.6	+8.8
MARC_2062	Pigeon Cove	*C. lupus*	Grey Wolf	Mandible	13.8	44.7	15.8	3.30	-18.8	+7.1
MARC_1926	Pigeon Cove	*C. lupus*	Grey Wolf	Mandible	14.6	46.5	16.6	3.27	-18.5	+7.0
MARC_1920	Pigeon Cove	*V. lagopus*	Arctic fox	Ulna	11.6	44.0	15.6	3.29	-17.1	+10.4
DMP26	Double Mer Point	*Rangifer tarandus*	Caribou	Long bone fragment	2.0	37.3	13.7	3.17	-18.0	+3.4

DMP27	Double Point	Mer	*Rangifer tarandus*	Caribou	Rib	5.9	42.2	16.0	3.08	-18.5	+3.3
DMP28	Double Point	Mer	*Rangifer tarandus*	Caribou	Skull	7.6	41.5	15.7	3.08	-17.8	+2.1
DMP29	Double Point	Mer	*Rangifer tarandus*	Caribou	Rib	2.3	43.5	15.3	3.32	-18.7	+3.3
DMP30	Double Point	Mer	*Pagophilus groenlandicus*	Harp seal	Left humerus	8.4	40.9	15.5	3.08	-14.9	+15.3
DMP31	Double Point	Mer	*Pagophilus groenlandicus*	Harp seal	Left humerus	6.0	36.4	13.7	3.11	-14.6	+15.6
DMP32	Double Point	Mer	*Pagophilus groenlandicus*	Harp seal	Right humerus	3.3	38.4	14.4	3.11	-14.2	+15.2
DMP46	Double Point	Mer	*Pagophilus groenlandicus*	Harp seal	Right mandible	13.3	40.7	15.2	3.13	-14.6	+14.3
DMP47	Double Point	Mer	*Pagophilus groenlandicus*	Harp seal	Left humerus	9.7	38.9	14.6	3.10	-14.5	+13.7
DMP33	Double Point	Mer	*Pusa hispida*	Ringed seal	Right humerus	12.4	42.6	16.1	3.09	-13.4	+16.0
DMP34	Double Point	Mer	*Pusa hispida*	Ringed seal	Right humerus	10.4	42.1	15.9	3.09	-13.3	+15.4
DMP35	Double Point	Mer	*Pusa hispida*	Ringed seal	Humerus	5.1	40.1	14.8	3.16	-14.4	+15.8
DMP36	Double Point	Mer	*Pusa hispida*	Ringed seal	Humerus	10.5	40.6	15.3	3.09	-13.8	+15.7
DMP37	Double Point	Mer	*Pusa hispida*	Ringed seal	Right humerus	11.6	40.2	15.1	3.11	-13.7	+16.9
DMP48	Double Point	Mer	*Pusa hispida*	Ringed seal	Left humerus	7.2	42.8	16.1	3.11	-13.5	+16.0

DMP49	Double Point	Mer	*Pusa hispida*	Ringed seal	Right humerus	5.4	42.7	16.0	3.12	-12.5	+17.0
DMP38	Double Point	Mer	*Erignathus barbatus*	Bearded seal	Long bone	9.3	40.2	15.0	3.13	-13.5	+14.6
DMP40	Double Point	Mer	*Erignathus barbatus*	Bearded seal	Auditory bulla	3.6	34.9	13.1	3.11	-12.9	+15.8
DMP41	Double Point	Mer	*Phoca vitulina*	Harbour seal	Auditory bulla	5.7	36.3	14.1	3.00	-12.4	+17.7
DMP42	Double Point	Mer	*Phoca vitulina*	Harbour seal	Auditory bulla	5.9	39.7	15.4	3.01	-13.8	+17.8
DMP43	Double Point	Mer	*Phoca vitulina*	Harbour seal	Left humerus	7.7	40.4	15.7	3.01	-12.3	+17.6
DMP44	Double Point	Mer	*Phoca vitulina*	Harbour seal	Auditory bulla	7.3	31.3	10.8	3.39	-14.3	+19.7
DMP50	Double Point	Mer	*Phoca vitulina*	Harbour seal	Radius	5.8	41.6	15.5	3.13	-14.4	+16.8
DMP51	Double Point	Mer	*Phoca vitulina*	Harbour seal	Left mandible	7.8	34.7	12.9	3.15	-13.0	+17.2
DMP52	Double Point	Mer	*Phoca vitulina*	Harbour seal	Auditory bulla	7.3	43.1	16.2	3.09	-13.3	+16.9
HI05	Huntingdon Island		*C. lupus*	Grey Wolf	Right Mandible	2.7	41.7	15.9	3.06	-15.0	+13.5
2593	Red Bay		*baleinidae*	Bowhead/Atlantic Right whale	Tympanic	5.1	42.9	13.8	3.62	-15.6	+14.3
2595	Red Bay		*baleinidae*	Bowhead/Atlantic Right whale	Tympanic	7.2	42.5	14.2	3.49	-15.4	+15.3
2596	Red Bay		*baleinidae*	Bowhead/Atlantic Right whale	Tympanic	7.3	42.2	14.2	3.46	-15.1	+15.7

		baleinidae	Bowhead/Atlantic	Tympanic						
2597	Red Bay		Right whale		9.2	42.2	14.0	3.51	-15.1	+14.4
		baleinidae	Bowhead/Atlantic	Tympanic						
2598	Red Bay		Right whale		4.3	42.0	14.2	3.45	-14.9	+14.0
		baleinidae	Bowhead/Atlantic	Tympanic						
2599	Red Bay		Right whale		3.9	42.8	13.8	3.63	-15.4	+14.3
		baleinidae	Bowhead/Atlantic	Tympanic						
2600	Red Bay		Right whale		6.7	43.0	14.3	3.51	-16.9	+12.0
		baleinidae	Bowhead/Atlantic	Tympanic						
2601	Red Bay		Right whale		4.6	39.8	13.5	3.44	-15.6	+16.0
		baleinidae	Bowhead/Atlantic	Tympanic						
2615	Red Bay		Right whale		16.4	42.8	15.3	3.25	-14.6	+13.2
2602	Red Bay	*Ursus maritimus*	Polar bear	Skull	18.5	42.1	15.3	3.21	-13.8	+18.1
2603	Red Bay	*Ursus maritimus*	Polar bear	Tibia	22.8	42.1	15.1	3.26	-14.0	+18.6
2612	Red Bay	*Phoca vitulina*	Harbour seal	Tympanic	6.0	41.8	14.0	3.48	-14.9	+17.2
		Pagophilus	Harp seal	Tympanic						
2613	Red Bay	*groenlandicus*			7.5	42.4	14.4	3.44	-15.2	+15.2
2614	Red Bay	*Orcinus orca*	Killer whale	Tooth	22.1	42.9	15.1	3.31	-13.4	+17.5

Appendix 3

This file contains supplementary tables 1–3 and supplementary figures 1–3.

Supplementary table 1. Sample origin, museum and lab IDs, genetic identification, mtDNA clade, biological sex and stable carbon and nitrogen isotope data.

Supplementary Table 1: Table of sample origin information

							Origin:													
Study ID:	Isotope ID:	Article ID:	Museum ID:	Macroscopic Species ID:	Genetic Taxa ID:	Item:	Country:	Location:	Lat.	Long	Age:	MT DNA coverage (Dog):	MT DNA coverage (non-Dog)	MT Dog clade:	Sex (Only for Canis)	Ameen et al 2019	d13C	d15N	Sequenced Reads	% Dog DNA	Diamond
TRF.02.48		K.265a	67462	C.l. familiaris	?	Boots (Leggings), Shaft	Scandi./Russia	Talma-byen	63.3	26.6	1912	0.0	0.1	NA	NA	no	NA	NA	2,916	45.0	Dog
TRF.02.42		Lu.805	94121	C.l. familiaris	?	Parka, Hood edge	Greenland	--	70.8	-48.4	--	0.0	NA	NA	NA	no	NA	NA	7,016	15.8	Dog
TRF.02.10		Kc.99	90710	C.l. familiaris	?		Siberia	Kap Dechnev	66.1	169.7	1860	0.0	NA	NA	NA	no	NA	NA	10,409	19.9	?
TRF.02.04			31369	C.l. familiaris	Canis		Greenland	Godthåb distrikt	64.2	-51.7	1892	36.9	NA	A1a		yes	NA	NA	14,320	19.2	Dog
TRF.02.52	KRK07	K.1160a	67201	C.l. familiaris	?	Coat, Sleeve edge	Siberia	Kamchatka Krai (Koryaks)	60.3	163.5	1961	0.1	NA	NA	NA	no	-20	7.9	17,328	60.5	Dog
TRF.02.51		K.1161a	67203	C.l. familiaris	?	Coat, Lower edge	Siberia	Kamchatka Krai (Koryaks)	60.3	163.5	1961	0.1	NA	NA	NA	no	NA	NA	19,800	37.3	Dog
TRF.02.46	GLN06	Ld.8a	31293	C.l. familiaris	?	Parka, Hood edge	Greenland	--	70.8	-48.4	1870	0.0	NA	NA	NA	no	-16.2	13.6	28,559	17.0	?
TRF.02.47	GLN02	L.9357	33000	C.l. familiaris	Canis	Stocking, Stocking edge	Greenland	Uummannaq	70.7	-52.1	1926	36.4	NA	A2a	F	no	-15.4	19.8	31,858	50.1	Dog
TRF.02.39	GLN01	L.2106	31597	C.l. familiaris	Ursus	Stocking, Stocking edge	Greenland	Kap York	75.9	-66.4	1905	0.0	0.2	NA	M	no	-15	18.5	51,733	3.1	?
TRF.02.34	CAN04	P.231a	36421	C.l. familiaris	?	Parka, Hood edge	Canada	Labrador (Coast)	54.7	-58.7	1922	0.1	NA	NA	NA	no	-14.4	18.3	95,648	48.1	
TRF.02.59		K.1171	19748	C.l. familiaris	Rangifer	Coat, Collar	Siberia	Kamchatka Krai (Koryaks)	60.3	163.5	1961	0.0	0.3	NA	NA	no	NA	NA	173,791	7.1	Dog
TRF.02.62	KHA04	K.3-9	90208	?	Vulpes lagopus	Coat, Collar	Siberia	Nenets/Khanti	63.2	73.9	1927	0.0	0.3	NA	NA	no	-22.3	9	180,130	55.5	Dog
TRF.02.18		Lu.798b	94114_b	C.l. familiaris	?	Parka, Hood edge	Greenland	--	70.8	-48.4	--	0.2	NA	NA	NA	no	NA	NA	188,493	38.4	?
TRF.02.35	CAN02	P.1358	20748	C.l. familiaris	Gulo	Belt	Canada	Mackenzie	67.6	-133.9	1936		1.7	NA	NA	no	-20.4	6.9	194,942	9.6	?
TRF.02.03	KRK05		19741	C.l. familiaris	Gulo		Siberia	Kamchatka Krai	60.3	163.5	1966	0.0	0.4	NA	NA	no	-20.2	6.7	229,678	5.3	?
TRF.02.11			91085	C.l. familiaris	?		Siberia	Obdorsk	66.5	66.6	1881	0.1	NA	NA	NA	no	NA	NA	435,734	40.4	?
TRF.02.53	KRK02	K.1161b	67204	C.l. familiaris	Canis	Coat, Lower edge	Siberia	Kamchatka Krai (Koryaks)	60.3	163.5	1961	149.5	NA	A1a	M	no	-19.8	6.5	449,839	76.0	Dog
TRF.02.44	GLN08	Lu.808	94192	C.l. familiaris	Canis	Parka, Hood edge	Greenland	--	70.8	-48.4	--	2.2	NA	A2a	M	no	-15.1	18.3	507,671	72.0	Dog
TRF.02.60		K.3-14b	67480	?	Rangifer	Boots, Sole	Siberia	Nenets/Khanti	63.2	73.9	1927	0.0	1.4	NA	NA	no	NA	NA	518,723	1.1	?
TRF.02.58	KRK10	K.1169	19747	C.l. familiaris	Canis	Suit, Sleeve edge	Siberia	Kamchatka Krai (Koryaks)	60.3	163.5	1961	2.0	NA	A1a	M	no	no data	no data	768,331	66.5	Dog
TRF.02.01			19451	C.l. familiaris	Canis		Siberia	Tjukotka	66.7	172.3	1927	43.1	NA	A1a	F	no	NA	NA	856,079	64.5	Dog
TRF.02.49		K.607	19448	C.l. familiaris	Canis	Suit, Sleeve edge	Siberia	Chuchki	64.4	-173.4	1927	63.0	NA	A1b	M	no	NA	NA	1,020,212	70.6	Dog
TRF.02.25	KHA01	K.3-7	90206_a	C.l. familiaris	Canis	Coat, Lower edge (Black)	Siberia	Nenets/Khanti	63.2	73.9	1927	44.5	NA	A1a	M	no	-20.3	8.5	1,087,531	56.9	Dog
TRF.02.56	KRK06	K.1170b	67208	C.l. familiaris	Gulo	Suit, Sleeve edge	Siberia	Kamchatka Krai (Koryaks)	60.3	163.5	1961	0.2	4.3	NA	NA	no	-18.9	8.2	1,256,998	5.8	?
TRF.02.45	GLN05	Lu.800	94113	C.l. familiaris	Canis	Parka, Hood edge	Greenland	--	70.8	-48.4	--	2.2	NA	A1a	M	no	-14.6	15.8	1,396,201	35.6	Dog
TRF.02.21		K.1-1a	89373_a	C.l. familiaris	Canis	Coat, Sleeve edge	Siberia	Nanai	50.9	137.6	1927	20.4	NA	A1b	F	no	NA	NA	1,411,141	67.7	Dog
TRF.02.50	KRK01	K.1165	19744	?	Gulo	Coat, Lower edge	Siberia	Kamchatka Krai (Koryaks)	60.3	163.5	1961	0.1	4.2	NA	NA	no	-21	6.6	1,659,657	4.1	?
TRF.02.32	CAN03	P26.2	69961	C.l. familiaris	Gulo	Parka, Hood edge	Canada	Labrador	53.3	-62.0	1924	0.2	4.5	NA	NA	no	-16.6	13.3	2,331,042	6.0	?
TRF.02.57	KRK03	K.1176	19753	C.l. familiaris	Canis	Hat, Hood band	Siberia	Kamchatka Krai (Koryaks)	60.3	163.5	1961	14.7	NA	A1a	F	no	-18	7.3	2,579,909	45.1	Dog
TRF.02.30	ALK01	P.6399	36679	C.l. familiaris	Gulo	Parka, Hood edge	Alaska	Alaska/Aleutian Islands	66.0	-152.1	1945	0.1	10.0	NA	NA	no	-22	6.3	2,830,206	5.0	Dog?
TRF.02.29	ALK06	P.6397	36677	C.l. familiaris	Canis	Parka, Hood edge	Alaska	Alaska/Aleutian Islands	66.0	-152.1	1945	101.2	NA	X	M	Yes	-16.4	13.3	3,096,011	52.7	Dog
TRF.02.40		Lu.979	95904	C.l. familiaris	Canis	Stocking, Stocking edge	Greenland	--	70.8	-48.4	1962	6.1	NA	A1a	M	yes	NA	NA	3,109,570	61.6	Dog
TRF.02.55	KRK09	K.1164	19743	?	Gulo	Coat, Lower edge	Siberia	Kamchatka Krai (Koryaks)	60.3	163.5	1961	0.2	5.4	NA	NA	no	-17.1	11.9	3,177,981	4.4	?
TRF.02.27	ALK07	P.6402	36681	C.l. familiaris	Canis	Parka, Hood edge	Alaska	Alaska/Aleutian Islands	66.0	-152.1	1945	4.9	NA	Wolf	F	Yes	-19.1	6.8	3,212,228	35.4	Dog
TRF.02.02			89594	C.l. familiaris	Lynx		Siberia	Yana North	71.4	136.3	1927	0.2	6.2	NA	NA	no	NA	NA	3,469,543	4.3	Lynx
TRF.02.14	ALK08	P.32.6	36963_b	C.l. familiaris	Canis	Parka, Lower edge	Alaska	Point Hope, AK	68.3	-166.8	1926	73.2	NA	A1a	M	Yes	-16.2	14.6	3,850,084	48.0	Dog
TRF.02.61	KHA03	K.3-12	90214	C.l. familiaris	Vulpes lagopus	Hat, Hood band	Siberia	Nenets/Khanti	63.2	73.9	1927	0.1	0.1	NA	NA	no	-19.4	11.9	3,956,840	0.4	?
TRF.02.38		L19.3	33560	C.l. familiaris	Canis	Earmuff	Greenland	Tasiilak	65.6	-37.6	1932	76.2	NA	A1b	M	Yes	NA	NA	4,254,696	60.7	Dog
TRF.02.19		Lu.788	94071	C.l. familiaris	Canis	Parka, Sleeve	Greenland	--	75.9	-66.4	--	10.9	NA	A1a	M	Yes	NA	NA	4,378,447	65.4	Dog
TRF.02.41	GLN09	L.18.194	33486	C.l. familiaris	Canis	Shoes, Shoe edge	Greenland	--	70.8	-48.4	1980	4.0	NA	A1a	F	yes	-16.3	17.7	5,059,876	69.2	Dog
TRF.02.54	KRK04	K.1160b	67202	C.l. familiaris	Canis	Coat, Lower edge	Siberia	Kamchatka Krai (Koryaks)	60.3	163.5	1961	14.7	NA	A1a	M	no	-20.4	12.3	5,372,465	70.4	Dog
TRF.02.28	ALK03	P.6396	36676	C.l. familiaris	Canis	Parka, Hood edge	Alaska	Alaska/Aleutian Islands	66.0	-152.1	1945	10.7	NA	Wolf	M	Yes	-19.3	6.7	5,650,576	62.4	Dog
TRF.02.31		K.6411a	69669	C.l. familiaris	Gulo	Coat, Hood edge	Alaska	Alaska/Aleutian Islands	66.0	-152.1	1945	0.1	5.8	NA	NA	no	NA	NA	5,656,517	3.7	?
TRF.02.65	ALK02	P.9597	95758	C.l. familiaris	Canis	Glove, Glove edge	Canada	Netsilik Inuit	68.8	-92.9	--	0.9	NA	NA	NA	no	-16.1	14	5,657,511	14.2	?
TRF.02.22		K.1-1b	89373_b	C.l. familiaris	Canis	Coat, Sleeve	Siberia	Nanai	50.9	137.6	1927	2.1	NA	A1b	M	no	NA	NA	6,618,514	60.0	Dog
TRF.02.23	KHA02	K.3-6	90205_a	C.l. familiaris	Canis	Coat, Lower edge (Black)	Siberia	Nenets/Khanti	63.2	73.9	1927	29.7	NA	A1a	M	no	-19.8	7.1	7,191,952	21.1	Dog
TRF.02.16	ALK05	P.1659	36636_b	C.l. familiaris	Canis	Parka, Hood edge	Alaska	St. Lawrence Island	63.3	-170.0	1939	155.4	NA	A1a	F	Yes	-14.2	18.3	7,274,547	47.9	Dog
TRF.02.26		K.3-7	90206_b	C.l. familiaris	Canis	Coat, Lower edge (White)	Siberia	Nenets/Khanti	63.2	73.9	1927	7.9	NA	A1a	M	no	NA	NA	7,311,062	67.8	Dog
TRF.02.24		K.3-6	90205_b	C.l. familiaris	Canis	Coat, Lower edge (White)	Siberia	Nenets/Khanti	63.2	73.9	1927	12.8	NA	B	F?	no	NA	NA	8,434,004	15.3	?
TRF.02.64		K.2-28	89609	C.l. familiaris	Spermophilus?	Hat, Hood band	Siberia	Yakuts	69.8	125.9	1927	0.1	2.6	NA	NA	no	NA	NA	8,861,445	0.8	Rodentia
TRF.02.37	GLN07	L.5083	32180	C.l. familiaris	Canis	Stocking, Stocking edge	Greenland	Tasiilak	65.6	-37.6	1911	10.9	NA	A1b	M	Yes	-15.3	16.4	9,162,548	20.3	Dog
TRF.02.12			19619	C.l. familiaris	Vulpes vulpes		Siberia	Sakhalin	51.0	143.0	1937		156.6	NA	NA	no	NA	NA	270,550,834	50.7	Dog
TRF.02.67	KHA05	K.3-13	90215	C.l. familiaris	--	Hat, Hood band	Siberia	Nenets/Khanti	63.2	73.9	1927	NA	NA	NA	NA	no	-23.4	7.5	NA	NA	NA
TRF.02.63	KHA06	Kd.13	91088	C.l. familiaris	--	Hat, Hood band	Siberia	Nenets/Khanti (Neutinsk)	63.2	73.9	1881	NA	NA	NA	NA	no	-23.2	8.7	NA	NA	NA
TRF.02.72	CAN05	P.31.1	37233	C.l. familiaris	--	Parka	Canada	Mackenzie River	67.6	-133.9	1926	0.0	NA	NA		no	-21.9	11.4	NA	NA	NA
TRF.02.66	GLN03	L.2103	31594	C.l. familiaris	--	Stocking, Shaft	Greenland	Kap York	75.9	-66.4	1905	NA	NA	NA	NA	no	-15.2	15.9	NA	NA	NA
TRF.02.43	GLN11	Lu.804	94118	C.l. familiaris	--	Parka, Hood edge	Greenland	--	70.8	-48.4	--	NA	NA	NA	NA	no	-15	15.7	NA	NA	NA
TRF.02.17	GLN10	Lu.798a	94114_a	C.l. familiaris	--	Parka, Hood	Greenland	--	70.8	-48.4	--	NA	NA	NA	NA	no	-14.9	18.3	NA	NA	NA
TRF.02.33	CAN01	P.229a	36410	C.l. familiaris	--	Parka, Lower edge	Canada	Labrador (Coast)	54.7	-58.7	1922	NA	NA	NA	NA	no	-13.8	19.7	NA	NA	NA
TRF.02.05			31588_a	C.l. familiaris	--		Greenland	Kap York	75.9	-66.4	1905	NA	NA	NA	NA	no	NA	NA	NA	NA	NA
TRF.02.06			31588_b	C.l. familiaris	--		Greenland	Kap York	75.9	-66.4	1905	NA	NA	NA	NA	no	NA	NA	NA	NA	NA
TRF.02.08			67733	C.l. familiaris	--		Siberia	Yenisei & Lena	60.8	89.8	1862	NA	NA	NA	NA	no	NA	NA	NA	NA	NA
TRF.02.36		Lu.930	95774	C.l. familiaris	--	Parka, Lower edge	Greenland	--	73.5	-43.9	--	NA	NA	NA	NA	no	NA	NA	NA	NA	NA
TRF.02.68		P.229e	36410	C.l. familiaris	--	Glove, Glove edge	Canada	Labrador (Coast)	54.7	-58.7	1922	NA	NA	NA	NA	no	NA	NA	NA	NA	NA
TRF.02.69a	ALK04	P30.9	37351_a	C.l. familiaris	Canis	Parka	Canada	Kent Peninsula	68.5	-107.0	1927	3.9	NA	Wolf	?	no	-18.5	7.8			--
TRF.02.70	GLN04	L.5082	32179	C.l. familiaris	Canis		Greenland	Tasiilaq	65.6	-37.6	1911	12.0	NA	A1b	F	no	-14.7	17.8			--
TRF.02.09			89375	C.l. familiaris	Canis		Siberia	Amur Delta	48.8	108.8	1927	36.0	NA	A1a		no	NA	NA			--
TRF.02.69			37351	C.l. familiaris	Canis	Parka	Canada	Kent Peninsula	68.5	-107.0	1927	37.0	NA	Wolf	?	no	NA	NA			--
1766				C. lupus	NA	Pelt	Greenland	Itivleriaq	66.7	-82.1	1922	NA	NA	NA	NA	NA			NA	NA	NA
2043				C. lupus	NA	Pelt	Canada	Southampton Island	73.9	-24.2	1922	NA	NA	NA	NA	NA			NA	NA	NA
2044				C. lupus	NA	Pelt	Greenland	Franklin Isthmus	64.4	-84.5	1922	NA	NA	NA	NA	NA			NA	NA	NA
2046				C. lupus	NA	Pelt	Greenland	Itibdjeriang	66.7	-82.1	1928	NA	NA	NA	NA	NA			NA	NA	NA
2047				C. lupus	NA	Pelt	Greenland	Itibdjeriang	66.7	-82.1	1928	NA	NA	NA	NA	NA			NA	NA	NA
2048				C. lupus	NA	Pelt	Greenland	Back River	66.1	-96.6	1923	NA	NA	NA	NA	NA			NA	NA	NA
2049				C. lupus	NA	Pelt	Greenland	Back River	66.1	-96.6	1923	NA	NA	NA	NA	NA			NA	NA	NA
2050				C. lupus	NA	Pelt	Greenland	Back River	66.1	-96.6	1923	NA	NA	NA	NA	NA			NA	NA	NA
4093				C. lupus	NA	Pelt	Canada	Eureka Sound	79.0	-87.0	1940	NA	NA	NA	NA	NA			NA	NA	NA
4094				C. lupus	NA	Pelt	Canada	Eureka Sound	79.0	-87.0	1940	NA	NA	NA	NA	NA			NA	NA	NA
Eunr				C. lupus	NA	Pelt	Canada	Ellesmere Island	80.2	-79.1	1900	NA	NA	NA	NA	NA			NA	NA	NA
3456				C. lupus	NA	Pelt	Canada	Ellesmere Island	80.2	-79.1	1898	NA	NA	NA	NA	NA			NA	NA	NA
1458				C. lupus	NA	Pelt	Canada	Axel Heibergs Land	79.4	-90.8	1912	NA	NA	NA	NA	NA			NA	NA	NA
1460				C. lupus	NA	Pelt	Canada	Axel Heibergs Land	79.4	-90.8	1914	NA	NA	NA	NA	NA			NA	NA	NA
1921				C. lupus	NA	Pelt	Greenland	Rosenvinge Bugt, Scoresby	70.5	-22.1	1925	NA	NA	NA	NA	NA			NA	NA	NA
1237				C. lupus	NA	Pelt	Greenland	Hvalrosodden	76.9	-20.1	1906	NA	NA	NA	NA	NA			NA	NA	NA
4903				C. lupus	NA	Pelt	Greenland	Kap Graah	79.5	-78.0	1926	NA	NA	NA	NA	NA			NA	NA	NA
8.1				C. lupus	NA	Pelt	Greenland	Northeast	74.0	-21.0	1901	NA	NA	NA	NA	NA			NA	NA	NA
1240				C. lupus	NA	Pelt	Greenland	Skibshavnen	76.8	-18.9	1908	NA	NA	NA	NA	NA			NA	NA	NA

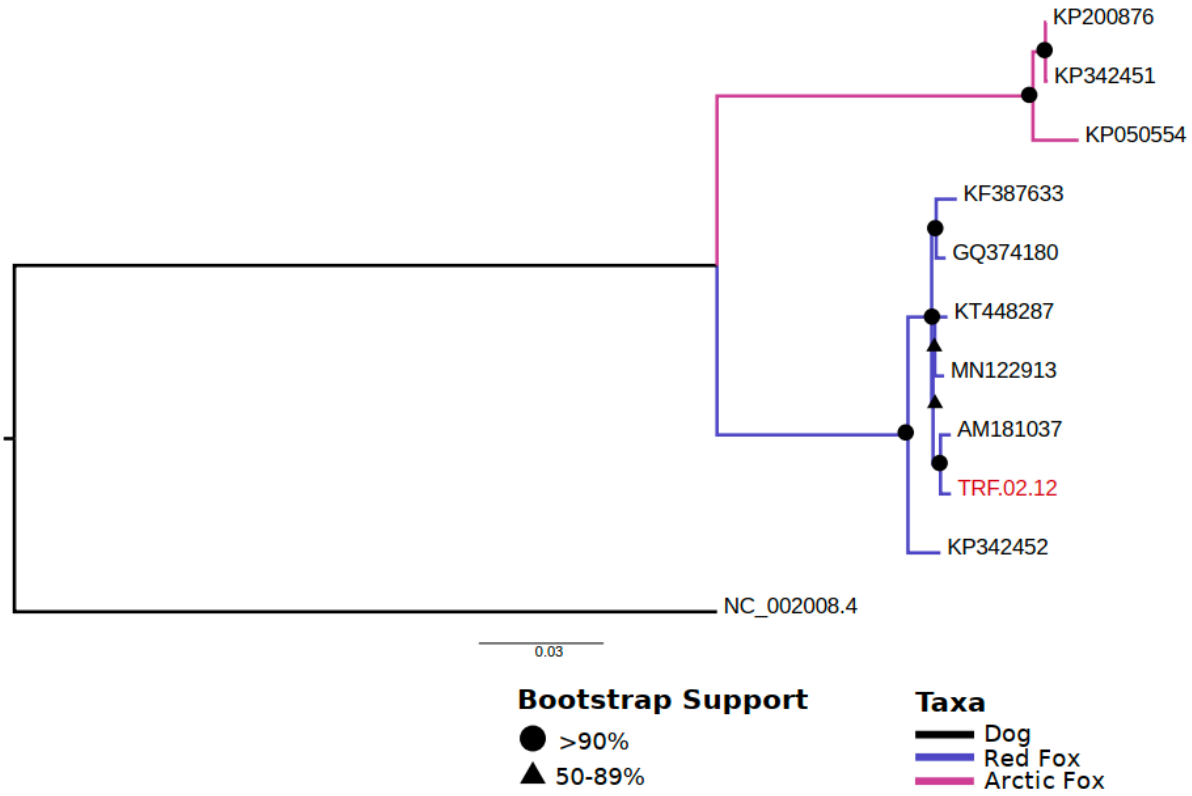
Supplementary Table 2: Table with read mapping counts

Ref_ID	NC_020677.1	NC_008415.3	NC_002008.4	NC_007704.2	NC_014703.1	NC_034313.1	NC_008426.1	NC_009685.1	NC_024043.1	NC_027083.1	NC_020642.1	NC_011579.1	NC_039173.1	NC_025516.1	NC_020641.1	NC_020631.1	KF892541.1	NC_001325.1	NC_008433.1	NC_007703.1	NC_027283.1	NC_025277.1	NC_003426.1	NC_003427.1	NC_003428.1	KT448286.1	JN711443.1
Scientific_Name	Alces alces	Callorhinus ursinus	Canis lupus familiaris	Cervus elaphus	Cervus elaphus songaricus	Dicrostonyx groenlandicus	Erignathus barbatus	Gulo gulo	Lepus americanus	Lynx lynx	Martes americana	Martes zibellina	Meles leucurus	Mustela erminea	Neovison vison	Ovibos moschatus	Panthera tigris tigris	Phoca vitulina	Pusa hispida	Rangifer tarandus	Spermophilus dauricus	Tamias sibiricus	Ursus americanus	Ursus arctos	Ursus maritimus	Vulpes lagopus	Vulpes vulpes
Common_Name	Moose	Northern fur seal	Dog	Red Deer	Elk/Whapati	Collared Lemming	Bearded Seal	Wolverine	Snowshoe hare	Lynx	Pine Marten	Sable	Asian badger	Stoat/ermine	Mink	Musk ox	Tiger	harbor seal	Ringed seal	reindeer	Daurian ground squirrel	Siberian chipmunk	American black bear	brown bear	polar bear	Arctic fox	red fox
TRF.02.01	1	4	24047	12	5	2	16	13	3	7	14	532	8.0	30.0	23	18	11	15	19	52	1.0	6	13	10	9	105	114
TRF.02.02	3	2	47	0	1	1	3	4	0	2272	1	507	2.0	1.0	2	1	15	4	0	2	1.0	1	1	0	1	1	1
TRF.02.03	0	0	1	0	0	0	0	169	0	0	4	5	0.0	1.0	0	0	0	1	0	0	0.0	0	1	0	0	0	0
TRF.02.04	29	46	42255	71	26	39	60	81	44	60	47	78640	129.0	84.0	78	71	60	72	63	82	14.0	39	54	28	41	326	264
TRF.02.05	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
TRF.02.06	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
TRF.02.08	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
TRF.02.09	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
TRF.02.10	1	0	1	0	0	1	0	0	0	0	1	0	0.0	0.0	1	0	0	0	0	1	0.0	2	0	1	1	0	2
TRF.02.11	220	145	247	168	156	258	163	201	246	144	148	270	212.0	167.0	170	187	201	135	125	245	280.0	297	183	137	145	204	211
TRF.02.12	972	1592	3121	998	931	677	1513	1271	597	1515	1412	1444	1433.0	1476.0	1533	662	1486	1431	1556	1745	521.0	525	1267	1261	1214	8613	27702
TRF.02.14	12	25	52172	38	23	15	67	79	20	15	33	4018	31.0	91.0	62	31	26	63	60	58	7.0	16	30	434	478	227	212
TRF.02.16	71	99	357690	315	88	78	329	204	91	129	166	19598	203.0	488.0	601	246	119	332	373	371	29.0	172	212	455	433	1087	1568
TRF.02.17	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
TRF.02.18	167	141	262	137	138	201	139	134	229	126	106	217	140.0	133.0	165	190	146	98	79	178	220.0	236	157	123	120	145	180
TRF.02.19	2	3	3780	3	1	3	6	4	0	7	2	240	2.0	7.0	5	5	0	2	2	4	1.0	2	3	2	7	21	31
TRF.02.20	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
TRF.02.21	4	7	6381	6	5	5	8	10	4	5	10	2291	15.0	18.0	7	10	8	9	11	11	7.0	13	6	18	16	49	66
TRF.02.22	11	8	860	10	5	19	9	17	16	6	9	927	15.0	13.0	13	14	17	9	14	10	10.0	11	8	10	11	19	32
TRF.02.23	9	13	19542	19	12	6	23	21	7	9	20	697	26.0	52.0	28	16	22	17	16	44	4.0	17	17	14	18	107	114
TRF.02.24	28	32	6332	30	14	33	19	22	35	26	23	375	28.0	43.0	35	33	30	29	19	70	36.0	38	33	23	42	87	82
TRF.02.25	5	26	31452	63	9	8	44	45	10	33	25	934	28.0	62.0	52	52	26	44	48	56	4.0	37	45	53	71	176	310
TRF.02.26	19	14	3287	15	14	22	13	15	24	24	27	482	19.0	28.0	24	11	16	14	13	27	25.0	19	20	14	20	49	53
TRF.02.27	0	1	1432	1	0	0	1	2	0	0	1	67	0.0	2.0	6	2	1	4	2	8	0.0	0	2	2	2	8	11
TRF.02.28	0	1	3476	2	1	1	9	3	0	5	5	211	3.0	6.0	4	4	4	7	5	6	1.0	1	1	3	7	21	36
TRF.02.29	3	2	4045	5	2	1	5	6	1	2	3	282	3.0	8.0	7	2	4	1	0	6	1.0	2	1	6	3	32	27
TRF.02.30	3	5	5	2	3	1	11	4385	2	2	75	620	47.0	35.0	17	9	6	9	9	73	1.0	0	3	4	4	3	5
TRF.02.31	1	1	0	2	0	0	1	1765	1	0	24	74	21.0	9.0	5	2	1	8	2	2	0.0	0	2	2	1	2	1
TRF.02.32	164	110	162	119	119	149	114	2684	194	122	138	479	172.0	103.0	153	156	119	69	80	220	207.0	228	104	81	84	118	133
TRF.02.33	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
TRF.02.34	80	60	94	52	48	66	56	54	81	44	29	52	59.0	34.0	55	60	58	33	42	57	78.0	89	50	48	43	47	44
TRF.02.35	0	0	2	1	0	0	0	69	0	0	0	2	0.0	1.0	0	0	0	0	0	0	0.0	0	0	0	0	0	0
TRF.02.36	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
TRF.02.37	4	3	5579	18	6	5	21	16	7	9	11	2195	14.0	15.0	15	5	11	12	17	18	2.0	5	8	12	12	52	45
TRF.02.38	21	20	61107	84	15	11	59	37	12	29	44	632	44.0	95.0	95	69	42	77	95	87	2.0	41	69	83	51	280	307
TRF.02.39	0	0	4	0	0	0	0	2	0	0	0	0	0.0	1.0	0	0	0	0	0	1	0.0	0	1	7	38	0	0
TRF.02.40	0	0	1805	1	0	0	3	2	0	0	1	81	1.0	0.0	4	2	1	0	2	2	0.0	0	6	0	1	10	12
TRF.02.41	0	1	1204	0	0	0	1	2	2	4	2	289	4.0	4.0	2	3	1	2	1	1	1.0	2	1	6	1	12	17
TRF.02.42	0	0	2	0	0	0	0	0	0	0	0	1	0.0	0.0	0	0	0	1	2	0	0.0	0	0	0	0	0	0
TRF.02.43	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
TRF.02.44	0	0	445	1	0	0	0	0	0	2	0	5	0.0	0.0	0	0	0	0	1	0	1.0	0	0	0	0	0	3
TRF.02.45	1	1	1153	4	0	0	2	1	0	5	4	240	1.0	3.0	4	0	3	1	2	4	0.0	2	1	1	2	9	11
TRF.02.46	1	0	9	0	0	1	0	4	2	1	0	1	2.0	1.0	1	0	2	1	0	3	5.0	0	1	0	0	0	1
TRF.02.47	0	0	35	0	0	0	0	0	0	0	0	3	0.0	0.0	0	0	0	0	0	0	0.0	0	0	0	0	0	0
TRF.02.48	0	0	1	0	0	0	0	0	0	0	0	1	0.0	0.0	0	0	0	0	0	0	0.0	0	0	0	0	0	0
TRF.02.49	11	29	38229	60	11	15	54	65	5	36	24	1749	38.0	79.0	85	39	20	61	57	72	4.0	25	43	57	49	241	322
TRF.02.50	0	0	6	0	0	0	1	1083	0	1	7	31	8.0	5.0	5	4	1	4	1	1	0.0	0	1	0	0	0	0
TRF.02.51	0	0	10	0	0	0	0	2	0	1	0	1	0.0	0.0	0	0	0	0	0	0	0.0	0	0	0	0	0	0
TRF.02.52	0	0	13	0	0	0	0	0	0	0	0	0	0.0	0.0	0	0	0	0	0	0	0.0	0	0	0	0	0	0
TRF.02.53	31	60	214379	213	44	24	199	131	29	84	86	4910	119.0	322.0	335	161	80	217	214	431	20.0	71	165	262	261	957	1227
TRF.02.54	1	3	4897	5	0	1	10	6	0	4	4	422	3.0	7.0	11	3	5	5	7	39	0.0	3	0	2	6	27	50
TRF.02.55	0	1	15	0	0	0	5	1656	0	0	20	139	21.0	4.0	10	2	0	4	0	1	0.0	0	2	0	0	1	1
TRF.02.56	0	0	40	1	1	0	5	1407	0	1	19	82	11.0	9.0	2	3	0	10	1	11	0.0	0	3	1	0	1	1
TRF.02.57	0	1	2279	1	1	0	2	3	0	3	2	125	2.0	4.0	0	2	1	3	0	6	0.0	1	4	2	1	7	10
TRF.02.58	0	0	265	1	0	0	1	0	0	0	0	23	1.0	0.0	0	0	0	1	0	1	0.0	0	0	0	1	2	0
TRF.02.59	4	0	0	2	1	0	0	0	0	0	0	9	0.0	0.0	0	1	0	0	0	114	0.0	0	0	0	0	0	0
TRF.02.60	14	0	3	9	9	0	1	2	0	1	1	13	1.0	0.0	0	2	0	0	1	548	2.0	2	1	1	0	0	1
TRF.02.61	0	0	18	1	0	0	0	0	0	0	0	5	0.0	0.0	0	0	0	0	0	3	0.0	1	0	0	0	65	6
TRF.02.62	0	0	0	0	0	0	0	0	0	0	0	25	0.0	0.0	0	0	0	0	1	0	0.0	0	0	1	1	154	7
TRF.02.63	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
TRF.02.64	4	4	5	5	3	10	3	4	3	5	1	97	5.0	1.0	3	0	0	4	1	0	108.0	65	0	1	1	3	1
TRF.02.65	2434	1610	3924	1728	1812	2528	1515	1518	3599	1736	1167	4397	1916.0	1653.0	2356	1989	1738	920	1036	4,444	3691.0	4186	1753	1426	1233	1706	1862
TRF.02.66	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
TRF.02.67	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
TRF.02.68	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
TRF.02.69	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
TRF.02.70	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
TRF.02.71	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
TRF.02.72	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Supplementary Table 3: Table with DIAMOND hit counts

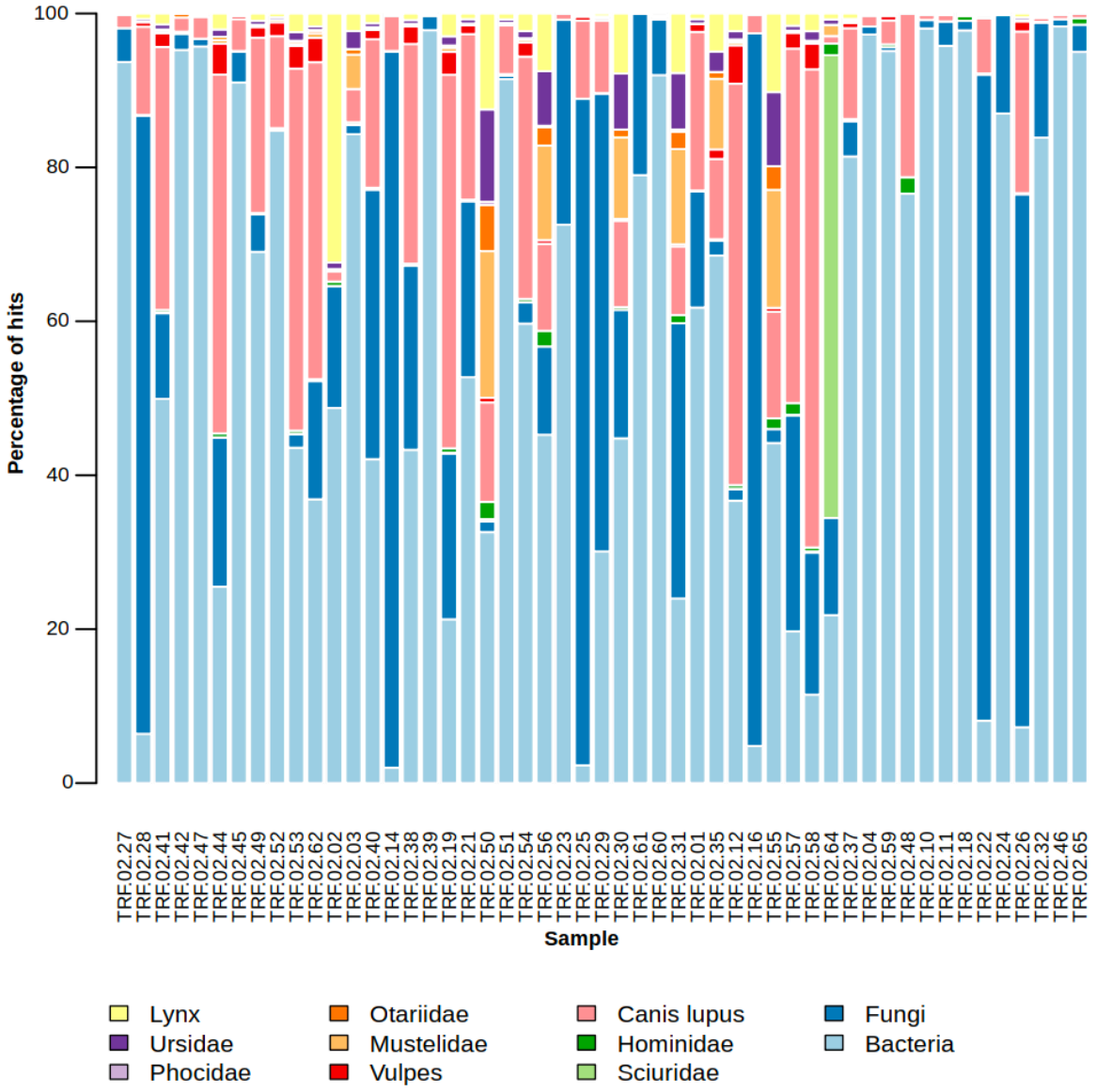
Sample	Bacteria	Fungi	Marmotini	Hominoidea	Canis lupus	Vulpes	Mustelidae	Otariidae	Ursidae	Lynx	Pecora
TRF.02.01	15	5	0	0	10	1	0	0	0	0	0
TRF.02.02	8	5	0	0	0	0	0	0	0	12	0
TRF.02.03	23	0	0	0	2	0	1	0	1	1	0
TRF.02.04	49	0	0	0	1	0	0	0	0	0	0
TRF.02.10	14	0	0	0	0	0	0	0	0	0	0
TRF.02.11	41	1	0	0	0	0	0	0	0	0	0
TRF.02.12	7	0	0	0	19	2	0	0	0	1	0
TRF.02.14	0	61	0	0	3	0	0	0	0	0	0
TRF.02.16	1	65	0	0	2	0	0	0	0	0	0
TRF.02.18	53	0	0	0	0	0	0	0	0	0	0
TRF.02.19	2	6	0	0	18	1	0	0	0	1	0
TRF.02.21	19	11	0	0	11	1	0	0	0	0	0
TRF.02.22	2	50	0	0	5	0	0	0	0	0	0
TRF.02.23	44	13	0	0	0	0	0	0	0	0	0
TRF.02.24	62	8	0	0	0	0	0	0	0	0	0
TRF.02.25	0	52	0	0	6	0	0	0	0	0	0
TRF.02.26	1	35	0	0	12	1	0	0	0	0	0
TRF.02.27	61	3	0	0	1	0	0	0	0	0	0
TRF.02.28	1	46	0	0	6	0	0	0	0	0	0
TRF.02.29	15	37	0	0	6	0	0	0	0	0	0
TRF.02.30	6	3	0	0	3	0	3	0	2	2	2
TRF.02.31	2	9	0	0	2	0	3	1	2	2	2
TRF.02.32	45	10	0	0	0	0	0	0	0	0	0
TRF.02.35	9	0	0	0	3	0	3	0	1	2	1
TRF.02.37	33	1	0	0	6	0	0	0	0	0	0
TRF.02.38	11	9	0	0	14	1	0	0	0	0	0
TRF.02.39	56	0	0	0	0	0	0	0	0	0	0
TRF.02.40	19	17	0	0	10	1	0	0	0	1	0
TRF.02.41	18	2	0	0	15	1	0	0	0	1	0
TRF.02.42	50	0	0	0	1	0	0	0	0	0	1
TRF.02.44	4	7	0	0	19	2	0	0	0	1	0
TRF.02.45	38	1	0	0	2	0	0	0	0	0	0
TRF.02.46	24	0	0	0	0	0	0	0	0	0	0
TRF.02.47	48	0	0	0	2	0	0	0	0	0	0
TRF.02.48	36	0	0	1	10	0	0	0	0	0	1
TRF.02.49	26	1	0	0	12	1	0	0	0	1	0
TRF.02.50	2	0	0	0	2	0	4	1	2	2	2
TRF.02.51	37	0	0	0	4	0	0	0	0	0	0
TRF.02.52	33	0	0	0	7	1	0	0	0	0	0
TRF.02.53	8	0	0	0	18	1	0	0	0	1	0
TRF.02.54	19	0	0	0	14	1	0	0	0	1	0
TRF.02.55	3	0	0	0	3	0	3	1	2	2	2
TRF.02.56	4	2	0	0	3	0	2	1	2	2	1
TRF.02.57	3	10	0	0	19	1	0	0	0	1	0
TRF.02.58	0	5	0	0	22	1	0	0	0	1	0
TRF.02.59	28	0	0	0	1	0	0	0	0	0	8
TRF.02.60	23	1	0	0	0	0	0	0	0	0	9
TRF.02.61	49	14	0	0	0	0	0	0	0	0	0
TRF.02.62	7	4	0	0	16	1	0	0	0	1	0
TRF.02.64	4	3	18	0	0	0	0	0	0	0	0
TRF.02.65	55	2	0	0	0	0	0	0	0	0	0

Supplementary Figure 1:



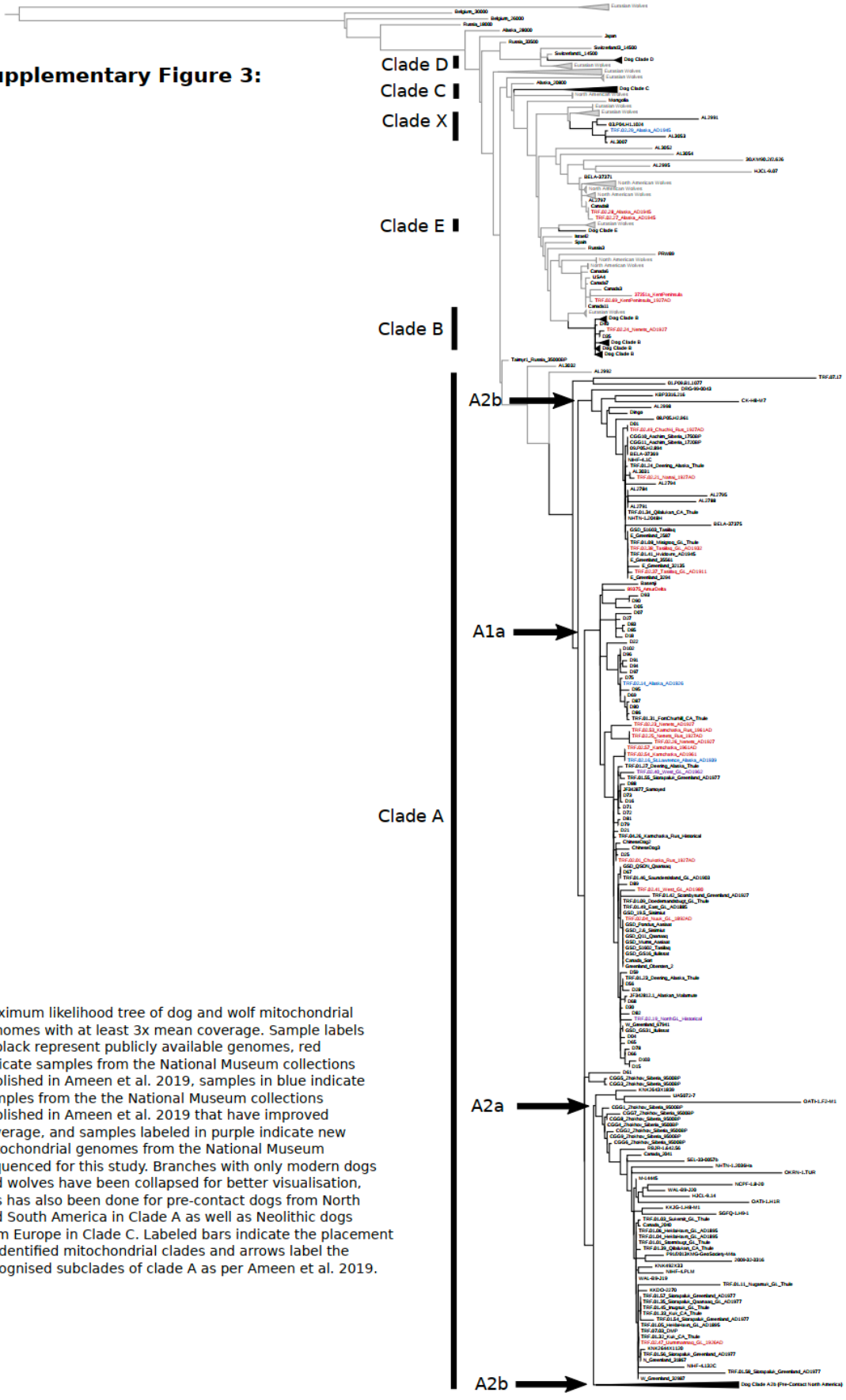
Maximum likelihood tree of foxes. A maximum likelihood tree of red and arctic foxes rooted with a dog. The tree was constructed with RAxML and run with 1,000 bootstrap replicates. Sample branches are coloured by the species and bootstrap support of the node is indicated by icon shape. The sample name in red indicates the mitochondrial genome sequenced in this study, all sample names in black are the NCBI accession numbers.

Supplementary Figure 2:



Percentage of DIAMOND hits per relevant taxonomic classification. Percentage of hits to proteins with DIAMOND per sample including hits for fungi and Bacteria.

Supplementary Figure 3:



Maximum likelihood tree of dog and wolf mitochondrial genomes with at least 3x mean coverage. Sample labels in black represent publicly available genomes, red indicate samples from the National Museum collections published in Ameen et al. 2019, samples in blue indicate samples from the the National Museum collections published in Ameen et al. 2019 that have improved coverage, and samples labeled in purple indicate new mitochondrial genomes from the National Museum sequenced for this study. Branches with only modern dogs and wolves have been collapsed for better visualisation, this has also been done for pre-contact dogs from North and South America in Clade A as well as Neolithic dogs from Europe in Clade C. Labeled bars indicate the placement of identified mitochondrial clades and arrows label the recognised subclades of clade A as per Ameen et al. 2019.

Appendix 4

This file includes:
The methods used in Paper V
Supporting tables 1-5
Supporting figures 1-23

Supporting information file 1: Methods

Collagen extraction

Collagen was extracted from permanent first molars at BioArCh, Department of Archaeology, University of York. Deciduous and permanent first molars were sectioned longitudinally using a Buehler Isomet 1000 precision saw fitted with a diamond wafering blade. The tooth halves were cleaned of adhering debris using a sterile scalpel. One half of each tooth was immersed in 8 ml of 0.6 M hydrochloric acid (HCl) and demineralised on a rocker table at 4°C. After one week, any adhering enamel was gently scraped from the crown, leaving the occlusal surface under enamel so as to protect the more delicate dentine cusps. Complete demineralization of each tooth half took approximately three weeks, after which time the samples were rinsed three times with deionized water. The tooth halves were sectioned into 1 mm increments beginning at the occlusal surface of the crown and moving towards the root apex using a sterile scalpel (Beaumont et al., 2013). The incremental samples gelatinised in a dilute HCl solution at a pH of 3 (80°C, 24-48 h). The gelatinised solutions were then cooled, frozen and lyophilised. Collagen was extracted from bone samples at the Archaeological Research Laboratory of Stockholm University. Bone samples of ~200-300 mg were snipped from the ends of ribs and long bones, and the exterior cortical bone surface was scraped clean of debris. The bone samples were immersed in chilled 0.5 M HCl and demineralized until a collagen pseudomorph remained (Sealy, 1986). The demineralized samples were rinsed to neutrality with DI water, and then leached with chilled 0.025 M NaOH. The NaOH solution was refreshed every 10 minutes until no further colour change was observed. Exposure time ranged

from 10 - 40 minutes. The samples were then rinsed to neutrality and gelatinised in a 0.001 M HCl solution (70°C, 48 h). The solubilised collagen was filtered with E-zee filters, frozen and lyophilised.

EA-IRMS analysis of bulk dentine and bone collagen samples

The collagen samples were weighed in duplicate into tin capsules (4 mm x 3.2 mm, OEA Laboratories, Cornwall, UK). The tin capsules were loaded into a Universal Sercon GSL preparation unit and combusted at 1000°C. The resulting gases were measured using a Sercon continuous flow 20-22 isotope ratio mass spectrometer in the BioArCh facility of the University of York. The raw isotope values were calibrated to the VPDB and AIR scales using international standards (Caffeine [IAEA 600] $\delta^{13}C$: –27.8±0.1‰, $\delta^{15}N$: +1.0±0.1‰; Cane sugar [IA-R006] $\delta^{13}C$: –11.6±0.1‰; and IAEA-N-2 $\delta^{15}N$: +20.3±0.2‰). Replicates of an internal fish gelatin standard ($\delta^{13}C$: –15.2±0.1‰, $\delta^{15}N$: +15.3±0.2‰) were run between every six samples to correct for instrumental drift. Three additional fish gelatin standards were used as check standards. The precision on replicate analyses of the samples was ±0.2‰ or better for $\delta^{13}C$ and $\delta^{15}N$.

Collagen hydrolysis

Collagen samples (1-2 mg) were hydrolysed (110°C, 24 h) in 200 µl of 6M HCl with 50 µl of Norleucine. The hydrolysates were cooled to room temperature and filtered with Nanosep® filters (Pall, 0.45 µm) to remove contaminants. The filtrates were transferred to sterile vials and treated with a 3:2 mixture of *n*-hexane and dichloromethane (1 ml x 3) to remove lipids. The samples were dried under a gentle stream of N2 at room temperature and stored at -18°C until required for derivatization.

Amino acid derivatization for compound specific isotope analysis

Collagen amino acids were derivatized using the methods of Corr et al. (2007) as modified by Styring et al. (2015) and Philben et al. (2018). The hydrolysates were dissolved in ~100 µl of 0.1 M HCl, vortexed and transferred to a 15 ml Hach tube. The procedure was repeated two times to maximize the recovery of amino acids. The samples were dried under a gentle stream of N_2 at room temperature. Amino acids were esterified by heating (100°C, 60 min) with 1 ml of an acidified 2-propanol solution

(4:1 2-propanol: acetyl chloride). The reaction was quenched at -18°C, then the reagent removed under a stream of N_2. The amino acid esters were redissolved twice in 300 µl of dichloromethane (DCM) to ensure removal of the derivatizing reagents. The DCM was removed under a stream of N_2 at room temperature. The samples were then acetylated by heating (60°C, 10 min) with 1 ml of a solution of HPLC grade acetone, triethylamine, and acetic anhydride (5:2:1 v/v/v). The reaction was quenched at -18°C and the reagents removed under a stream of N_2. Phase separation was achieved through the addition of 2 ml of ethyl acetate and 1 ml of a saturated NaCl solution to each sample. The samples were vortexed, and the organic phase transferred to a clean Hach tube. The procedure was repeated with 1 ml of ethyl acetate. Trace water was removed from each sample with molecular sieves (Sodium aluminium silicate 0.3 nm, Merck KGaA, Darmstadt, Germany). The samples were transferred to sterile 2 ml GC vials, and blown to dryness. The amino acid derivatives were dried with two successive additions of 1 ml of DCM. The samples were redissolved in ethyl acetate and aliquoted to sterile GC vials with fixed glass inserts. Samples were stored at -18°C until analysis. Each batch of derivatized samples included one mixture of international amino acid standards (50 µl each of Glu, Asp, Hyp, Leu, Val, Gly, Phe, Ala, Nle), one blank containing 50 µl of Nle.

GC-C-IRMS analysis of amino acid derivatives

GC-C-IRMS measurements of the amino acids were conducted using a Delta V Plus isotope ratio mass spectrometer (Thermo Fisher, Bremen, Germany) linked to a Trace Ultra gas chromatograph (Thermo Fisher, Bremen, Germany) with a GC Isolink II interface fitted with a Cu/Ni combustion reactor maintained at 1000°C. Ultra-high-purity-grade helium with a flow rate of 1.4 mL min^{-1} was used as the carrier gas, and parallel acquisition of Flame Ionisation data was achieved by diverting a small part of the flow to an integrated FID (Thermo Fisher). Ethyl acetate was used to dilute the samples, and 1 µL of each sample and 2 µL of each standard was injected at 240ºC with a 3.5s pre-injection dwell time, onto a custom DB-35 fused-silica column (60 m × 0.32 mm × 0.50 µm; Agilent J&W Scientific technologies, Folsom, CA, USA). All samples were injected in duplicate or triplicate. The oven temperature programme used for samples and standards was as follows: 40 °C (hold 5 min) then increasing by

15 ºC min^{-1} up to 120 ºC, then by 3ºC min^{-1} up to 180 ºC, then by 1.5 ºC min^{-1} up to 210 ºC, then by 5 ºC min^{-1} up to 280 ºC (hold 8 min).

A nafion membrane removed water and a cryogenic trap was employed in order to remove CO_2 from the oxidised and reduced samples. Ion intensities of *m/z* 28, 29, and 30 were monitored in order to automatically compute the $^{15}N/^{14}N$ ratio of each peak in the samples. Computations were made with Isodat (version 3.0; Thermo Fisher) and were based on comparisons with a repeatedly measured high purity standard reference gas (CO_2 or N_2). The results from the analysis are reported in parts per mil (‰) relative to an international standard. Each reported value is a mean of triplicated or duplicated $\delta^{15}N$ measurements. An AA international standard mixture, comprising AAs whose $\delta^{15}N$ was run after every three sample injections in order to monitor instrument performance and drift. The AA standard mixture used for $\delta^{15}N$ determinations comprised 8 international standards (University of Indiana, USA and SHOKO Science, Japan) with the addition of Norleucine from Sigma Aldrich ($\delta^{15}N$ values determined in-house via Sercon EA-IRMS; Crewe, UK). The International mixture included: Ala, +43.25±0.07(‰); Gly, +1.76±0.06(‰); Val, –5.21±0.05(‰) Leu, +6.22(‰); Nle, +14.47±0.23(‰); Asp, +35.2±?(‰), Glu, –4.52±0.06(‰); Hyp, –9.17±?(‰); Phe, +1.7±0.06(‰).

Amino acid isotope data treatment

The amino acid $\delta^{15}N$ values were normalised to the internal standard, Nle, and then corrected using the compound specific correction described in Yarnes and Herszage (2017).

Assignment of age to dentine increments

Dentine increments were assigned approximate ages after Beaumont and Montgomery (2015). Assuming that tooth dentine grows at a regular rate then incremental samples of the same size will each represent an equal fraction of formation time. Each dentine increment is assigned a median age, but it should be noted that the ages assigned to each increment are estimations and are not exact. This assumption is not completely supported by the morphology and variable growth rate of human teeth: Human teeth grow incrementally in overlapping dentine cones

that form at an increasingly oblique angle with proximity to the root tip; the rate of growth also changes over the formation of the tooth (Dean and Cole, 2013).

Statistical analysis

Non-parametric tests were conducted in SPSS v. 25 to investigate patterns in the isotopic data. A Mann Whitney U test was used to investigate possible differences between males and females.

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SI Table 1. Summary data for human AA samples

Sample ID	Age	Bulk $\delta^{15}N$	Bulk $\delta^{13}C$	Ala	Val	Glx	Pro	Hyp	Asx	Gly	Ser	Thr	Phe	Lys
Marine diet														
EKV18_A	0.3	+24.9	–11.3	+28.9 (0.2)	+30.3 (0.5)	+30.3 (0.5)	+34.3 (0.4)	+33.8 (0.4)	+27.8 (0.5)	+27.9 (0.4)	+24.1 (0.6)	–22.4 (0.8)	+9.4 (1.5)	+10.1 (0.8)
EKV18_C	1.5	+22.4	–11.6	+28.8 (0.8)	+29.9 (0.5)	+30.1 (0.7)	+32.6 (0.6)	+32.1 (0.3)	+27.0 (0.2)	+23.9 (0.6)	+18.5 (0.7)	–23.2 (1.4)		+10.3 (1.4)
EKV18_F	3.4	+20.8	–11.8	+28.3 (0.4)	+28.5 (0.6)	+28.7 (0.3)	+28.1 (0.3)	+26.8 (0.3)	+24.2 (0.6)	+21.9 (0.2)	+18.0 (0.6)	–22.2 (0.8)	+8.3 (1.5)	+8.1 (1.0)
EKV18_Q	10.0	+21.2	–11.6	+28.1 (0.1)	+28.6 (0.1)	+29.2 (0.2)	+27.9 (0.1)	+27.9 (0.1)	+24.8 (0.4)	+22.1 (0.1)	+19.5 (0.2)	–23.6 (0.1)	+9.6 (0.6)	+7.2 (0.3)
$\Delta^{15}N_{1st\text{-}3rd}$		4.1	0.5	0.6	1.8	1.6	6.2	7.0	3.6	6.0	6.1	0.2	0.7	2.0
EKV23_A	0.3	+23.8	–11.6	+28.2 (0.2)	+30.2 (0.4)	+30.6 (0.7)	+33.0 (0.3)	+32.7 (0.7)	+28.1 (0.4)	+26.4 (0.3)		–28.5 (1.0)	+8.6 (0.4)	+10.6 (0.6)
EKV23_B	0.9	+22.8	–11.8	+28.3 (0.5)	+30.5 (0.4)	+30.6 (0.5)	+33.6 (0.4)	+31.9 (0.5)	+ 28.0 (0.6)	+25.2 (0.3)		–25.4 (0.5)	+7.1 (0.9)	+11.0 (0.9)
EKV23_D	2.0	+21.4	–11.7	+27.9 (0.5)	+29.3 (0.1)	+29.4 (0.4)	+31.2 (0.4)	+30.0 (0.3)	+26.6 (0.2)	+22.2 (0.3)	+17.7 (0.7)	–26.0 (1.4)		+10.7 (0.8)

EKV23_F	3.2	+20.7	–11.9	+27.3 (0.2)	+28.5 (0.5)	+29.5 (0.6)	+30.4 (0.1)	+29.0 (0.4)	+26.4 (0.3)	+21.5 (0.3)		–24.3 (1.8)	+5.3 (0.7)	+10.7 (0.5)
EKV23_H	4.3	+20.5	–11.8	+28.2 (0.5)	+29.9 (0.1)	+29.7 (0.4)	+29.8 (0.4)	+29.5 (0.7)	+26.1 (0.2)	+21.6 (0.3)	+17.2 (0.4)	–27.2 (1.0)		+10.2 (0.5)
$\Delta^{15}N_{1st\text{-}5th}$		3.3	0.2	0.0	0.3	0.9	3.2	3.2	2.0	4.8	0.5	–1.3	3.3	0.4
Mixed C3-Marine diet														
SK45_1	0.3			+18.1 (0.3)	+22.2 (0.6)	+20.5 (0.3)	+21.9 (0.2)	+22.3 (0.5)	+19.2 (0.4)	+17.0 (0.1)	+13.9 (0.5)	–14.8 (0.6)	+9.7 (1.1)	+5.1 (1.0)
SK45_2	0.9	+13.8	–19.8	+18.0 (0.3)	+18.8 (0.9)	+20.7 (0.9)	+22.1 (0.5)	+22.3 (0.1)	+18.5 (0.4)	+18.1 (0.2)		–14.9 (1.7)		+5.3 (0.7)
SK45_3	1.4	+13.6	–19.6	+16.8 (0.1)	+19.0 (0.5)	+20.0 (0.7)	+18.8 (0.1)	+19.0 (0.2)	+17.0 (0.5)	+15.3 (0.2)	+14.0 (0.9)	–12.6 (1.1)	+11.2 (1.4)	+6.3 (1.3)
SK45_6	3.2	+12.9	–19.6	+14.5 (0.6)		+18.6 (0.5)	+17.5 (0.7)	+17.6 (0.5)	+17.2 (0.7)	+13.8 (0.8)	+13.3 (0.1)	–9.9 (0.7)	+11.7 (1.5)	+6.4 (1.1)
SK45_18	10.0	+13.9	–18.4	+17.4 (0.8)	+18.7 (1.2)	+19.4 (0.9)	+19.5 (0.4)	+19.9 (1.3)	+17.0 (1.0)	+15.7 (0.5)	+14.8 (0.3)			+4.2 (1.3)
$\Delta^{15}N_{1st\text{-}4th}$				3.6		1.9	4.4	4.7	2.0	3.2	0.6	4.9	–2.0	–1.4

SK58_1	0.3	+14.6	–19.1	+16.6 (0.8)	+19.3 (1.0)	+19.3 (0.6)	+20.5 (0.4)	+20.1 (0.9)	+17.2 (0.6)	+15.8 (0.7)	+14.5 (1.7)	–16.6 (0.6)		+3.2 (1.8)
SK58_2	0.8	+13.1	–19.2	+15.6 (1.0)	+15.6 (0.5)	+17.5 (0.8)	+18.4 (0.9)	+17.4 (1.5)	+14.6 (0.6)	+14.0 (0.4)	+16.1 (1.1)	–14.8 (1.6)		+0.5 (0.5)
SK58_3	1.2	+12.1	–19.4	+14.5 (0.1)	+16.5 (0.4)	+17.3 (0.4)	+17.2 (0.2)	+17.2 (0.2)	+15.7 (0.9)	+11.7 (0.2)		–16.9 (1.1)		+2.1 (0.5)
SK58_4	1.7	+12.0	–19.5	+14.0 (0.7)	+18.5 (1.1)	+17.6 (0.7)	+16.3 (0.4)	+16.6 (0.7)	+15.8 (1.0)	+10.8 (0.7)	+11.6 (1.8)	–15.7 (0.8)		+3.3 (1.6)
$\Delta^{15}N_{1st\text{-}4th}$		2.6	0.4	2.6	0.8	1.7	4.2	3.5	1.4	5.0	2.9	0.9		–0.1
Mixed C3-C4 diet														
RUS9_1	0.3	+12.8	–16.7	+16.0 (0.4)	+18.1 (0.4)	+18.0 (0.1)	+18.8 (0.2)	+19.0 (0.1)	+15.7 (0.1)	+14.6 (0.1)	+11.9 (1.2)	–10.5 (0.1)	+13.7 (1.4)	+6.1 (0.1)
RUS9_2	1.0	+12.4	–16.5	+15.0 (0.4)	+16.2 (0.1)	+16.2 (0.8)	+17.4 (0.1)	+16.7 (0.6)	+14.1 (0.5)	+13.2 (0.3)	+10.1 (0.3)	–11.5 (1.2)	+11.3 (1.7)	+5.7 (0.3)
RUS9_4	2.4	+11.2	–15.4	+14.3 (0.1)	+14.7 (0.7)	+15.8 (0.1)	+16.2 (0.0)	+17.0 (0.3)	+13.9 (0.1)	+11.9 (0.2)	+10.4 (0.5)	–11.9 (0.6)	+12.4 (0.4)	+4.0 (0.2)
RUS9_9	5.8	+10.8	–16.6	+14.6 (0.2)	+14.7 (0.4)	+15.5 (0.4)	+16.0 (0.6)	+16.1 (0.3)	+14.0 (0.9)	+10.3 (0.6)	+9.5 (0.1)	–12.6 (0.8)	+9.5 (0.1)	+4.6 (0.5)
$\Delta^{15}N_{1st\text{-}3rd}$		2.0	–0.1	1.4	3.4	2.5	2.8	2.9	1.7	4.3	2.4	2.1	4.2	1.5

SI Table 2. Stable isotope values, collagen quality indicators, and estimated age at dentine increment formation for all Ekven samples.

Burial	Age at death	Sex	Tooth	Sample ID	% C	% N	C/N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Approximate age
281	~12 yrs	Unknown	Ldm_1	EKV01 1	44.3	15.6	3.3	–12.1	+24.0	0.1
				EKV01 2	42.6	15.2	3.3	–11.8	+23.9	0.5
				EKV01 3	42.7	15.5	3.2	–11.8	+23.3	0.9
				EKV01 4	42.4	15.3	3.2	–11.9	+22.3	1.3
				EKV01 5	42.8	15.6	3.2	–11.5	+21.6	1.7
				EKV01 6	41.2	14.9	3.2	–11.6	+21.4	2.0
				EKV01 7	41.9	15.2	3.2	–11.5	+21.5	2.4
				EKV01 8	42.0	15.2	3.2	–11.7	+21.7	2.8
				EKV01 9	42.0	15.2	3.2	–11.6	+21.4	3.2
				EKV01 10	40.9	14.6	3.3	–11.8	+21.4	3.6
			LM_1	EKV02 1	42.5	15.5	3.2	–11.8	+23.0	0.3
				EKV02 2	42.2	15.4	3.2	–11.7	+21.3	0.9
				EKV02 3	42.3	15.3	3.2	–11.8	+21.1	1.6
				EKV02 4	42.8	15.7	3.2	–11.5	+21.4	2.2
				EKV02 5	41.6	15.2	3.2	–11.6	+21.1	2.9
				EKV02 6	42.3	15.3	3.2	–11.6	+21.0	3.5
				EKV02 7	42.9	15.6	3.2	–11.4	+21.0	4.2
				EKV02 8	43.4	15.7	3.2	–11.3	+21.1	4.8
				EKV02 9	43.1	15.6	3.2	–11.3	+21.2	5.5
				EKV02 10	42.7	15.5	3.2	–11.2	+21.0	6.1

				EKV02 11	42.5	15.4	3.2	–11.1	+20.8	6.8
				EKV02 12	42.8	15.5	3.2	–10.9	+20.8	7.4
				EKV02 13	42.9	15.4	3.3	–11.1	+21.0	8.1
				EKV02 14	42.7	15.3	3.3	–11.2	+21.0	8.7
				EKV02 15	42.8	15.4	3.2	–11.4	+21.1	9.4
				EKV02 16	42.7	15.1	3.3	–11.9	+21.7	10.0
310	Adult	Male	RM_1	EKV04 1	44.9	16.4	3.2	–11.6	+21.6	0.3
				EKV04 2	44.5	16.2	3.2	–11.6	+21.1	0.9
				EKV04 3	44.4	16.1	3.2	–11.4	+21.0	1.4
				EKV04 4	44.2	16.0	3.2	–11.4	+20.7	2.0
				EKV04 5	44.0	16.0	3.2	–11.4	+20.5	2.6
				EKV04 6	44.3	16.2	3.2	–11.1	+20.2	3.2
				EKV04 7	44.4	16.2	3.2	–11.1	+20.5	3.7
				EKV04 8	45.2	16.5	3.2	–11.2	+20.5	4.3
				EKV04 9	44.4	16.2	3.2	–11.1	+20.6	4.9
				EKV04 10	43.3	15.7	3.2	–11.1	+20.5	5.4
				EKV04 11	43.3	15.6	3.2	–11.1	+20.6	6.0
				EKV04 12	42.9	15.5	3.2	–11.2	+20.6	6.6
				EKV04 13	44.0	15.9	3.2	–11.3	+20.6	7.2
				EKV04 14	44.4	16.0	3.2	–11.4	+20.5	7.7
				EKV04 15	45.0	16.5	3.2	–11.3	+20.6	8.3
				EKV04 16	45.8	16.3	3.3	–11.9	+20.6	8.9
				EKV04 17	44.3	15.9	3.3	–11.9	+20.9	9.4
				EKV04 18	44.6	16.0	3.3	–11.9	+21.4	10.0

308	Adolescent	Male	RM_1	EKV05 1	42.0	15.3	3.2	–11.5	+20.5	0.3
				EKV05 2	41.6	15.0	3.2	–11.7	+20.7	1.2
				EKV05 3	42.3	15.4	3.2	–11.5	+20.7	2.1
				EKV05 4	42.8	15.7	3.2	–11.4	+20.8	2.9
				EKV05 5	42.5	15.5	3.2	–11.3	+20.6	3.8
				EKV05 6	42.3	15.5	3.2	–11.2	+20.7	4.7
				EKV05 7	42.4	15.4	3.2	–11.3	+21.1	5.6
				EKV05 8	42.4	15.5	3.2	–11.4	+21.3	6.5
				EKV05 9	42.4	15.5	3.2	–11.6	+21.5	7.4
				EKV05 10	42.8	15.4	3.2	–11.9	+21.7	8.2
				EKV05 11	42.3	15.4	3.2	–11.7	+21.8	9.1
				EKV05 12	43.9	15.6	3.3	–11.8	+22.1	10.0
320	Adult	Male	RM_1	EKV07 1	45.3	16.3	3.3	–11.6	+22.3	0.3
				EKV07 2	48.0	17.5	3.2	–11.1	+21.1	1.1
				EKV07 3	44.6	16.2	3.2	–11.3	+21.2	1.9
				~~EKV07 4~~	~~46.0~~	~~15.5~~	~~3.5~~	~~–12.9~~	~~+21.4~~	~~2.7~~
				EKV07 5	44.3	16.1	3.2	–11.6	+21.2	3.5
				EKV07 6	43.6	15.9	3.2	–11.5	+20.8	4.3
				EKV07 7	44.6	16.1	3.2	–11.4	+20.8	5.1
				EKV07 8	44.4	16.2	3.2	–11.2	+20.6	6.0
				EKV07 9	44.6	16.2	3.2	–11.3	+20.5	6.8
				EKV07 10	43.9	15.9	3.2	–11.3	+20.3	7.6
				EKV07 11	43.8	15.9	3.2	–11.2	+20.5	8.4

				EKV07 12	43.0	15.7	3.2	–11.3	+20.5	9.2
				EKV07 13	42.9	15.5	3.2	–11.4	+20.7	10.0
291	Adult	Female	RM_1	EKV08 1	42.6	15.6	3.2	–11.4	+22.0	0.3
				EKV08 2	43.1	15.8	3.2	–11.5	+20.9	1.0
				EKV08 3	43.5	15.8	3.2	–11.6	+21.0	1.7
				EKV08 4	43.6	15.8	3.2	–11.5	+21.2	2.4
				EKV08 5	43.2	15.7	3.2	–11.5	+21.4	3.1
				EKV08 6	43.2	15.7	3.2	–11.4	+21.8	3.8
				EKV08 7	45.4	16.1	3.3	–11.6	+22.0	4.5
				EKV08 8	43.4	15.8	3.2	–11.3	+21.9	5.2
				EKV08 9	42.9	15.2	3.2	–11.8	+22.0	5.8
				EKV08 10	42.0	15.2	3.2	–11.4	+21.9	6.5
				EKV08 11	42.4	15.5	3.2	–11.4	+21.9	7.2
				EKV08 12	42.6	15.6	3.2	–11.4	+21.3	7.9
				EKV08 13	43.3	15.7	3.2	–11.3	+21.4	8.6
				EKV08 14	43.1	15.6	3.2	–11.6	+21.6	9.3
				EKV08 15	43.7	15.5	3.3	–12.1	+21.3	10.0
318	Adult	Female	RM_1	EKV10 1	47.2	17.1	3.2	–11.5	+21.5	0.3
				EKV10 2	47.0	16.9	3.2	–11.6	+20.3	0.9
				EKV10 3	47.0	17.0	3.2	–11.7	+20.3	1.6
				EKV10 4	47.5	17.0	3.3	–11.7	+20.4	2.2
				EKV10 5	46.4	16.8	3.2	–11.7	+20.4	2.9
				EKV10 6	44.1	15.9	3.2	–11.7	+20.4	3.5
				EKV10 7	45.2	16.3	3.3	–11.5	+20.2	4.2

				EKV10 8	44.7	16.0	3.3	–11.6	+20.2	4.8
				EKV10 9	43.7	15.7	3.3	–11.5	+20.7	5.5
				EKV10 10	42.6	15.5	3.2	–11.7	+20.7	6.1
				EKV10 11	43.2	15.4	3.3	–12.0	+20.7	6.8
				EKV10 12	43.1	15.5	3.2	–12.0	+20.7	7.4
				EKV10 13	43.4	15.6	3.2	–11.8	+20.5	8.1
				EKV10 14	44.5	15.9	3.3	–11.7	+20.6	8.7
				EKV10 15	44.4	15.7	3.3	–12.0	+21.1	9.4
				EKV10 16	43.9	15.5	3.3	–11.9	+21.0	10.0
276	Adult	Female	RM_1	EKV11 1	40.9	14.6	3.3	–12.3	+21.9	0.3
				EKV11 2	40.4	14.6	3.2	–12.0	+20.5	0.9
				EKV11 3	41.4	15.0	3.2	–11.9	+20.7	1.4
				EKV11 4	41.5	15.0	3.2	–11.7	+20.9	2.0
				EKV11 5	~~33.2~~	~~11.3~~	~~3.4~~	~~–13.1~~	+20.3	2.6
				EKV11 6	43.2	15.7	3.2	–11.8	+21.0	3.2
				EKV11 7	42.4	15.4	3.2	–11.9	+20.9	3.7
				EKV11 8	~~46.3~~	~~13.5~~	~~4.0~~	~~–11.9~~	~~+20.9~~	4.3
				EKV11 9	41.9	15.2	3.2	–12.0	+20.8	4.9
				EKV11 10	41.2	14.9	3.2	–12.1	+20.8	5.4
				EKV11 11	41.9	15.2	3.2	–11.9	+21.0	6.0
				EKV11 12	40.8	14.7	3.3	–11.8	+21.3	6.6
				EKV11 13	41.8	15.0	3.2	–11.7	+21.4	7.2
				EKV11 14	42.2	15.2	3.3	–11.7	+21.3	7.7
				EKV11 15	42.3	15.4	3.2	–11.4	+20.9	8.3

				EKV11 16	42.2	15.1	3.3	–11.7	+20.8	8.9
				EKV11 17	44.6	15.0	3.5	–11.3	+21.2	9.4
				EKV11 18	42.8	15.2	3.3	–12.0	+21.2	10.0
220	<12 years	Unknown	Rdm_1	EKV 33 1	41.3	15.0	3.2	–11.7	+23.6	-0.2
				EKV 33 2	42.7	15.6	3.2	–11.6	+23.7	0.1
				EKV 33 3	43.0	15.7	3.2	–11.5	+24.1	0.4
				EKV 33 4	42.6	15.5	3.2	–11.7	+24.4	0.7
				EKV 33 5	42.7	15.7	3.2	–11.8	+23.8	1.0
				EKV 33 6	42.8	15.7	3.2	–11.7	+23.3	1.3
				EKV 33 7	42.7	15.7	3.2	–11.7	+23.5	1.6
				EKV 33 8	42.5	15.6	3.2	–11.7	+23.3	1.8
				EKV 33 9	42.4	15.6	3.2	–11.9	+22.6	2.1
				EKV 33 10	42.8	15.8	3.2	–12.0	+21.8	2.4
				EKV 33 11	42.6	15.7	3.2	–11.9	+21.4	2.7
				EKV 33 12	42.4	15.6	3.2	–11.9	+21.5	3.0
				EKV 33 13	42.9	15.7	3.2	–11.8	+21.8	3.3
			RM_1	EKV12 1	43.9	16.0	3.2	–11.7	+22.6	1.6
				EKV12 2	44.2	15.7	3.3	–12.3	+20.5	2.9
				EKV12 3	43.8	15.9	3.2	–11.9	+20.7	3.3
				EKV12 4	43.5	15.6	3.3	–12.1	+20.6	3.6
				EKV12 5	43.6	15.7	3.2	–12.0	+20.7	4.0
				EKV12 6	41.4	15.1	3.2	–11.8	+21.0	4.6
				EKV12 7	44.5	16.3	3.2	–11.7	+20.9	5.3
				EKV12 8	44.9	16.4	3.2	–11.7	+20.3	6.0

				EKV12 9	45.6	16.4	3.2	–11.8	+20.0	6.4
				EKV12 10	46.0	16.7	3.2	–11.6	+20.2	7.1
				EKV12 11	45.3	16.4	3.3	–11.9	+20.5	7.8
				EKV12 12	43.9	15.8	3.2	–12.4	+20.9	8.1
				EKV12 13	43.3	15.8	3.2	–12.2	+21.5	8.8
				EKV12 14	46.3	15.7	3.2	–12.2	+21.6	9.5
				EKV12 15	42.8	15.3	3.3	–11.8	+20.9	10.2
300	Adult	Male	LM_1	EKV14 1	42.6	15.5	3.2	–11.5	+22.3	0.3
				EKV14 2	42.5	15.5	3.2	–11.4	+21.6	1.0
				EKV14 3	43.2	15.7	3.2	–11.6	+20.9	1.7
				EKV14 4	43.1	15.4	3.3	–11.8	+21.2	2.4
				EKV14 5	43.2	15.5	3.3	–11.5	+21.2	3.1
				EKV14 6	42.7	15.5	3.2	–11.3	+21.1	3.8
				EKV14 7	44.7	16.0	3.3	–11.5	+21.2	4.5
				EKV14 8	43.6	15.7	3.2	–11.3	+21.2	5.2
				EKV14 9	42.3	15.4	3.2	–11.3	+20.9	5.8
				EKV14 10	43.0	15.5	3.2	–11.4	+20.9	6.5
				EKV14 11	42.8	15.5	3.2	–11.4	+21.1	7.2
				EKV14 12	43.4	15.6	3.2	–11.5	+21.6	7.9
				EKV14 13	42.7	15.4	3.2	–11.5	+21.6	8.6
				EKV14 14	42.5	15.5	3.2	–11.7	+21.4	9.3
				EKV14 15	41.6	14.9	3.3	–12.0	+21.1	10.0
280	Subadult	Unknown	RM_1	EKV16 1	41.9	14.8	3.3	–11.9	+22.6	0.3
				EKV16 2	41.9	15.3	3.2	–11.2	+21.4	0.9

				EKV16 3	42.9	15.5	3.2	–11.3	+21.1	1.6
				EKV16 4	42.6	15.6	3.2	–11.0	+20.9	2.2
				EKV16 5	41.5	15.3	3.2	–11.1	+21.0	2.9
				EKV16 6	42.1	15.4	3.2	–11.2	+21.3	3.5
				EKV16 7	41.8	15.3	3.2	–11.3	+21.1	4.2
				EKV16 8	41.4	14.8	3.3	–11.7	+21.0	4.8
				EKV16 9	41.8	15.4	3.2	–11.4	+20.8	5.5
				EKV16 10	41.6	15.3	3.2	–11.5	+20.8	6.1
				EKV16 11	41.6	15.4	3.2	–11.3	+20.8	6.8
				EKV16 12	41.8	15.4	3.2	–11.1	+20.6	7.4
				EKV16 13				double drop		8.1
				EKV16 14	41.6	15.2	3.2	–11.2	+20.4	8.7
				EKV16 15	41.7	15.2	3.2	–11.3	+20.6	9.4
				EKV16 16	41.1	14.8	3.2	–11.8	+20.7	10.0
285- Г	Subadult	Unknown	RM_1	EKV17 1	47.5	17.1	3.2	–11.4	+22.9	0.3
				EKV17 2	47.5	17.1	3.2	–11.6	+21.9	0.9
				EKV17 3	45.7	16.7	3.2	–11.6	+21.4	1.5
				EKV17 4	44.0	16.0	3.2	–11.4	+21.1	2.1
				EKV17 5	41.8	15.3	3.2	–11.4	+20.5	2.7
				EKV17 6	41.9	15.4	3.2	–11.3	+20.3	3.4
				EKV17 7	42.1	15.4	3.2	–11.3	+20.3	4.0
				EKV17 8	42.1	15.4	3.2	–11.1	+20.4	4.6
				EKV17 9	42.1	15.4	3.2	–11.2	+20.6	5.2
				EKV17 10	42.2	15.4	3.2	–11.1	+20.6	5.8

				EKV17 11	42.2	15.2	3.2	–11.5	+20.8	6.4
				EKV17 12	42.0	15.4	3.2	–11.3	+21.0	7.0
				EKV17 13	42.5	15.5	3.2	–11.4	+21.1	7.6
				EKV17 14	42.4	15.5	3.2	–11.5	+21.1	8.2
				EKV17 15	42.0	15.3	3.2	–11.6	+21.4	8.8
				EKV17 16	41.1	14.9	3.2	–11.7	+21.2	9.5
				EKV17 17	41.3	14.7	3.3	–12.0	+21.6	10.1
327	Adolescent	Unknown	LM_1	EKV18 1	44.5	16.0	3.2	–11.3	+24.9	0.3
				EKV18 2	44.0	16.0	3.2	–11.4	+24.3	0.9
				EKV18 3	43.2	15.7	3.2	–11.6	+22.4	1.5
				EKV18 4	43.1	15.7	3.2	–11.5	+21.3	2.1
				EKV18 5	43.0	15.7	3.2	–11.7	+21.0	2.7
				EKV18 6	43.8	16.0	3.2	–11.8	+20.8	3.4
				EKV18 7	43.7	16.0	3.2	–11.8	+20.9	4.0
				EKV18 8	43.7	15.9	3.2	–11.4	+21.0	4.6
				EKV18 9	43.1	15.8	3.2	–11.3	+21.1	5.2
				EKV18 10	42.8	15.6	3.2	–11.4	+20.9	5.8
				EKV18 11						6.4
				EKV18 12	42.3	15.4	3.2	–11.4	+21.1	7.0
				EKV18 13						7.6
				EKV18 14	44.1	16.1	3.2	–11.4	+21.5	8.2
				EKV18 15	44.0	16.0	3.2	–11.4	+21.4	8.8
				EKV18 16	43.8	16.0	3.2	–11.3	+21.3	9.5

				EKV18 17	44.1	16.0	3.2	–11.6	+21.2	10.1
284	Young adult	Female	LM_1	EKV20 1	44.6	15.6	3.3	–12.5	+22.8	0.3
				EKV20 2	44.4	16.2	3.2	–12.1	+22.2	0.8
				EKV20 3	43.7	15.5	3.3	–12.7	+22.8	1.4
				EKV20 4	38.8	14.4	3.1	–11.9	+20.8	1.9
				EKV20 5	40.8	15.0	3.2	–11.8	+20.5	2.5
				EKV20 6	39.9	14.6	3.2	–11.7	+20.9	3.0
				EKV20 7	41.9	15.4	3.2	–11.7	+21.2	3.5
				EKV20 8	42.5	15.4	3.2	–12.0	+22.0	4.1
				EKV20 9	42.7	15.6	3.2	–12.0	+21.8	4.6
				EKV20 10	41.7	15.2	3.2	–12.1	+21.2	5.2
				EKV20 11	41.9	15.3	3.2	–12.1	+21.0	5.7
				EKV20 12	41.4	15.1	3.2	–12.2	+21.1	6.2
				EKV20 13	40.3	14.4	3.3	–12.6	+21.0	6.8
				EKV20 14	40.9	15.0	3.2	–12.0	+21.2	7.3
				EKV20 15	41.2	15.1	3.2	–11.9	+21.1	7.9
				EKV20 16	40.8	15.0	3.2	–11.8	+20.6	8.4
				EKV20 17	40.7	14.9	3.2	–11.7	+21.0	8.9
				EKV20 18	40.7	14.9	3.2	–12.0	+21.3	9.5
				EKV20 19	38.1	13.9	3.2	–11.9	+21.6	10.0
325	Adult	Female	LM_1	EKV21 1	40.6	14.5	3.3	–11.8	+23.8	0.3
				EKV21 2	40.9	14.9	3.2	–11.9	+22.9	0.7
				EKV21 3	41.2	15.0	3.2	–12.0	+22.5	1.2

				EKV21 4	41.2	15.2	3.2	–11.9	+22.0	1.6
				EKV21 5	40.9	15.0	3.2	–11.9	+22.3	2.1
				EKV21 6	41.0	15.0	3.2	–11.8	+21.6	2.5
				EKV21 7	40.7	14.7	3.2	–11.9	+21.4	2.9
				EKV21 8	41.2	15.1	3.2	–11.7	+21.2	3.4
				EKV21 9	41.5	15.1	3.2	–11.5	+21.1	3.8
				EKV21 10	40.9	14.9	3.2	–11.5	+21.1	4.3
				EKV21 11	41.4	15.1	3.2	–11.5	+20.9	4.7
				EKV21 12	41.0	14.9	3.2	–11.5	+20.9	5.1
				EKV21 13	41.8	15.3	3.2	–11.5	+20.8	5.6
				EKV21 14	40.5	14.8	3.2	–11.5	+20.8	6.0
				EKV21 15	40.8	14.9	3.2	–11.4	+21.1	6.5
				EKV21 16	40.5	14.8	3.2	–11.3	+21.2	6.9
				EKV21 17	40.2	14.7	3.2	–11.4	+21.1	7.3
				EKV21 18	39.4	14.4	3.2	–11.5	+21.2	7.8
				EKV21 19	41.6	15.3	3.2	–11.5	+21.7	8.2
				EKV21 20	41.8	15.4	3.2	–11.3	+21.2	8.7
				EKV21 21	41.9	15.3	3.2	–11.4	+20.6	9.1
				EKV21 22	41.5	15.1	3.2	–11.6	+20.7	9.5
				EKV21 23	41.6	15.2	3.2	–11.5	+21.3	10.0
216	Adult	Male	RM_1	EKV22 1	41.9	15.5	3.2	–11.8	+22.7	0.7
				EKV22 2	42.5	15.4	3.2	–11.7	+21.3	1.3
				EKV22 3	42.4	15.4	3.2	–11.6	+21.4	2.0
				EKV22 4	41.8	15.3	3.2	–11.5	+21.2	2.7

				EKV22 5	41.9	15.2	3.2	–11.5	+21.0	3.4
				EKV22 6	41.9	15.3	3.2	–11.5	+20.7	4.7
				EKV22 7	41.7	15.0	3.2	–11.7	+20.5	5.4
				EKV22 8	41.3	15.2	3.2	–11.6	+20.9	6.1
				EKV22 9	40.9	15.0	3.2	–11.5	+21.0	6.8
				EKV22 10	40.8	14.8	3.2	–11.5	+21.1	7.2
				EKV22 11	40.5	14.8	3.2	–11.5	+21.2	7.8
				EKV22 12	40.7	14.8	3.2	–11.3	+21.3	8.5
				EKV22 13	40.6	14.8	3.2	–11.4	+21.3	8.9
				EKV22 14	41.0	14.8	3.2	–11.5	+21.1	9.6
				EKV22 15	40.2	14.5	3.2	–11.7	+21.0	10.3
				EKV22 16	40.1	14.3	3.3	–12.0	+21.2	11.0
326	Adult	Female	RM_1	EKV23 1	41.5	15.2	3.2	–11.6	+23.8	0.3
				EKV23 2	41.2	15.1	3.2	–11.8	+22.8	0.9
				EKV23 3	40.8	14.9	3.2	–11.7	+22.5	1.4
				EKV23 4	41.9	15.5	3.2	–11.7	+21.4	2.0
				EKV23 5	41.4	15.1	3.2	–11.8	+21.2	2.6
				EKV23 6	42.2	15.4	3.2	–11.9	+20.7	3.2
				EKV23 7	41.4	15.2	3.2	–12.1	+20.8	3.7
				EKV23 8	41.9	15.5	3.2	–11.8	+20.5	4.3
				EKV23 9	41.6	15.2	3.2	–11.7	+20.6	4.9
				EKV23 10	41.5	15.2	3.2	–11.6	+20.8	5.4
				EKV23 11	41.7	15.4	3.2	–11.5	+21.2	6.0
				EKV23 12	41.6	15.3	3.2	–11.5	+21.4	6.6

				EKV23 13	41.1	15.2	3.2	–11.6	+21.1	7.1
				EKV23 14	41.5	15.2	3.2	–11.5	+21.0	7.7
				EKV23 15	42.3	15.4	3.2	–11.6	+20.8	8.3
				EKV23 16	41.8	15.2	3.2	–11.4	+21.1	8.9
				EKV23 17	41.8	15.2	3.2	–11.4	+21.2	9.4
				EKV23 18	41.8	15.3	3.2	–11.6	+20.7	10.0
323	Adult	Female	RM_1	EKV25 1	41.9	15.1	3.2	–11.4	+24.3	0.3
				EKV25 2	42.4	15.6	3.2	–11.3	+23.6	0.9
				EKV25 3	42.1	15.4	3.2	–11.5	+23.1	1.5
				EKV25 4	43.2	15.7	3.2	–11.5	+22.0	2.1
				EKV25 5	42.7	15.5	3.2	–11.5	+21.5	2.7
				EKV25 6	42.9	15.6	3.2	–11.6	+21.1	3.4
				EKV25 7	42.1	15.4	3.2	–11.5	+20.5	4.0
				EKV25 8	43.7	16.0	3.2	–11.5	+20.5	4.6
				EKV25 9	41.9	15.3	3.2	–11.5	+20.4	5.2
				EKV25 10	42.1	15.4	3.2	–11.6	+20.6	5.8
				EKV25 11	42.3	15.6	3.2	–11.5	+20.8	6.4
				EKV25 12	41.6	15.2	3.2	–11.4	+21.0	7.0
				EKV25 13	42.3	15.5	3.2	–11.5	+21.1	7.6
				EKV25 14	42.3	15.5	3.2	–11.5	+21.0	8.2
				EKV25 15	41.8	15.4	3.2	–11.6	+20.4	8.8
				EKV25 16	41.7	15.5	3.2	–11.5	+21.1	9.5
				EKV25 17	41.7	15.4	3.2	–11.7	+21.2	10.1
321	Adult	Male	RM_1	EKV27 1	40.4	14.7	3.2	–12.3	+21.6	0.3

				EKV27 2	41.3	15.1	3.2	–12.3	+20.4	1.0
				EKV27 3	42.4	15.1	3.3	–12.5	+20.4	1.6
				EKV27 4	41.9	15.5	3.2	–12.2	+20.4	2.3
				EKV27 5	42.7	15.6	3.2	–12.2	+20.8	2.9
				EKV27 6	42.9	15.1	3.3	–12.3	+20.9	3.6
				EKV27 7	42.3	15.3	3.2	–11.9	+20.6	4.2
				EKV27 8	44.0	14.7	3.5	–11.8	+20.4	4.9
				EKV27 9	42.2	15.2	3.3	–11.7	+20.5	5.5
				EKV27 10	42.9	15.4	3.3	–11.9	+20.4	6.2
				EKV27 11	43.5	15.5	3.3	–11.9	+21.0	6.8
				EKV27 12	42.5	15.5	3.2	–11.8	+21.0	7.5
				EKV27 13	42.5	15.3	3.2	–11.9	+21.1	8.1
				EKV27 14	42.3	15.5	3.2	–12.1	+21.3	8.8
				EKV27 15	42.4	15.5	3.2	–11.9	+21.4	9.4
				EKV27 16	43.2	15.5	3.3	–12.0	+21.3	10.1
277	Adult	Female	RM_1	EKV29 1	40.5	14.7	3.2	–12.0	+23.1	0.3
				EKV29 2	41.4	15.0	3.2	–12.0	+21.8	0.8
				EKV29 3	41.9	15.3	3.2	–11.8	+20.3	1.3
				EKV29 4	41.5	15.2	3.2	–11.4	+21.1	1.8
				EKV29 5	42.4	15.4	3.2	–11.6	+21.7	2.3
				EKV29 6	41.6	15.0	3.2	–11.8	+20.4	2.9
				EKV29 7	42.3	15.5	3.2	–11.7	+20.0	3.4
				EKV29 8	42.1	15.4	3.2	–11.7	+19.8	3.9
				EKV29 9	42.4	15.5	3.2	–11.6	+19.8	4.4

				EKV29 10	42.5	15.5	3.2	–11.4	+20.0	4.9
				EKV29 11	42.1	15.4	3.2	–11.5	+20.1	5.4
				EKV29 12	42.8	15.5	3.2	–11.4	+20.3	5.9
				EKV29 13	42.1	15.4	3.2	–11.4	+20.1	6.4
				EKV29 14	43.9	16.0	3.2	–11.4	+20.4	6.9
				EKV29 15	42.2	15.4	3.2	–11.6	+20.5	7.4
				EKV29 16	42.2	15.5	3.2	–11.5	+20.4	8.0
				EKV29 17	42.3	15.5	3.2	–11.6	+20.3	8.5
				EKV29 18	43.1	15.7	3.2	–11.5	+20.3	9.0
				EKV29 19	42.9	15.7	3.2	–11.6	+21.0	9.5
				EKV29 20	42.8	15.6	3.2	–11.7	+21.4	10.0
311	Young adult	Male	LM_1	EKV31_1	42.7	15.6	3.2	–11.5	+25.1	0.3
				EKV31_2	43.5	16.1	3.2	–11.3	+23.6	0.8
				EKV31_3	43.9	16.2	3.2	–11.5	+22.6	1.4
				EKV31_4	43.6	16.2	3.1	–11.5	+22.5	1.9
				EKV31_5	44.6	16.6	3.1	–11.5	+21.9	2.5
				EKV31_6	45.1	16.6	3.2	–11.5	+21.5	3.0
				EKV31_7	45.7	16.8	3.2	–11.4	+21.5	3.5
				EKV31_8	45.0	16.5	3.2	–11.3	+21.6	4.1
				EKV31_9	44.7	16.4	3.2	–11.4	+21.7	4.6
				EKV31_10	44.8	16.4	3.2	–11.4	+21.5	5.2
				EKV31_11	43.3	16.0	3.2	–11.6	+21.2	5.7
				EKV31_12	43.4	16.0	3.2	–11.6	+21.4	6.2

				EKV31_13	43.0	15.8	3.2	–11.6	+21.4	6.8
				EKV31_14	43.3	16.0	3.2	–11.6	+21.5	7.3
				EKV31_15	43.1	15.8	3.2	–11.6	+21.4	7.8
				EKV31_16	43.4	15.9	3.2	–11.6	+21.2	8.4
				EKV31_17	44.1	16.2	3.2	–11.6	+21.1	8.9
				EKV31_18	44.4	16.3	3.2	–11.6	+21.5	9.5
				EKV31_19	45.1	16.4	3.2	–11.6	+21.6	10.0
279	Infant	Unknown	Ldm_1	EKV34_1	43.2	16.0	3.2	–11.9	+22.9	-0.2
				EKV34_2	44.1	16.2	3.2	–11.3	+22.9	0.1
				EKV34_3	44.1	16.3	3.2	–11.2	+23.2	0.4
				EKV34_4	43.1	15.9	3.2	–11.3	+23.4	0.7
				EKV34_5	43.5	16.0	3.2	–11.2	+23.6	1.0
				EKV34_6	43.0	15.8	3.2	–11.3	+23.6	1.3
				EKV34_7	43.8	16.0	3.2	–11.3	+23.8	1.6
				EKV34_8	43.5	15.9	3.2	–11.3	+23.4	1.9
				EKV34_9	43.5	16.0	3.2	–11.3	+22.9	2.2
				EKV34_10	42.8	15.7	3.2	–11.4	+22.9	2.5
				EKV34_11	41.5	15.2	3.2	–11.7	+23.1	2.8
298	Infant	Unknown	Rdm_1	EKV35_1				Insufficient collagen		
				EKV35_2	41.1	15.2		–12.4	+21.0	0.1
				EKV35_3	42.5	15.6		–12.1	+21.9	0.4
				EKV35_4	43.3	15.8		–12.0	+22.0	0.7
				EKV35_5	43.0	15.6		–12.1	+22.2	0.9

				EKV35_6	43.1	15.8		–12.2	+22.0	1.2
				EKV35_7	42.7	15.7		–12.1	+21.9	1.5
				EKV35_8	42.6	15.6		–12.1	+21.6	1.8
				EKV35_9	43.4	15.9		–12.2	+21.8	2.1
45	29	Female	M1	SK45_1				no data		0.3
				SK45_2	45.2	16.7	3.2	–19.8	+13.8	0.9
				SK45_3	44.4	16.3	3.2	–18.4	+13.6	1.4
				SK45_4	43.0	15.9	3.2	–20.0	+12.9	2.0
				SK45_5	43.2	15.8	3.2	–19.7	+12.7	2.6
				SK45_6	42.9	15.8	3.2	–19.6	+12.9	3.2
				SK45_7	43.3	15.9	3.2	–19.1	+13.1	3.7
				SK45_8	43.6	17.2	3.1	–18.4	+13.8	4.3
				SK45_9	43.9	16.0	3.2	–17.8	+13.2	4.9
				SK45_10	43.9	16.0	3.2	–17.4	+13.8	5.4
				SK45_11	42.7	15.6	3.2	–17.1	+13.3	6.0
				SK45_12	43.1	15.9	3.2	–17.1	+13.4	6.6
				SK45_13				no data		7.1
				SK45_14	42.8	15.8	3.2	–17.2	+13.4	7.7
				SK45_15	42.8	15.7	3.2	–17.4	+13.4	8.3
				SK45_16	43.0	15.7	3.2	–17.8	+13.5	8.9
				SK45_17	43.0	15.7	3.2	–18.2	+13.8	9.4
				SK45_18	43.8	15.9	3.2	–18.4	+13.9	10
58	51	Male	M1	SK58_1				no data		0.3
				SK58_2	44.3	16.2	3.2	–19.2	+13.1	0.8

				SK58_3	43.2	15.9	3.2	–19.4	+12.1	1.2
				SK58_4	43.4	16.0	3.2	–19.5	+12.0	1.7
				SK58_5	42.3	15.6	3.2	–19.6	+12.2	2.1
				SK58_6	44.4	16.1	3.2	–20.1	+12.6	2.6
				SK58_7	43.8	16.0	3.2	–19.5	+12.4	3.1
				SK58_8	43.2	15.8	3.2	–19.5	+12.1	3.5
				SK58_9	43.1	15.8	3.2	–19.5	+12.3	4.0
9	Young adult	Female	M1	RUS9_1	42.4	15.5	3.2	–16.7	+12.8	0.3
				RUS9_2	41.8	15.3	3.2	–16.5	+12.4	1.0
				RUS9_3	42.5	15.5	3.2	–16.0	+11.6	1.7
				RUS9_4	41.9	15.3	3.2	–15.4	+11.2	2.4
				RUS9_5	42.2	15.4	3.2	–15.4	+10.9	3.1
				RUS9_6	42.0	15.4	3.2	–15.7	+10.8	3.8
				RUS9_7	42.8	15.7	3.2	–16.1	+10.9	4.4
				RUS9_8	43.3	15.8	3.2	–16.4	+11.0	5.1
				RUS9_9	43.8	15.9	3.2	–16.6	+10.8	5.8
				RUS9_10	43.2	15.8	3.2	–15.9	+10.6	6.5
				RUS9_11	43.6	15.8	3.2	–15.8	+10.3	7.2
				RUS9_12	43.3	15.8	3.2	–15.9	+10.1	7.9
				RUS9_13				–17.0	+10.1	8.6
				RUS9_14	42.8	15.5	3.2	–16.0	+9.8	9.3
				RUS9_15	42.3	15.2	3.3	–15.0	+9.7	10.0

SI Table 3. Stable carbon and nitrogen isotope values of Ekven bone collagen samples

Burial	Sample ID	Sex	Age	%C	%N	C/N	δ^{13}C (‰)	δ^{15}N (‰)
276	EKV11	F	Adult	44.3	16.5	3.1	–12.0	+20.3
277	EKV29	F	Adult	46.0	17.0	3.2	–11.6	+19.6
278	EKV150	?	Adult	46.1	17.1	3.1	–12.1	+20.3
279	EKV34	?	Infant	43.9	16.3	3.1	–11.5	+22.6
280	EKV16	?	Subadult	41.9	15.5	3.2	–11.6	+19.4
281	EKV1	?	<12 yrs	44.0	16.3	3.2	–11.4	+20.7
283A	EKV137	F	Adult	45.5	16.8	3.2	–11.7	+20.8
283B	EKV127	?	Adolescent	36.6	13.4	3.2	–12.3	+20.0
284	EKV20	F	Adolescent	45.4	16.6	3.2	–12.0	+20.1
285Г	EKV17	?	Adolescent	43.5	16.1	3.2	–11.7	+20.6
288	EKV123	?	Adult	44.6	16.5	3.2	–12.1	+19.8
289	EKV131	M	Adult	44.1	16.4	3.1	–11.7	+20.5
290	EKV145	?	Mature adult	44.8	16.5	3.2	–12.2	+20.3
291	EKV8	F	Adult	41.0	15.2	3.2	–11.5	+20.6
294	EKV122	?	Infant	45.1	16.5	3.2	–12.4	+22.4
296	EKV119	?	Adult	44.8	16.6	3.2	–11.6	+20.8
297	EKV147	M	Mature adult	41.6	15.0	3.2	–12.0	+21.0
298	EKV35	?	<3 yrs	44.1	16.3	3.2	–12.3	+21.8
299	EKV140	?	Adult	42.0	15.5	3.2	–12.4	+20.7
300	EKV14	M	Adult	45.9	17.1	3.1	–11.2	+20.2
308	EKV5	M	Adolescent	42.9	15.9	3.1	–11.4	+21.0

309	EKV134	F	Mature adult	44.6	16.4	3.2	–11.8	+20.7
310	EKV4	M	Adult	44.0	16.2	3.2	–11.6	+20.6
311	EKV31	M	Young adult	45.0	16.6	3.2	–12.0	+20.0
312	EKV129	F	Young adult	42.7	15.9	3.1	–11.5	+20.3
314	EKV121	F	Adult	46.5	17.2	3.2	–11.4	+20.9
318	EKV10	F	Adult	46.4	17.3	3.1	–11.3	+19.7
320	EKV7	M	Adult	44.2	16.3	3.2	–11.3	+20.7
321	EKV27	M	Adult	45.1	16.7	3.2	–12.2	+20.3
322	EKV146	?	Infant	42.9	15.8	3.2	–12.7	+20.8
323	EKV25	F	Young adult	41.8	15.5	3.1	–11.6	+20.3
324	EKV133	M	Mature adult	45.5	16.9	3.1	–11.5	+20.9
325	EKV21	F	Adult	46.1	17.1	3.2	–11.9	+20.5
326	EKV23	F	Young adult	44.5	16.2	3.2	–11.8	+20.7
327	EKV18	?	Adolescent	45.9	16.7	3.2	–12.1	+21.0

SI Table 4. Amino acid nitrogen isotope values of wild fauna from Nunalleq, Alaska.

Species	Sample ID	Ala	Gly	Val	Leu	Ile	Thr	Ser	Pro	Asx	Glx	Hyp	Phe	Lys
Bearded seal	AK_491	23.69	9.86	30.49	25.46	25.73	-7.59	18.36	23.08	25.35	23.43	25.57	13.06	10.46
	AK_491	23.74	12.01	28.33	25.43	26.50	-9.12	20.02	24.37	25.89	22.64	25.94	12.63	11.11
	AK_491	23.71	10.83	25.15	24.70	24.75	-10.50	19.01	23.96	24.72	22.22	25.42	11.69	9.76
	AVERAGE	**23.72**	**10.90**	**27.99**	**25.19**	**25.66**	**-9.07**	**19.13**	**23.80**	**25.32**	**22.76**	**25.64**	**12.46**	**10.44**
	SD	0.03	1.07	2.69	0.43	0.87	1.46	0.83	0.66	0.59	0.61	0.27	0.70	0.68
	Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
Beluga	AK_463_a	25.68	11.87	31.30	27.57	30.18	-21.61	13.19	28.59	26.86	29.84	29.71	10.71	8.23
	AK_463_a	26.86	11.87	28.63	26.99	28.59	-23.83	12.38	28.56	26.03	29.25	29.30	10.15	8.32
	AK_463_a	26.14	11.91	27.10	26.44	26.84	-24.12	12.71	28.43	25.71	29.10	28.89	9.93	8.07
	AVERAGE	**26.22**	**11.88**	**29.01**	**27.00**	**28.54**	**-23.19**	**12.76**	**28.53**	**26.20**	**29.39**	**29.30**	**10.27**	**8.21**
	SD	0.59	0.02	2.13	0.56	1.67	1.37	0.41	0.09	0.60	0.39	0.41	0.40	0.12
	Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
Beluga	AK_462_a	27.22	15.40	30.72	28.44	31.15	-23.43	17.48	29.65	27.74	31.03	30.35	10.65	9.11
	AK_462_a	28.21	14.68	28.31	27.79	31.05	-25.02	15.79	29.51	27.38	31.10	30.72	12.21	10.36
	AK_462_a	27.46	14.22	28.36	27.77	28.74	-25.25	14.51	28.67	26.81	30.30	30.20	10.85	9.76
	AVERAGE	**27.63**	**14.77**	**29.13**	**28.00**	**30.31**	**-24.57**	**15.93**	**29.28**	**27.31**	**30.81**	**30.42**	**11.24**	**9.74**
	SD	0.52	0.60	1.38	0.38	1.36	0.99	1.49	0.53	0.47	0.45	0.27	0.85	0.62
	Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
Bearded seal	AK_492_a	24.58	10.96	26.90	24.27	26.84	-12.83	19.31	24.47	24.94	27.99	25.94	10.07	9.22

	AK_492_a	24.61	10.63	25.49	23.98	24.38	-13.77	17.11	24.47	24.18	27.24	25.78	10.55	8.41
	AK_492_a	24.19	10.61	25.56	23.49	24.18	-14.35	15.13	24.17	24.44	27.16	25.14	9.94	9.19
	AVERAGE	**24.46**	**10.73**	**25.98**	**23.91**	**25.13**	**-13.65**	**17.18**	**24.37**	**24.52**	**27.46**	**25.62**	**10.19**	**8.94**
	SD	0.23	0.20	0.80	0.40	1.48	0.77	2.09	0.17	0.39	0.46	0.42	0.32	0.46
	Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
Beluga	AK_461_a	27.00	12.29	27.93	27.33	27.80	-24.41	12.52	28.09	26.70	30.08	27.88	10.41	8.92
	AK_461_a	27.52	11.83	26.87	27.20	26.81	-25.43	11.73	27.65	26.60	29.31	26.35	7.89	7.76
	AK_461_a	26.49	11.10	26.48	25.92	26.76	-25.37	11.55	26.73	24.80	28.69	26.76	10.67	8.84
	AVERAGE	**27.00**	**11.74**	**27.09**	**26.82**	**27.13**	**-25.07**	**11.93**	**27.49**	**26.03**	**29.36**	**27.00**	**9.66**	**8.51**
	SD	0.52	0.60	0.75	0.78	0.59	0.57	0.52	0.69	1.07	0.70	0.79	1.53	0.65
	Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
Caribou	AK_453_a	2.33	-0.87	7.61	4.95	4.93	-9.19	2.98	5.06	5.98	5.40	5.30	5.77	-0.41
	AK_453_a	2.74	-1.66	5.92	4.37	4.16	-9.37	1.56	5.33	5.18	5.30	6.97	6.05	-0.74
	AK_453_a	2.06	-1.88	4.84	4.14	2.62	-10.98	0.85	5.39	5.27	5.21	6.37	5.76	-0.38
	AVERAGE	**2.38**	**-1.47**	**6.13**	**4.49**	**3.90**	**-9.85**	**1.80**	**5.26**	**5.48**	**5.31**	**6.21**	**5.86**	**-0.51**
	STDEV	0.34	0.53	1.40	0.42	1.17	0.99	1.08	0.17	0.44	0.09	0.85	0.17	0.20
	Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
Caribou	AK_450_a	3.48	-2.15	10.96	8.85	7.50	-7.85	-0.20	4.23	6.28	5.22	5.20	5.73	0.12
	AK_450_a	4.26	-1.12	12.65	10.35	9.05	-8.70	1.16	4.53	7.35	6.49	5.91	6.83	-0.90
	AK_450_a	2.95	-1.51	13.45	8.64	8.91	-8.92	1.45	4.41	7.11	5.81	5.66	8.35	-0.14
	AVERAGE	**3.56**	**-1.59**	**12.35**	**9.28**	**8.49**	**-8.49**	**0.80**	**4.39**	**6.91**	**5.84**	**5.59**	**6.97**	**-0.31**
	SD	0.66	0.52	1.27	0.93	0.85	0.57	0.88	0.15	0.56	0.63	0.36	1.31	0.53
	Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**

Caribou	AK_452_a	3.50	-3.38	10.66	7.98	8.26	-7.71	0.08	3.74	5.50	4.98	4.53	7.05	-0.73
	AK_452_a	2.94	-3.10	11.96	8.09	8.24	-7.78	-0.96	2.56	6.07	5.25	4.85	7.49	-1.09
	AK_452_a	2.44	-2.82	12.14	9.29	7.05	-7.33	-0.76	3.26	6.39	5.96	5.27	6.31	-0.41
	AVERAGE	**2.96**	**-3.10**	**11.59**	**8.45**	**7.85**	**-7.60**	**-0.55**	**3.19**	**5.99**	**5.40**	**4.88**	**6.95**	**-0.74**
	SD	0.53	0.28	0.81	0.73	0.69	0.24	0.56	0.60	0.45	0.51	0.37	0.59	0.34
	Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
Walrus	AK_469_a	20.86	8.53	26.44	24.26	23.80	-11.58	10.79	19.03	19.36	22.18	20.13	12.07	10.03
	AK_469_a	20.96	9.54	27.55	24.82	22.86	-10.06	11.85	19.19	20.83	22.21	21.08	13.98	11.43
	AK_469_a	19.47	9.21	28.61	24.52	24.29	-8.76	12.32	19.27	20.68	22.55	20.51	13.85	11.28
	AVERAGE	**20.43**	**9.09**	**27.53**	**24.53**	**23.65**	**-10.13**	**11.65**	**19.16**	**20.29**	**22.31**	**20.57**	**13.30**	**10.92**
	SD	0.83	0.52	1.08	0.28	0.73	1.41	0.78	0.12	0.81	0.20	0.47	1.07	0.77
	Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
Ringed seal	AK_499_a	26.14	10.61	29.22	27.83	No data	-17.91	14.05	23.98	23.79	28.15	24.75	11.02	8.68
	AK_499_a	26.26	11.10	31.39	29.61	No data	-17.35	14.01	23.77	23.77	27.57	25.45	12.12	9.39
	AK_499_a	24.01	10.88	31.43	29.37	No data	-17.12	14.30	22.93	22.84	26.67	24.73	12.09	8.42
	AVERAGE	**25.47**	**10.86**	**30.68**	**28.93**	**No data**	**-17.46**	**14.12**	**23.56**	**23.47**	**27.46**	**24.98**	**11.74**	**8.83**
	SD	1.26	0.25	1.27	0.96	No data	0.41	0.16	0.55	0.54	0.74	0.41	0.63	0.50
	Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
Walrus	AK_470_a	20.36	9.04	28.24	21.98	22.97	-11.94	5.66	19.57	20.47	21.78	20.38	11.73	10.25
	AK_470_a	18.19	7.44	25.79	22.29	22.23	-9.71	10.62	18.55	19.94	21.66	19.66	11.72	8.84
	AK_470_a	16.56	6.82	24.88	21.08	22.40	-10.11	10.39	17.91	19.39	21.05	18.90	10.74	8.88

AVERAGE	**18.37**	**7.77**	**26.30**	**21.78**	**22.53**	**-10.59**	**8.89**	**18.67**	**19.93**	**21.50**	**19.65**	**11.40**	**9.32**
SD	1.90	1.14	1.74	0.63	0.39	1.19	2.80	0.84	0.54	0.39	0.74	0.57	0.80

SI Table 5 Stable nitrogen isotope values of human amino acids.

Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
EKV18_A	28.69	27.91	30.34	25.67	26.22	-23.35	24.05	34.43	27.86	30.66	33.81	10.91	9.63
EKV18_A	29.13	28.35	30.84	42.28	26.90	-21.47	24.90	34.84	28.50	30.80	34.24	10.44	11.24
EKV18_A	28.78	27.40	29.55	25.19	26.42	-22.60	23.58	34.11	27.51	29.75	33.37	8.10	9.94
EKV18_A	28.89	27.74	30.39	39.48	27.85	-22.22	23.78	33.88	27.38	30.15	33.82	7.96	9.43
AVERAGE	**28.87**	**27.85**	**30.28**	**33.15**	**26.85**	**-22.41**	**24.08**	**34.32**	**27.81**	**30.34**	**33.81**	**9.35**	**10.06**
SD	0.19	0.40	0.53	9.00	0.73	0.78	0.58	0.42	0.50	0.48	0.35	1.54	0.81
Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
EKV18_C	28.40	23.14	29.30	26.27	26.52	-24.81	17.76	31.88	26.83	29.28	31.83	12.38	8.94
EKV18_C	29.68	24.26	30.21	27.31	27.63	-22.44	19.02	32.73	27.26	30.62	32.28	14.13	10.29
EKV18_C	28.22	24.21	30.11	27.02	27.23	-22.14	18.83	33.11	26.98	30.24	32.29	18.21	11.78
AVERAGE	**28.77**	**23.87**	**29.87**	**27.02**	**27.23**	**-23.16**	**18.54**	**32.57**	**27.02**	**30.05**	**32.13**	**14.91**	**10.34**
SD	0.80	0.63	0.50	0.65	0.62	1.44	0.68	0.63	0.22	0.69	0.26	2.99	1.42
Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
EKV18_F	27.84	22.09	28.29	26.27	26.52	-21.39	18.57	27.79	24.87	28.48	26.95	9.23	7.43
EKV18_F	28.66	21.71	28.07	24.52	23.91	-22.94	17.38	28.14	24.03	28.45	26.48	6.57	7.64
EKV18_F	28.29	21.79	29.26	24.95	24.63	-22.14	17.99	28.43	23.70	29.06	27.08	9.04	9.24
AVERAGE	**28.26**	**21.86**	**28.54**	**24.92**	**24.60**	**-22.16**	**17.98**	**28.12**	**24.20**	**28.66**	**26.83**	**8.28**	**8.10**
SD	0.41	0.20	0.63	0.38	0.67	0.78	0.60	0.32	0.60	0.34	0.32	1.48	0.99

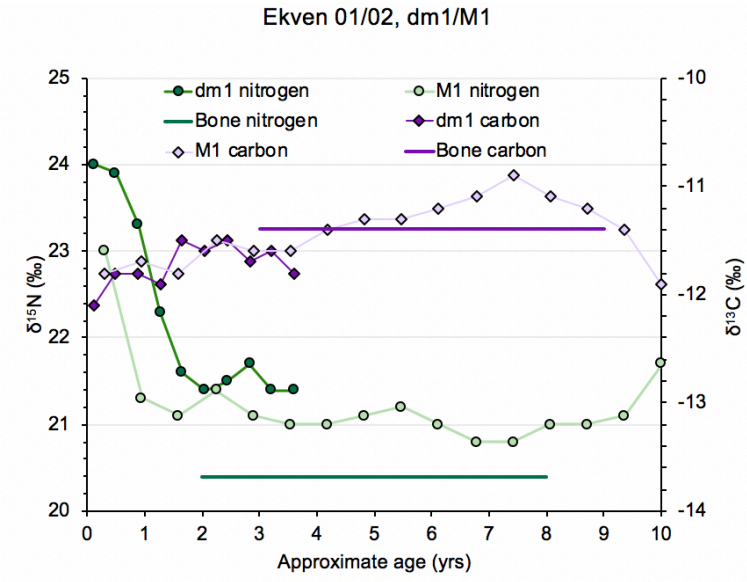
Sample ID	Ala	Gly	Val	Leu	Ile	Thr	Ser	Pro	Asx	Glx	Hyp	Phe	Lys
EKV18_Q	28.16	22.01	28.48	26.52	26.31	-23.50	19.60	27.87	24.57	29.35	27.93	9.14	7.39
EKV18_Q	28.10	22.12	28.65	27.04	28.80	-23.60	19.30	27.94	25.08	29.11	27.93	10.01	7.01
AVERAGE	**28.13**	**22.06**	**28.57**	**26.78**	**27.56**	**-23.55**	**19.45**	**27.90**	**24.82**	**29.23**	**27.93**	**9.58**	**7.20**
Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
EKV23_A	28.46	26.50	30.66	23.64	28.46	-28.17	25.03	33.11	28.06	30.38	32.56	8.94	10.97
EKV23_A	28.18	26.56	30.12	23.09	23.45	-29.62	25.27	33.23	28.43	31.39	33.46	8.53	10.95
EKV23_A	28.04	26.09	29.84	22.12	26.33	-27.70	21.75	32.63	27.68	30.12	32.19	8.25	9.86
AVERAGE	**28.23**	**26.38**	**30.21**	**22.95**	**26.08**	**-28.50**	**24.02**	**32.99**	**28.06**	**30.64**	**32.74**	**8.58**	**10.60**
SD	0.21	0.26	0.42	0.77	2.52	1.00	1.97	0.31	0.38	0.67	0.65	0.35	0.63
Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
EKV23_H	28.44	21.59	29.85	26.87	27.33	-28.36	16.97	30.12	26.30	29.96	29.81	8.19	9.84
EKV23_H	28.49	21.91	30.08	26.05	27.01	-26.57	17.72	29.94	26.14	30.03	29.98	7.09	10.77
EKV23_H	27.69	21.24	29.85	25.66	22.09	-26.56	17.01	29.37	25.84	29.24	28.75	15.65	9.91
AVERAGE	**28.21**	**21.58**	**29.93**	**26.19**	**25.48**	**-27.16**	**17.23**	**29.81**	**26.09**	**29.74**	**29.51**	**10.31**	**10.17**
SD	0.45	0.33	0.13	0.62	2.93	1.03	0.42	0.39	0.23	0.43	0.66	4.66	0.52
Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
EKV23_D	27.39	21.88	29.40	26.01	29.00	-27.48	16.93	30.74	26.39	29.00	29.74	-0.94	9.70
EKV23_D	28.20	22.39	29.14	26.32	24.61	-25.55	17.77	31.58	26.53	29.72	30.29	5.33	11.20
EKV23_D	28.15	22.39	29.32	26.41	27.92	-24.82	18.36	31.37	26.71	29.52	30.03	7.01	11.05
AVERAGE	**27.91**	**22.22**	**29.28**	**26.25**	**27.18**	**-25.95**	**17.69**	**31.23**	**26.55**	**29.41**	**30.02**	**3.80**	**10.65**
SD	0.45	0.29	0.13	0.21	2.29	1.37	0.72	0.44	0.16	0.37	0.28	4.19	0.83
Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**

EKV23_B	27.73	24.94	30.08	23.87	27.50	-25.85	20.62	33.10	27.83	31.11	31.41	6.33	11.35
EKV23_B	28.31	25.28	30.53	26.89	24.97	-25.27	26.61	33.63	27.54	30.13	32.21	8.14	10.02
EKV23_B	28.71	25.51	30.79	24.05	26.49	-24.97	26.15	33.97	28.60	30.43	32.18	6.91	11.69
AVERAGE	**28.25**	**25.24**	**30.46**	**24.94**	**26.32**	**-25.36**	**24.46**	**33.57**	**27.99**	**30.55**	**31.93**	**7.13**	**11.02**
SD	0.49	0.29	0.36	1.70	1.27	0.45	3.33	0.44	0.55	0.50	0.45	0.92	0.88
Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
EKV23_F	27.50	21.36	28.16	21.70	25.44	-25.25	22.76	30.34	26.59	29.73	28.77	6.08	10.72
EKV23_F	27.18	21.39	28.24	24.25	25.84	-25.41	23.93	30.39	26.04	28.75	29.37	4.98	11.22
EKV23_F	27.25	21.80	28.99	24.40	23.92	-22.23	19.43	30.33	26.56	29.95	28.73	4.85	10.14
AVERAGE	**27.31**	**21.52**	**28.46**	**23.45**	**25.07**	**-24.30**	**22.04**	**30.35**	**26.39**	**29.48**	**28.96**	**5.30**	**10.69**
SD	0.17	0.25	0.46	1.52	1.01	1.79	2.33	0.03	0.31	0.64	0.36	0.68	0.54
Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
RUS09_M	14.27	11.76	14.16	12.84	12.56	-12.36	10.05	16.21	13.77	15.88	16.80	12.62	4.19
RUS09_M	14.30	12.10	15.14	13.16	13.81	-11.51	10.70	16.16	13.96	15.74	17.21	12.11	3.89
AVERAGE	**14.28**	**11.93**	**14.65**	**13.00**	**13.19**	**-11.93**	**10.38**	**16.18**	**13.86**	**15.81**	**17.00**	**12.37**	**4.04**
SD	0.02	0.24	0.69	0.23	0.88	0.60	0.46	0.03	0.13	0.10	0.29	0.36	0.21
Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
RUS09_H	14.42	9.89	14.97	12.59	11.87	-12.01	9.54	15.61	13.37	15.23	15.84	9.61	4.22
RUS09_H	14.74	10.69	14.38	12.48	9.78	-13.12	9.45	16.40	14.57	15.80	16.30	9.42	4.98
AVERAGE	**14.58**	**10.29**	**14.67**	**12.54**	**10.82**	**-12.56**	**9.50**	**16.00**	**13.97**	**15.51**	**16.07**	**9.51**	**4.60**
SD	0.23	0.56	0.42	0.08	1.48	0.78	0.06	0.56	0.85	0.40	0.33	0.13	0.54
Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
RUS09_O	14.73	13.02	16.16	13.76	No data	-12.28	9.90	17.34	13.70	15.70	16.24	10.06	5.90

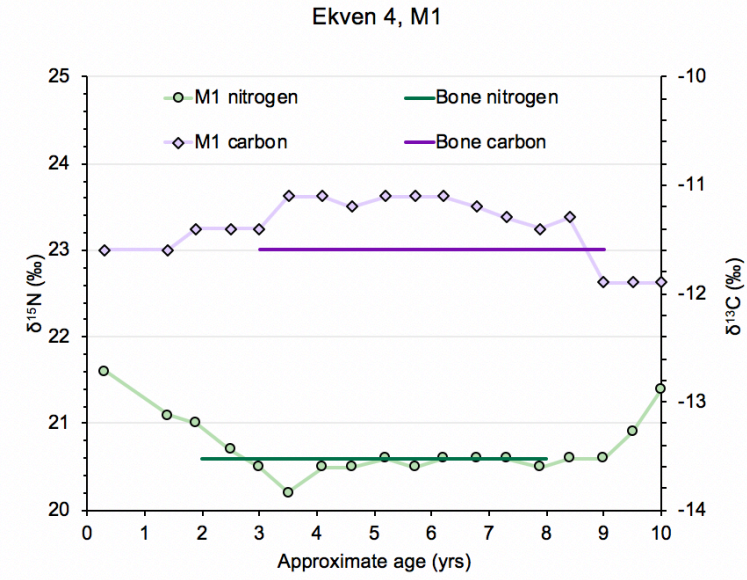
RUS09_O	15.23	13.37	16.15	13.93	No data	-10.63	10.32	17.42	14.41	16.78	17.08	12.46	5.53
AVERAGE	**14.98**	**13.20**	**16.16**	**13.93**	No data	**-12.56**	**10.11**	**17.38**	**14.05**	**16.24**	**16.66**	**11.26**	**5.71**
SD	0.36	0.25	0.01	0.24	No data	1.17	0.29	0.05	0.50	0.76	0.60	1.70	0.26
Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
RUS09_P	15.74	14.55	17.84	13.60	14.96	-10.54	11.07	18.72	15.74	17.98	18.92	12.70	6.04
RUS09_P	16.26	14.61	18.39	14.67	14.54	-10.40	12.74	18.94	15.63	18.06	19.06	14.67	6.12
AVERAGE	**16.00**	**14.58**	**18.11**	**14.13**	**14.54**	**-10.47**	**11.90**	**18.83**	**15.69**	**18.02**	**18.99**	**13.68**	**6.08**
SD	0.37	0.04	0.39	0.75	0.60	0.10	1.17	0.15	0.08	0.05	0.10	1.40	0.06
Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
SK45_6	14.27	13.54	23.00	0.45	17.31	-10.70	13.43	17.65	17.13	18.69	17.27	13.34	5.20
SK45_6	15.19	14.62	23.87	33.67	16.15	-9.36	14.25	18.14	17.89	19.07	18.18	11.40	7.02
SK45_6	13.98	13.14	20.13	31.24	no data	-9.72	12.25	16.82	16.51	18.10	17.32	10.41	7.01
AVERAGE	**14.48**	**13.77**	**22.33**	**21.79**	**11.23**	**-9.93**	**13.31**	**17.54**	**17.18**	**18.62**	**17.59**	**11.72**	**6.41**
SD	0.63	0.77	1.96	18.52	9.54	0.69	1.00	0.67	0.69	0.49	0.51	1.49	1.05
Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
SK45_1	17.92	16.96	22.60	31.89	No data	-14.54	14.20	21.96	19.70	20.43	21.95	10.50	4.83
SK45_1	18.44	16.99	22.41	30.26	No data	-14.24	14.07	21.99	19.06	20.85	22.19	10.04	4.28
SK45_1	17.82	17.17	21.46	31.75	No data	-15.45	13.34	21.66	18.95	20.22	22.88	8.50	6.25
AVERAGE	**18.06**	**17.04**	**22.16**	**31.30**	**No data**	**-14.75**	**13.87**	**21.87**	**19.23**	**20.50**	**22.34**	**9.68**	**5.12**
SD	0.34	0.11	0.61	0.91	No data	0.63	0.46	0.18	0.40	0.32	0.48	1.05	1.01
Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
SK45_3	16.84	15.19	19.37	27.91	15.16	-12.93	14.25	18.76	17.54	20.48	18.76	10.02	5.74
SK45_3	16.66	15.30	18.44	26.78	13.88	-11.30	12.99	18.69	16.84	20.31	19.05	12.78	7.75

SK45_3	16.74	15.52	19.07	26.81	No data	-13.43	14.60	18.86	16.68	19.25	19.12	10.77	5.28
AVERAGE	16.75	15.34	18.96	27.17	9.73	-12.55	13.95	18.77	17.02	20.01	18.98	11.19	6.26
SD	0.09	0.17	0.47	0.65	8.33	1.11	0.85	0.09	0.46	0.66	0.19	1.43	1.32
Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
SK45_18	16.51	15.16	19.41	15.15	0.06	No data	14.54	19.09	15.92	18.34	18.59	0.06	5.36
SK45_18	17.60	15.79	17.31	17.13	0.95	No data	14.79	19.60	17.25	19.74	19.97	0.95	4.48
SK45_18	17.96	16.05	19.41	16.01	1.28	No data	15.10	19.82	17.83	20.04	21.15	1.28	2.87
AVERAGE	**17.36**	**15.67**	**18.71**	**16.10**	**0.77**	**No data**	**14.81**	**19.50**	**17.00**	**19.37**	**19.90**	**0.77**	**4.24**
SD	0.75	0.46	1.21	1.00	0.63	No data	0.28	0.37	0.98	0.91	1.28	0.63	1.26
Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
SK45_2	17.72	17.90	17.80	15.99	No data	-16.85	16.21	21.61	18.03	20.18	22.22	13.58	4.74
SK45_2	18.04	18.21	19.28	16.29	No data	-13.67	17.07	22.35	18.67	20.16	22.19	0.01	6.04
SK45_2	18.35	18.24	19.30	17.36	No data	-14.04	11.19	22.42	18.71	21.74	22.43	0.06	5.04
AVERAGE	**18.03**	**18.12**	**18.80**	**16.55**	**No data**	**-14.85**	**14.82**	**22.13**	**18.47**	**20.70**	**22.28**	**4.55**	**5.27**
SD	0.32	0.19	0.86	0.72	No data	1.74	3.18	0.45	0.38	0.91	0.13	7.82	0.68
Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
SK58_4	14.78	11.63	19.72	26.74	13.00	-14.83	12.55	16.76	16.97	18.15	17.20	12.69	5.01
SK58_4	13.71	10.59	18.17	24.83	12.24	-15.85	12.65	16.04	15.36	17.73	16.83	8.96	2.94
SK58_4	13.44	10.23	17.66	24.14	15.77	-16.37	9.49	16.08	15.04	16.80	15.84	9.07	1.94
AVERAGE	**13.97**	**10.81**	**18.51**	**25.24**	**13.67**	**-15.68**	**11.56**	**16.29**	**15.79**	**17.56**	**16.62**	**10.24**	**3.30**
SD	0.71	0.72	1.07	1.35	1.86	0.78	1.80	0.40	1.03	0.69	0.71	2.12	1.57
Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
SK58_1	15.86	15.13	19.56	36.27	No data	-16.16	15.09	20.11	17.11	18.65	19.45	8.88	1.58

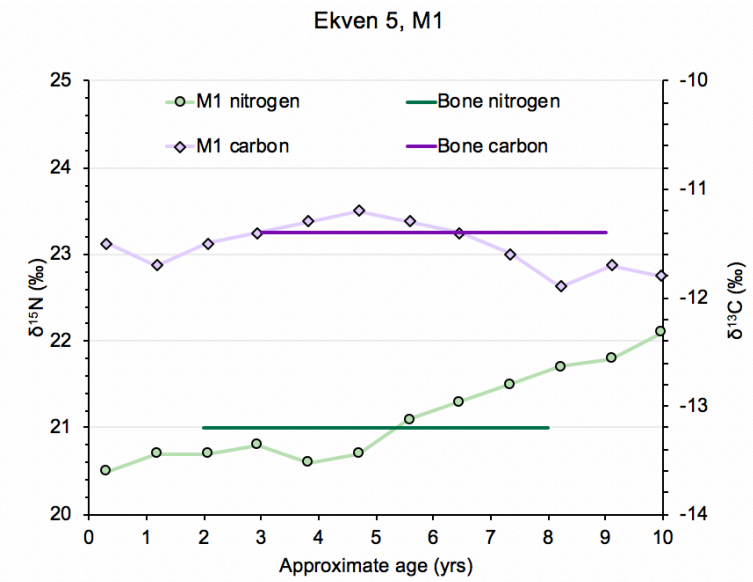
SK58_1	17.37	16.44	20.06	34.47	No data	-16.32	12.61	20.96	17.82	19.90	21.18	11.75	5.05
SK58_1	16.69	15.81	18.20	31.27	No data	-17.28	15.89	20.47	16.66	19.29	19.72	6.38	2.90
AVERAGE	**16.64**	**15.79**	**19.27**	**34.00**	**No data**	**-16.58**	**14.53**	**20.51**	**17.20**	**19.28**	**20.12**	**9.00**	**3.18**
SD	0.76	0.66	0.96	2.53	No data	0.61	1.71	0.43	0.58	0.62	0.93	2.69	1.75
Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
SK58_3	14.42	11.60	16.49	14.42	No data	-17.17	8.80	17.35	15.54	17.65	17.05	12.74	1.66
SK58_3	14.42	11.49	16.83	14.82	No data	-17.87	7.83	16.99	16.61	17.30	17.38	7.74	2.59
SK58_3	14.57	11.92	16.11	14.33	No data	-15.64	13.16	17.09	14.90	16.94	17.28	12.96	2.02
AVERAGE	**14.47**	**11.67**	**16.48**	**14.52**	**No data**	**-16.89**	**9.93**	**17.15**	**15.69**	**17.30**	**17.24**	**11.14**	**2.09**
SD	0.08	0.22	0.36	0.26	No data	1.14	2.84	0.19	0.86	0.35	0.17	2.95	0.47
Sample ID	**Ala**	**Gly**	**Val**	**Leu**	**Ile**	**Thr**	**Ser**	**Pro**	**Asx**	**Glx**	**Hyp**	**Phe**	**Lys**
SK58_2	15.88	14.63	15.57	18.55	No data	-16.22	15.10	18.22	15.44	17.46	18.48	1.58	1.08
SK58_2	14.46	13.49	15.18	15.29	No data	-14.94	16.20	17.65	14.23	16.75	15.59	10.46	-0.24
SK58_2	16.49	13.85	16.06	15.23	No data	-13.29	16.99	19.28	14.16	18.30	18.21	15.81	0.51
AVERAGE	**15.61**	**13.99**	**15.60**	**16.36**	**No data**	**-14.82**	**16.10**	**18.38**	**14.61**	**17.50**	**17.43**	**9.28**	**0.45**
SD	1.04	0.58	0.44	1.90	No data	1.47	0.95	0.83	0.72	0.77	1.60	7.19	0.66



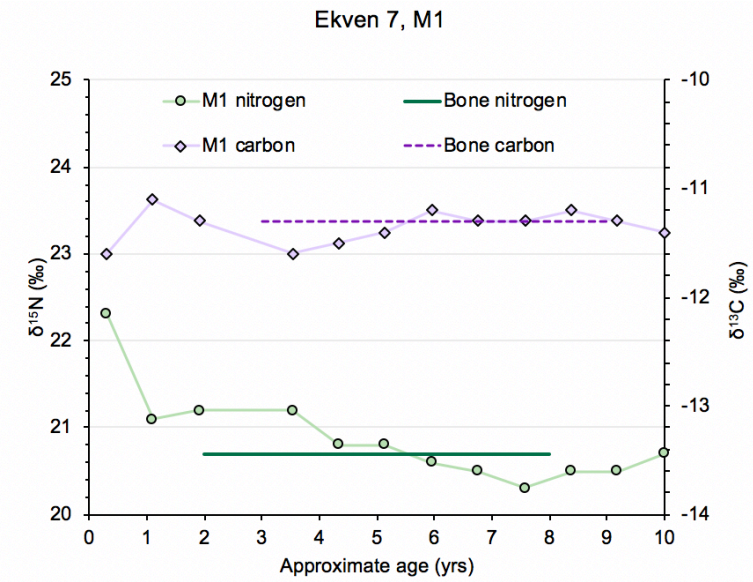
SI fig. 1. Burial 281 (EKV01/02), subadult of unknown sex. Bone collagen values do not correspond to the x-axis.



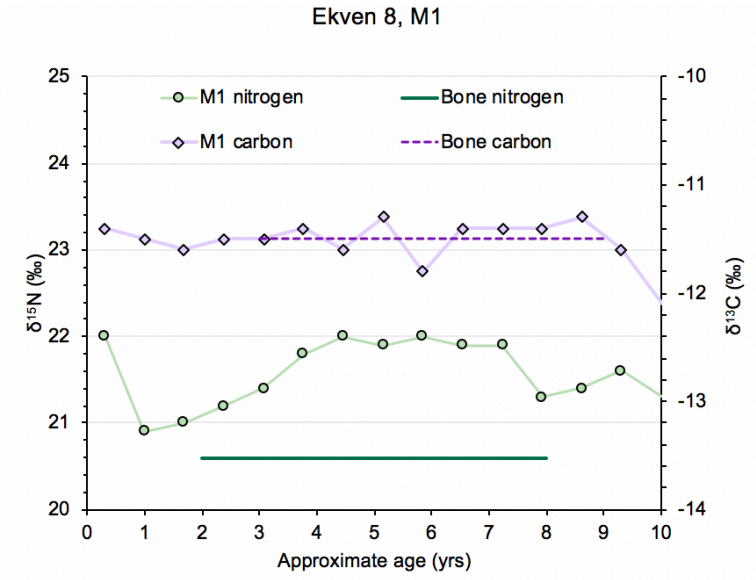
SI fig. 2 Burial 310 (EKV4), adult male. Bone collagen values do not correspond to the x-axis.



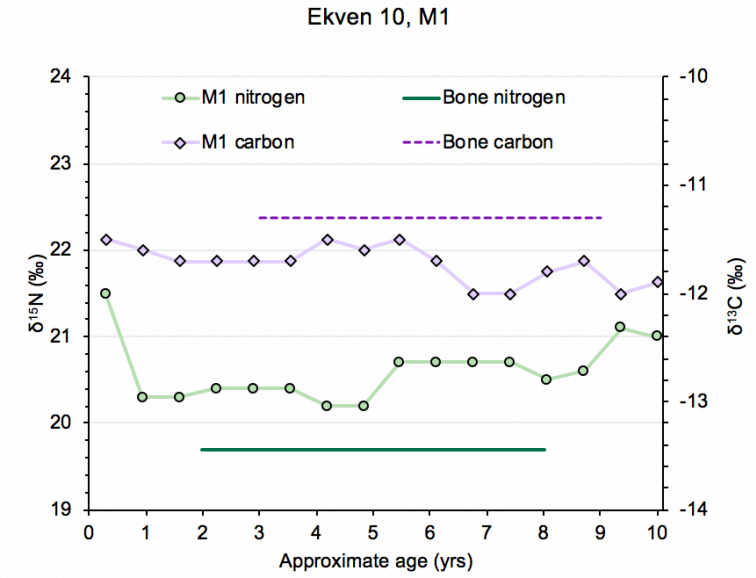
SI fig. Burial 308 (EKV5), adolescent male. Bone collagen values do not correspond to the x-axis.



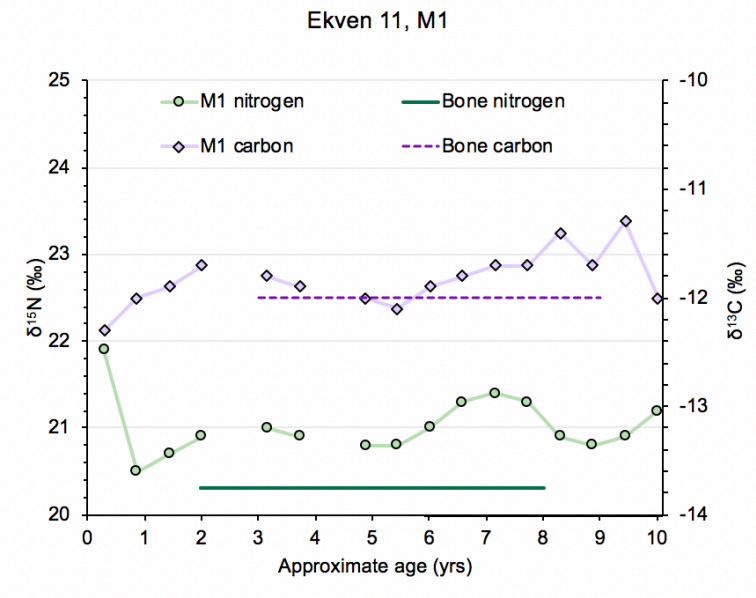
SI Fig. 4 Burial 320 (EKV07), adult male. Bone collagen values do not correspond to the x-axis.



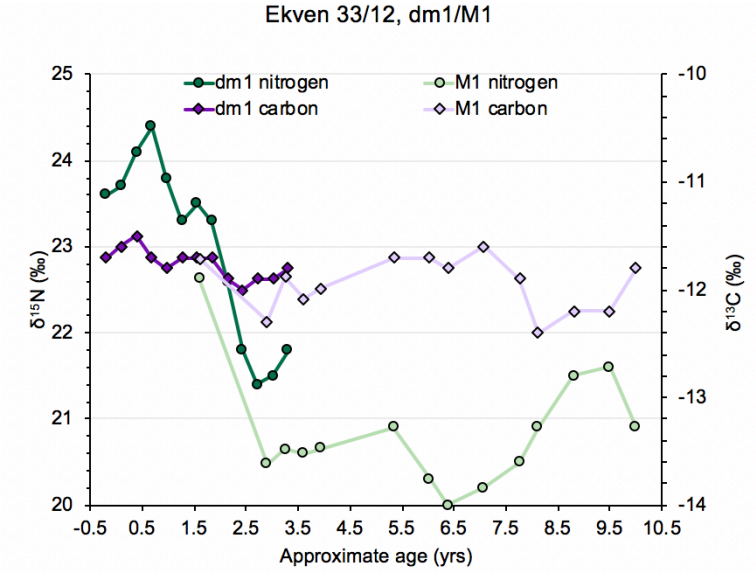
SI Fig. 5 Burial 291 (EKV08), adult female. Bone collagen values do not correspond to the x-axis.



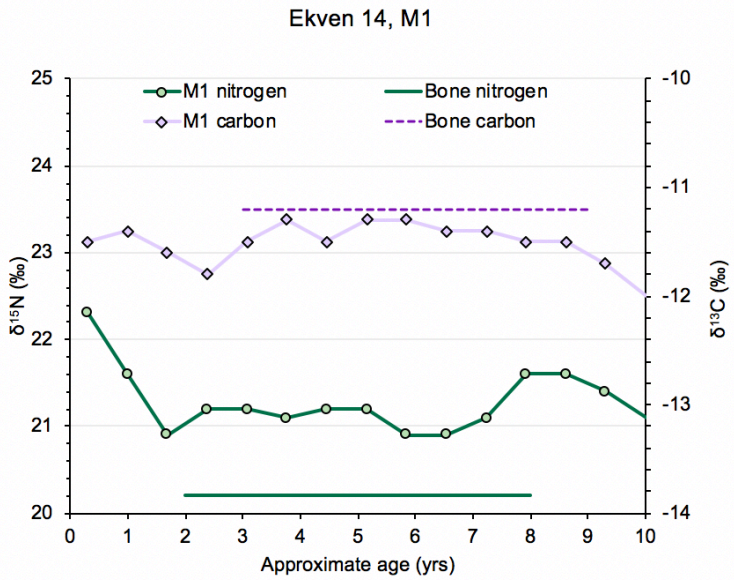
SI Fig. 6 Burial 318 (EKV10), adult female. Bone collagen values do not correspond to the x-axis.



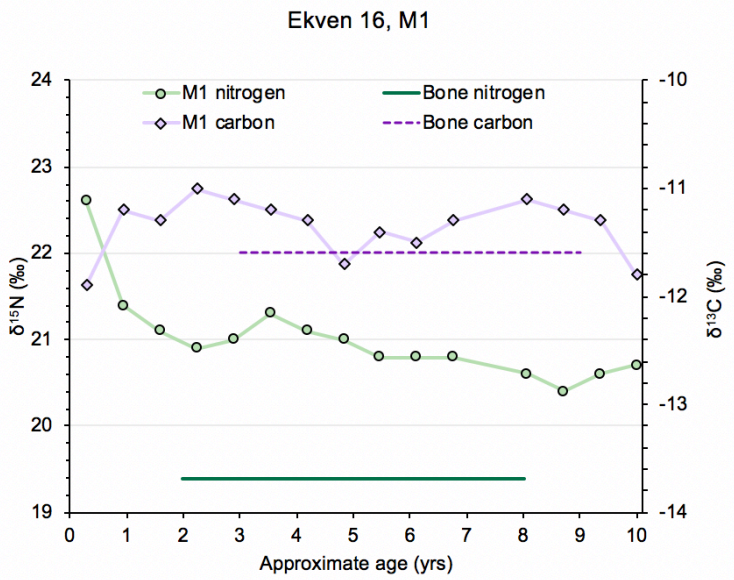
SI Fig 7 Burial 276 (EKV11), adult female. Bone collagen values do not correspond to the x-axis.



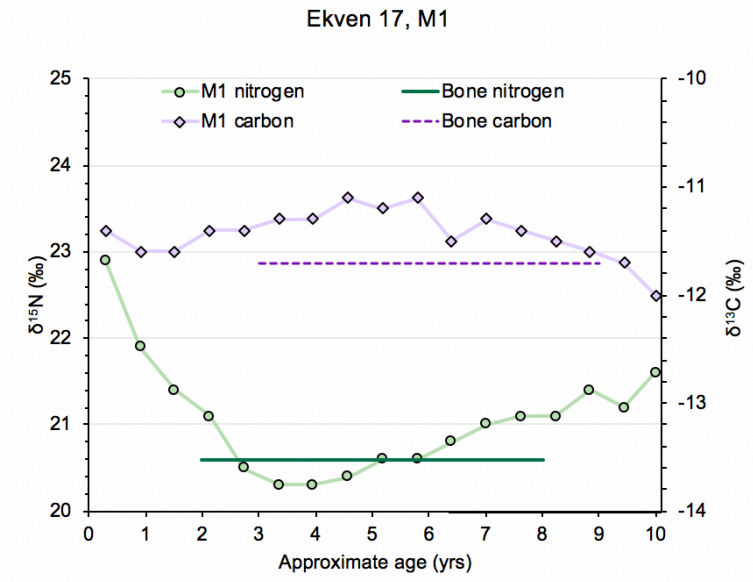
SI Fig. 8. Burial 220 (EKV33/12), subadult of unknown sex. Bone collagen values do not correspond to the x-axis.



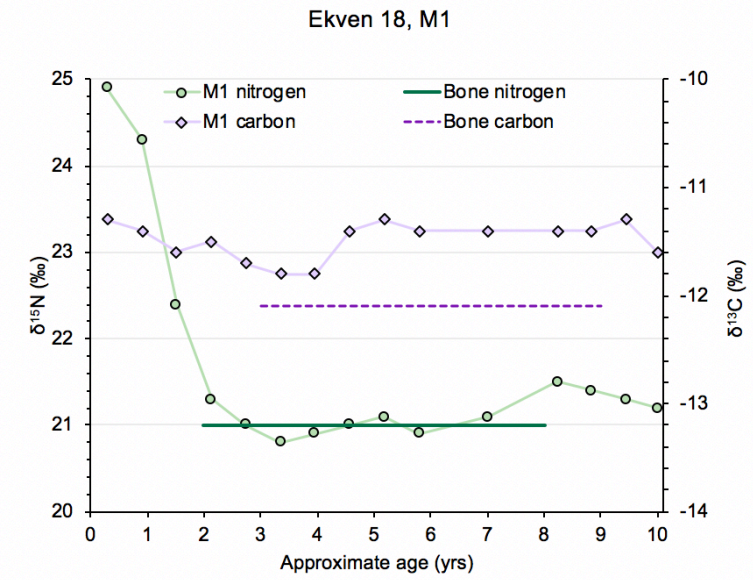
SI Fig. 9 Burial 300 (EKV14), adult male. Bone collagen values do not correspond to the x-axis.



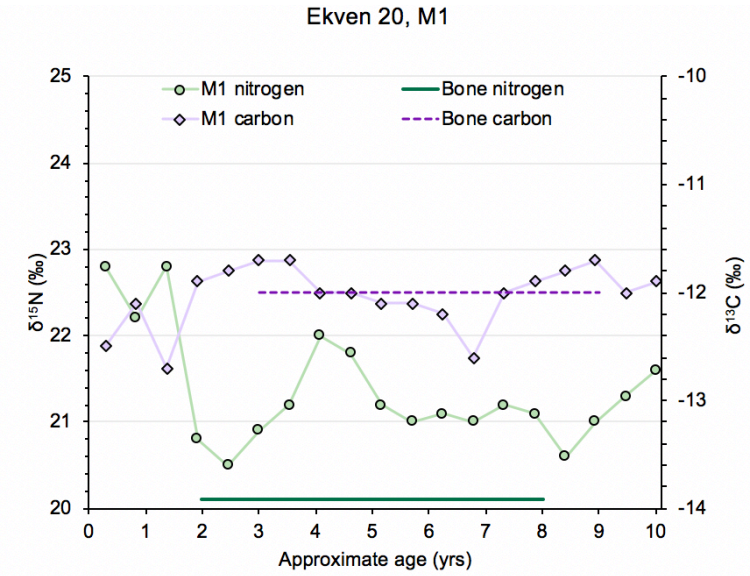
SI Fig. 10. Burial 280 (EKV16), subadult of unknown sex. Bone collagen values do not correspond to the x-axis.



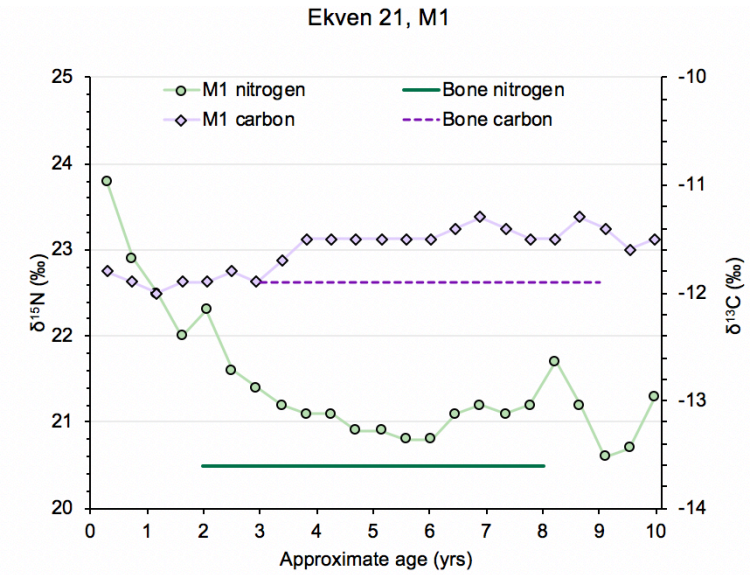
SI Fig. 11 Burial 285Г (EKV17), adolescent of unknown sex. Bone collagen values do not correspond to the x-axis.



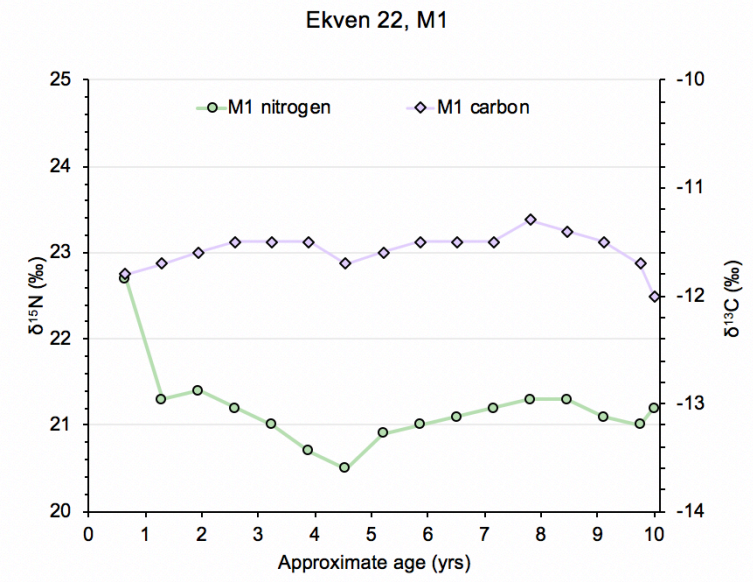
SI Fig. 12. Burial 327 (EKV18), adolescent of unknown sex. Bone collagen values do not correspond to the x-axis.



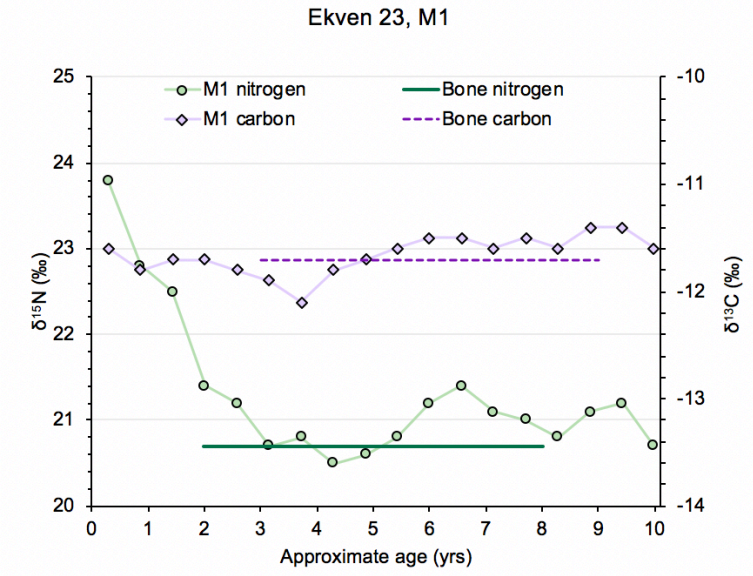
SI Fig. 13 Burial 284 (EKV20), adolescent female. Bone collagen values do not correspond to the x-axis.



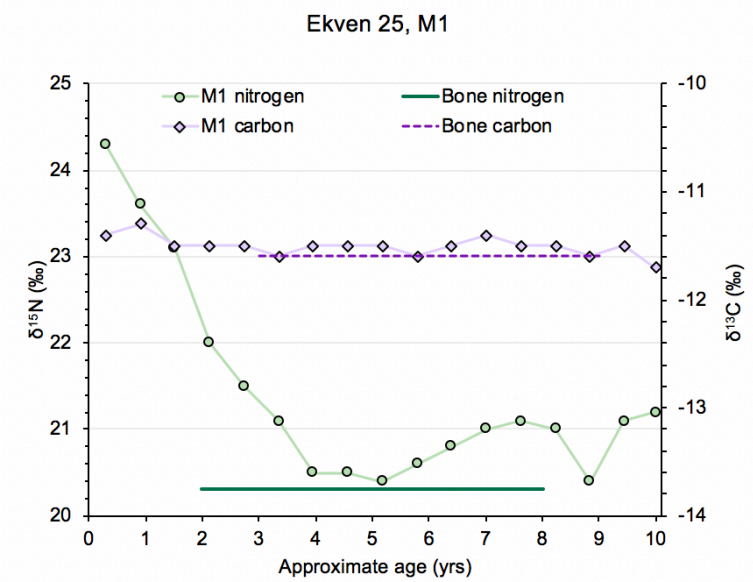
SI Fig. 14 Burial 325 (EKV21), adult female. Bone collagen values do not correspond to the x-axis.



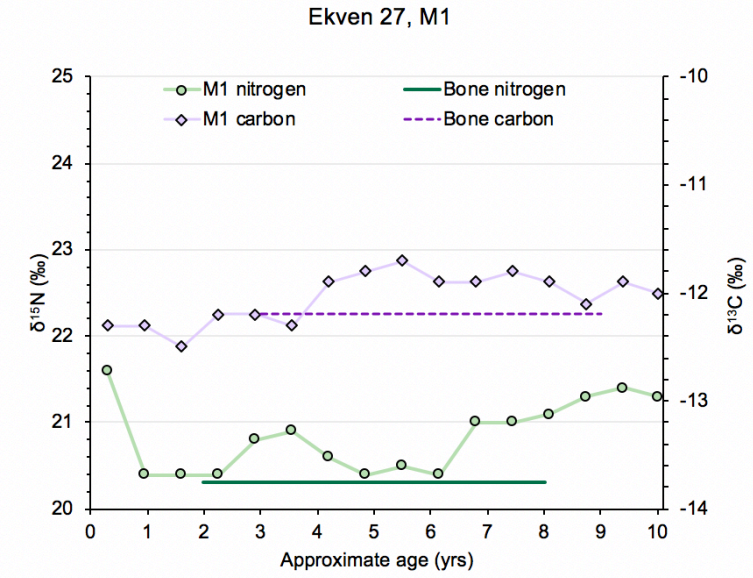
SI Fig. 15. Burial 216 (EKV22), adult male. A bone sample was not available for this individual.



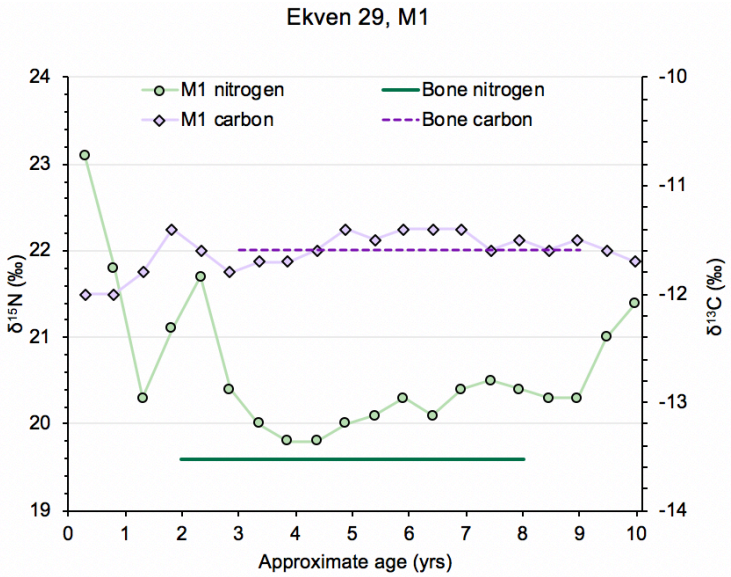
SI Fig. 16 Burial 326 (EKV23), adult female. Bone collagen values do not correspond to the x-axis.



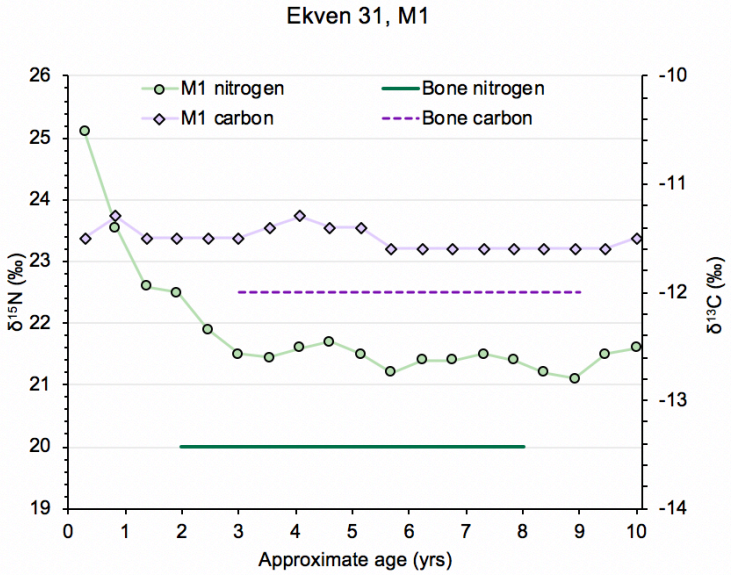
SI Fig. 17. Burial 323 (EKV25), adult female. Bone collagen values do not correspond to the x-axis.



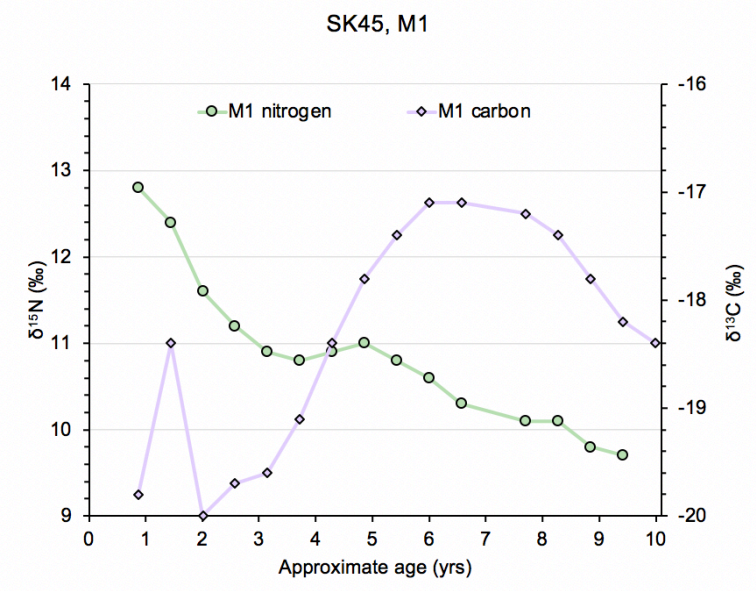
SI Fig. 18 Burial 321 (EKV27), adult male. Bone collagen values do not correspond to the x-axis.



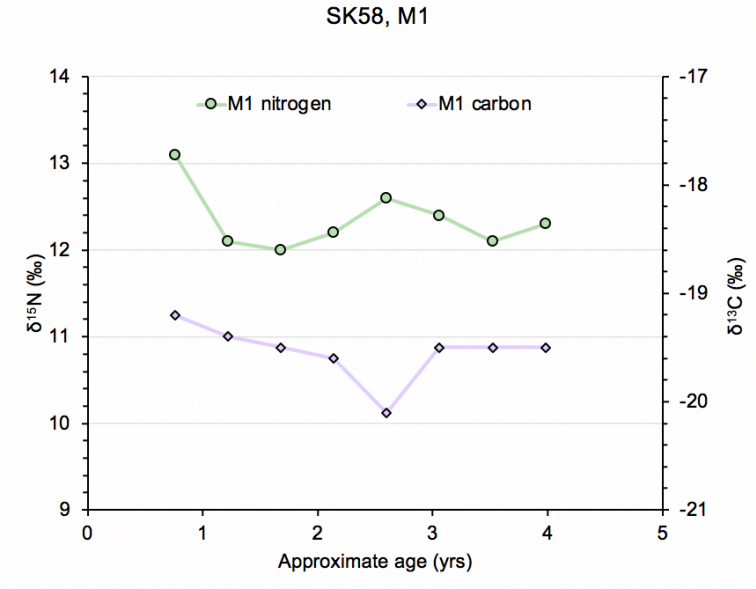
SI Fig. 19 Burial 277 (EKV29), adult female. Bone collagen values do not correspond to the x-axis.



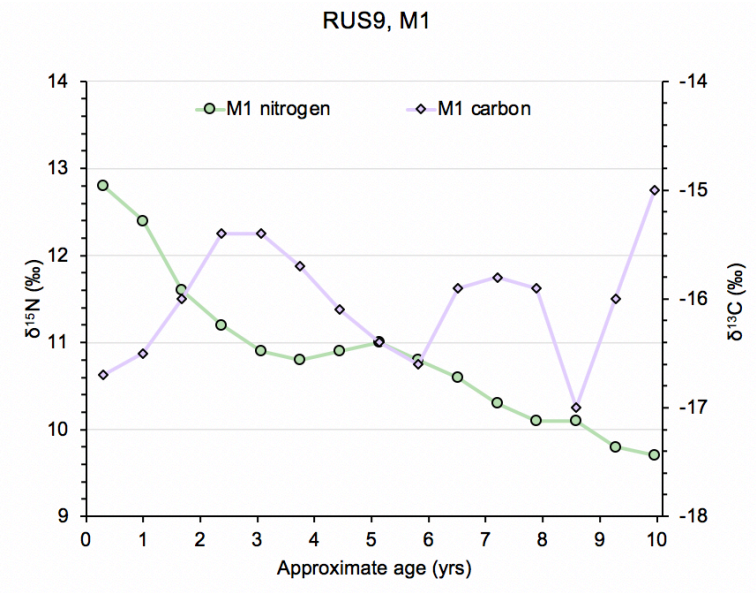
SI Fig. 20. Burial 311 (EKV31), adult male. Bone collagen values do not correspond to the x-axis.



SI Fig. 21. SK 45, 29-year-old female from London, UK.



SI Fig. 22. SK58 51-year-old male from London, UK.



SI Fig. 23 RUS 9, young adult female from Russia.