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Reconstructing caribou seasonal biogeography in Little Ice Age (late Holocene) Western Alaska using intra-tooth strontium and oxygen isotope analysis

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ABSTRACT

The palaeobiogeography of key prey-species can provide valuable insights into animal-human interactions, human subsistence activities and landscape use in the past. In many contemporary indigenous Arctic societies, caribou (*Rangifer tarandus* spp.) are an important seasonal subsistence species, and recent climatic shifts have influenced the seasonal and spatial distribution and migrations of herds. The impact of larger scale climatic change on this species, such as that experienced during the Little Ice Age (LIA), is not known, but may provide vital clues about future variability. Here we present sequential strontium ($^{87}Sr/^{86}Sr$) and oxygen ($\delta^{18}O_{CO3}$) isotope data from archaeological caribou tooth enamel from Nunalleq, a 15th to 17th century AD pre-contact Yup'ik village site in Western Alaska, to reconstruct caribou movement patterns in this region during the LIA. The results of these analyses highlight variation in ranging habits over the period of time that the site was occupied, and indicate different ranging behaviours in the region in the past compared to modern herds in the area today. The isotopic data presented here complement the wealth of data derived from other research at Nunalleq, illuminating the influence of changing climatic conditions on prey-species palaeoecology and human-animal interactions at the site.

1. Introduction

Isotopic analyses of sequentially sampled, incrementally-formed tissues are increasingly being utilised in archaeology and palaeoecology to identify and reconstruct seasonal dietary and migratory behaviours in wild animal species in the past (e.g. Britton et al., 2011; Feranec and MacFadden, 2000; Henton et al., 2017; Julien et al., 2012; Metcalfe and Longstaffe, 2014; Pellegrini et al., 2008; Price et al., 2017). Incrementally-developed tissues, such as tooth enamel and dentine, are formed over a relatively short period of time with no remodelling so the sequential sampling of these materials can provide time-series isotopic profiles. In this way, the episodic nature of isotopic variations measured within the tissues – brought about by variations in isotopic inputs related to changes in diet, ingested water, or location during tooth formation – can be established. Strontium isotope measurements in teeth, for example, are related to (geological) location during formation (Bentley, 2006), and – given that oxygen isotope ratios of precipitation vary seasonally at mid-/high-latitudes – oxygen isotope data can be utilised alongside strontium to 'anchor' data within a seasonal context. The utility of intra-tooth strontium and oxygen isotope analysis for the reconstruction of seasonal migratory behaviour in caribou/reindeer (*Rangifer tarandus*) has been recently demonstrated using migratory modern caribou (Britton et al., 2009; Britton, 2010), and has since been applied to European Middle and Late Palaeolithic reindeer (Britton et al., 2011; Price et al., 2017).

When focused on archaeologically-important prey-species, isotope zooarchaeology (the isotope analysis of archaeofaunal remains) studies not only serve to reconstruct the seasonal movements of important extinct and ancestral extant taxa, but also offer insights into animal-human interactions, animal landscape use and past human subsistence strategies. Isotope zooarchaeology also has the potential to allow archaeologists and palaeoecologists to explore changes in animal ecological behaviours over time periods not achievable in modern ecological studies. The influence of modern-day climate and environmental

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fluctuations, including anthropogenically-induced ones, on prey-species ecology, and specifically their migrations, has been observed for a number of modern wild animal species including terrestrial and marine mammals and birds (e.g. Blois and Hadly, 2009; Post et al., 2009; Root et al., 2003; Tape et al., 2016). Considering this, and other factors, the ecological behaviours of archaeological species (even in extant species) should not simply be assumed using modern analogues (see Britton, in press). Furthermore, the isotope zooarchaeological record, particularly within the context of large scale climatic shifts, can inform on continuity and change in faunal palaeoecology and the impact of environmental changes on faunal species, and illuminate species adaptability and niche plasticity or conservatism (see Britton, in press). To date, however, few studies have utilised these approaches to assess behavioural changes, though a limited number of studies have sought to demonstrate changes in palaeoecological behaviours over time at a single site- or on a regional/population-specific level (e.g. Britton, in press; Price et al., 2017). Further studies are warranted to better understand the impact of environmental change on the behaviour of medium- and large-sized herbivores, both in the past and in the future, particularly given the rate and scale of present-day global warming-induced environmental instability.

Caribou and reindeer (*Rangifer tarandus*) are amongst the most important seasonal subsistence taxa in the circumpolar North, particularly for contemporary Indigenous communities. North American caribou have both sedentary and migratory ecotypes; sedentary caribou 'space out', moving only during calving to avoid predation, whilst migratory caribou 'space away', undertaking long-range seasonal movements usually on a North-South trajectory (Bergerud, 1988:77). Migratory herds demonstrate cyclical movements, showing fidelity to calving sites and geographic ranges (Gunn and Miller, 1986; Skoog, 1968), although the size and actual location of the range can vary depending on herd numbers, forage abundance, predation and modern infrastructure (Dahle et al., 2008; Gunn and Miller, 1986; Hemming, 1971; Hinzman et al., 2005). Modern-day climatic shifts have also been shown to influence caribou seasonal movements and range use (e.g. Abraham et al., 2012; Brotton and Wall, 1997; Jacobs et al., 1996; Masood et al., 2017; Weladji et al., 2002). Extrinsic markers such as telemetry, satellite transmitters and aerial photography can provide detailed information on caribou herd range use and movements (Hobson, 1999), however other methods – such as isotope analysis – are required to reconstruct caribou migratory habits and range use in the recent historical and archaeological past.

Here, we present coupled $^{87}Sr/^{86}Sr$ and $\delta^{18}O_{CO3}$ isotopic measurements of sequentially-sampled *Rangifer* tooth enamel from the late Holocene site of Nunalleq in the Yukon-Kuskokwim Delta of Western Alaska. The pre-contact Yup'ik village site was primarily occupied between the 15th to 17th centuries (Britton et al., 2016; Ledger et al., 2016), during a period of global climatic disruption known as the Little Ice Age. The research goals of our study are: (i) to identify if these caribou undertook seasonal migrations in the past; (ii) to identify any differences in calving ground area and/or range use in the past compared to the region's present-day caribou population; and (iii) to utilise this new isotopic evidence for the (possible) seasonal movements of caribou in the Yukon-Kuskokwim Delta to better understand the nature of caribou exploitation at the site.

2. Reconstructing faunal migration using stable isotope analysis

Initial applications of stable isotope analysis demonstrated that the isotopic ratios of foods consumed during life are reflected in the isotopic ratios of body tissues (DeNiro and Epstein, 1978, 1981). Subsequent studies introduced and furthered the notion of applying the technique to reconstruct human palaeodiet (e.g. Tauber, 1981; Chisholm et al., 1982; Schoeninger et al., 1983). Since these initial studies, the use of isotope analysis in archaeology has expanded substantially, with studies now also encompassing the reconstruction of past animal diets (e.g. Balasse et al., 2006; Craig et al., 2006; Feranec et al., 2009; Sayle et al., 2016); human and animal mobility (e.g. Bentley and Knipper, 2005; Hoppe et al., 1999; Montgomery et al., 2007; Price et al., 2000); human and animal behaviours such as weaning (e.g. Britton et al., 2015; Fuller et al., 2003) and birth seasonality (e.g. Balasse et al., 2003; Buchan et al., 2016), and the reconstruction of palaeoenvironments and palaeoclimate (e.g. Domingo et al., 2015; Fricke et al., 1998; Hedges et al., 2004; Stevens et al., 2014; Tütken et al., 2008; Wißing et al., 2015). Early studies primarily utilised 'bulk' measurements of bones and teeth, giving averaged values of different ontogenetic periods (depending on the formation and/or remodelling time of the hard tissue in question). The desire for higher-resolution isotopic data, however, has led to an increase in the sequential sampling of incrementally-formed tissues such as enamel, dentine, and antler.

The accumulative nature of enamel growth, whereby enamel is laid down in successive layers and then mineralises, occurs over a relatively conservative period during sub-adulthood. Unlike bone, these incremental layers of tissue do not remodel over time, such that the isotopic composition of the diet consumed during their growth is fixed within these tissues. Intra-tooth isotopic analysis often involves sampling an enamel face horizontally across these bands of growth, therefore providing time-series isotopic data. Some biases, such as isotopic attenuation due to sample homogenisation across multiple phases of growth and within-tooth variations in growth-rates, can occur during sampling (Balasse, 2003; Bendrey et al., 2015; Zazzo et al., 2006, 2012). In archaeofaunal studies, such sampling has enabled a deeper understanding of seasonal dietary behaviour (e.g. Balasse et al., 2006; Feranec et al., 2009), animal husbandry practices (e.g. Balasse et al., 2012; Balasse and Tresset, 2002) and seasonal mobility (e.g. Britton et al., 2011; Julien et al., 2012; Widga et al., 2010). The period of time represented depends on the rate of tooth growth, which can vary species-to-species, and the tooth selected, with a single tooth from a high-crowned herbivore taking over a year to fully form and that of a small animal taking just weeks (Kohn and Cerling, 2002). For caribou and reindeer, estimations of enamel formation and mineralisation derive from studies of other deer species (e.g. Brown and Chapman, 1991a, 1991b). Based on these studies, and a recent case study using modern caribou (Britton et al., 2009), it is estimated that a full unworn *Rangifer* molar will represent between 6 and 9 months of growth, although consideration must be given to the influence that dental attrition and wear will have on this (Britton et al., 2009; Britton, 2010: 91). It must also be noted that sequential-sampling in this way does serve to homogenise enamel of each section into one datum point and, given the rapid mineralization time of these low-crowned teeth and the geometry of enamel growth, this may limit the resolution achievable.

The application of isotope analysis to mobility studies in archaeology and palaeoecology is made possible by the presumed relationship between the local environment (geology, climate) and the isotopic signatures of foods consumed by an individual. The use of strontium ($^{87}Sr/^{86}Sr$) and oxygen ($\delta^{18}O$) isotope compositions from dental enamel (or 'bioapatite') are perhaps now the most established approaches in isotope palaeomobility studies, and have been utilised to investigate movements and migrations of both humans and animals in the past in a variety of geographical and temporal contexts (e.g. Britton et al., 2009; Eckardt et al., 2009; Evans et al., 2006; Henton et al., 2017; Hoppe, 2004; Valenzuela-Lamas et al., 2016). Strontium isotope approaches are based on the relationship between the characteristic strontium isotopic signatures of underlying lithologies and, by extension, location during tissue formation (see review in Bentley, 2006). Since strontium can substitute for calcium in hydroxyapatite, the mineral component of bone and tooth (McConnell, 1973) the $^{87}Sr/^{86}Sr$ ratios of faunal bioapatite can therefore be related to the region in which an organism sourced its food. This is particularly effective for wild herbivores, and the movements of archaeological and modern herbivores have been reconstructed using their strontium isotope composition (e.g. Britton

et al., 2009, 2011; Feranec et al., 2007; Hoppe et al., 1999).

The $^{87}Sr/^{86}Sr$ of underlying bedrock varies primarily according to the age of the rock, as in geologically older rocks more of the radioactive mother isotope ^{87}Rb has, over time, decayed to the radiogenic daughter isotope ^{87}Sr. Therefore, older rocks have higher concentrations of ^{87}Sr, and thus higher $^{87}Sr/^{86}Sr$ (Capo et al., 1998). Although the geological age of rock is the primary influence on the $^{87}Sr/^{86}Sr$, other factors such as rock composition (i.e. ^{87}Rb content) and mineralogy can affect this. Furthermore, while the isotopic 'signature' of soils or plants at any location ('bioavailable' strontium) is primarily influenced by the parent material/underlying lithology, other factors influence local bioavailable $^{87}Sr/^{86}Sr$, such as differential weathering processes, groundwater and precipitation, and atmospheric deposition such as sea spray (Bentley, 2006; Green et al., 2004; Montgomery et al., 2007; Vitousek et al., 1999). There are a number of approaches that can be used to estimate bioavailable $^{87}Sr/^{86}Sr$ at a particular location, including the sampling of modern vegetation, soils, or near-ranging (micro-)fauna, or even the sampling of archaeological bone or dentine which (due to their susceptibility to diagenetic alteration) can provide an indication of the $^{87}Sr/^{86}Sr$ ratios of the surrounding burial environment at a site (Bentley and Knipper, 2005; Budd et al., 2000; Maurer et al., 2012; Price et al., 2002).

The $\delta^{18}O$ values of precipitation are determined by climatic and environmental factors, primarily local temperature, but also altitude, humidity, and proximity to the coast (e.g. Dansgaard, 1964; Gat, 1980, 1996). In light of this, and the relationship between the $\delta^{18}O$ values of mineralised tissues and that of ingested water (Bryant et al., 1994; Bryant and Froelich, 1995; Longinelli, 1984; Luz et al., 1984), oxygen isotopes can be utilised as a secondary indicator of geographical (climatic) origin in archaeological case studies. Furthermore, given that $\delta^{18}O$ values of precipitation at mid- to high- latitudes vary seasonally, $\delta^{18}O$ values can be used to 'anchor' strontium data within a seasonal context to further inform on seasonal movements and migrations (e.g. Britton et al., 2009; Julien et al., 2012; Pellegrini et al., 2008; Widga et al., 2010), while intra-tooth $\delta^{18}O$ values (both the phosphate and carbonate components) can also be used to track local climatic conditions that occurred during tissue formation. The attenuation ('dampening') of the intra-tooth isotope signature, relative to the isotopic signatures of inputs (i.e. drinking water or food), occurs as a result of physiological factors, sampling strategy, and the nature, process and three-dimensional geometry of tooth mineralisation itself (Balasse, 2002; Kohn, 1996; Kohn, 2004; Kohn et al., 1996; Kohn and Cerling, 2002; Passey and Cerling, 2002). Additionally, it has been demonstrated that animal ranging behaviours, such as rapid, long-distance 'thermo-stress' migrations and altitudinal ranging, can further influence the nature of these attenuations (Britton et al., 2009; Tornero et al., 2016, 2017). It is on this basis that it has been suggested that attenuated oxygen isotope intra-tooth profiles in animals from areas of pronounced seasonal temperature variations (i.e. at mid- to high-latitudes) could indicate the scale and mode of seasonal ranging (near versus far ranging; rapid or gradual movements) undertaken by an animal (Britton et al., 2009).

3. The Nunalleq site

3.1. Background

The Nunalleq site (59° 44′ N, 161° 54′ W) is a pre-contact Yup'ik village located in the Yukon-Kuskokwim Delta on the coast of the Bering Sea close to the village of Quinhagak, Western Alaska (Fig. 1). Investigations at the site followed a series of recent climatic changes that have resulted in, amongst things, an increase in unpredictable weather conditions in the region resulting in increased storms, a reduction in permafrost and, through this, coastal erosion which exposed the site in profile along the beach close to Quinhagak. Research and recovery efforts were subsequently undertaken at the request of the local Yup'ik descendant community. Between 2009 and 2015, excavations carried out by archaeologists from the University of Aberdeen uncovered a semi-subterranean multi-room sod house complex, which spans at least three different occupation phases between the 15th to 17th century AD (Britton et al., 2016; Ledger et al., 2016). The presence of discontinuous permafrost at the site has resulted in extremely-well preserved artefacts and ecofacts (including wooden tools, lithics, pottery, grass work, human hair, fur, animal bones and insects), a number of which have been the focus of recent studies (Britton et al., 2013, 2016; Farrell et al., 2014; Forbes et al., 2015; Ledger et al., 2016; McManus-Fry et al., 2016), contributing a wealth of data and building a wider picture of pre-contact life at Nunalleq. In a region that is sensitive to modern day climate change, and amongst communities that are suffering from its effects (Berkes and Jolly, 2001; Ford et al., 2006; Hansman, 2016; Pilkington, 2008). Nunalleq offers the chance to reconstruct and assess the impact that the most recent hemisphere-wide large scale climatic event (The Little Ice Age) had on the lives of the people of Nunalleq and the environment and animals around them, an especially important consideration given the modern-day context of similar environmental fragility.

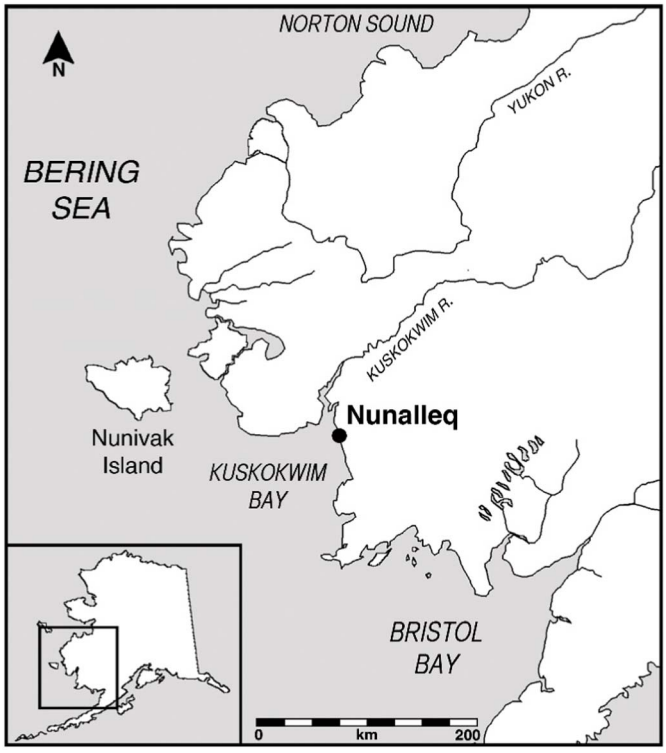

Fig. 1. Map of Western Alaska showing the location of the Nunalleq site. (Source: adapted from Britton et al., 2013).

3.2. Regional climate, topography, and lithology

Nunalleq is located in the Yukon-Kuskokwim Delta region, an environment typified by a flat, waterlogged, tundra landscape. This area of Alaska is classified as subarctic Dfc in the Köppen climate classification, with a maritime influence from the Bering Sea. This climate type is defined as being a snow climate, fully humid with cool summers and cold winters (Kottek et al., 2006, after Köppen, 1900). Mean winter (January) temperatures in this area are between − 13 and − 10 °C (8.6 and 14°F), and between 11 and 18 °C (51.8 and 64.4°F) (mean) in summer (July) (Fleming et al., 2000). While only limited strontium isotope bioavailability data is available for Alaska, a recent geostatistical framework has been published for the state (based on measured lithological samples), creating a predictive model for both bedrock and

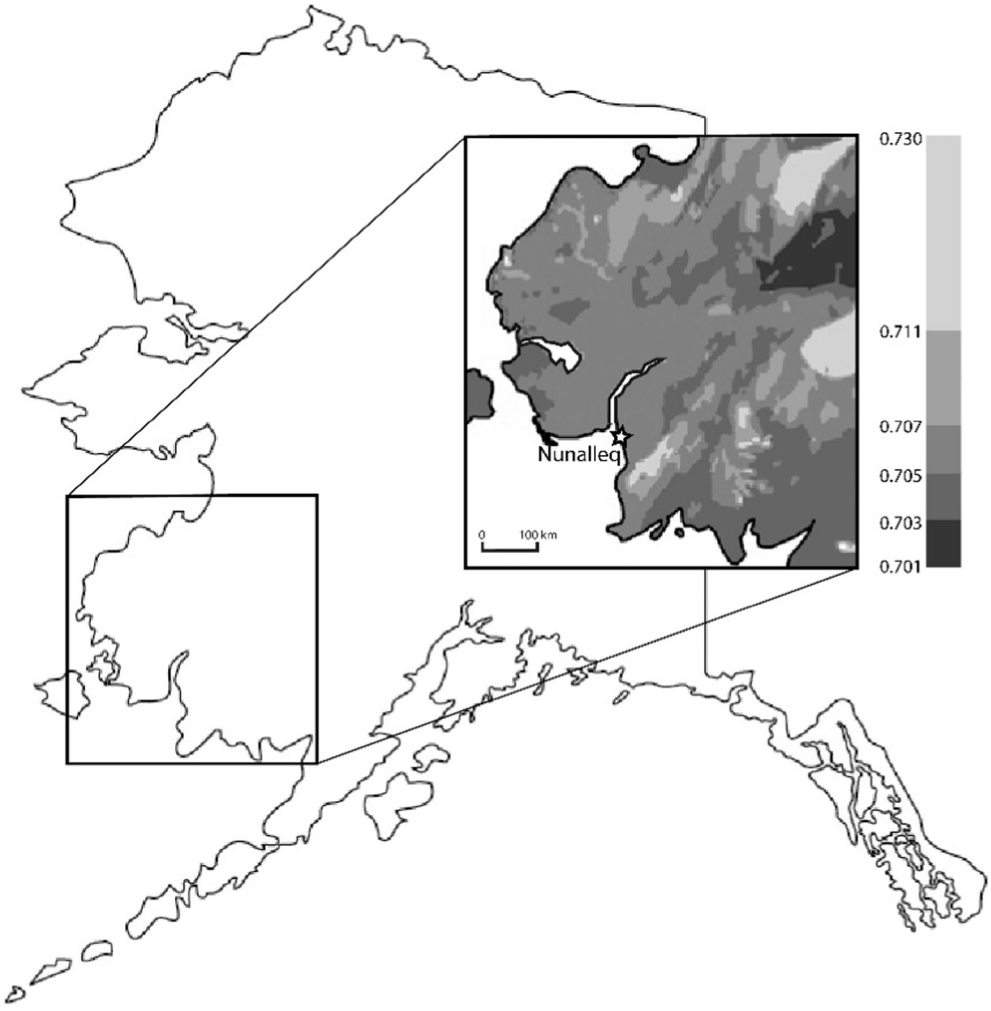

Fig. 2. Predicted $^{87}Sr/^{86}Sr$ (median values) in bedrock in area surrounding the Nunalleq site and the modern Mulchatna herd range area (Source: adapted from Bataille et al., 2014: 6, Fig. 3B). Location of the Nunalleq site is shown.

river $^{87}Sr/^{86}Sr$ (Bataille et al., 2014). Median values from the Bataille et al. (2014) study suggest $^{87}Sr/^{86}Sr$ of local bedrock for the area around the site vary between 0.705 and 0.707 (see Fig. 2, adapted from Bataille et al., 2014: 6, Fig. 3B).

The site's main occupation period during the 15th to 17th century AD coincided with the Little Ice Age, a large scale climatic event that saw increased glaciation and generally cooler conditions. In the Northern hemisphere the period AD 1400 to 1900 is thought to have been around 0.8 °C (33.4°F) colder than the late 20th century, with the 17th and 19th century in particular being the coldest within this entire period (Mann et al., 1999; Mann, 2002). In most cases there appears to have been increased climatic variability, with intermittent periods of warmth punctuating the generally colder climate (Bradley and Jones, 1993; Pfister, 1995). Tree-ring palaeoclimate data from the Seward Peninsula (N.W. Alaska) confirms this, demonstrating cold conditions from the early to middle 1600s and again in the late 1700s to mid-1800s, with the most severe cold episode occurring around AD 1780 (D'Arrigo et al., 2005).

3.3. Caribou: past and present

The archaeological record at Nunalleq highlights the important role of caribou in the pre-contact Yup'ik world. Zooarchaeological evidence demonstrates that caribou carcasses were being brought to the site for processing (McManus-Fry, 2015: 160), skinning, consumption (meat and marrow) and for use as raw material in the osseous industry (antler and bone), with caribou remains making up approximately 22% of the faunal assemblage (total faunal NISP = 9852; Edouard Masson-MacLean, pers. comm. 2017). While stable isotope evidence of human hair from Nunalleq suggests that salmon were likely the dominant protein source, diet at the site was mixed, incorporating terrestrial protein (likely caribou), fish (particularly anadromous species) and marine mammals (Britton et al., 2013, 2016). On the basis of isotopic mixing models, it has been estimated that caribou meat contributed approximately 9% of total dietary protein at Nunalleq (Britton et al., 2016), with domestic dogs at the site consuming proportionally a little more caribou meat than the human inhabitants of the site (McManus-Fry et al., 2016). Caribou are not just represented in the bioarchaeological record of Nunalleq, but are common in manufacturing-waste, artwork, and other finished pieces. Antler (debitage and artefacts) is a common find at the site, and examples of finished pieces featuring representations of caribou at the site include an antler engraved with a running caribou and hunting pendants in the shape of caribou hooves, attesting to the important relationship between this species and the inhabitants of Nunalleq.

Caribou remain an important subsistence species for the Yup'ik today, not only economically but culturally too, and like many animals they are traditionally considered sentient beings or 'non-human persons' (Fienup-Riordan, 2000; Simon-Sakurai, 2013). Contemporary changes in environmental conditions, however, appear to be affecting the availability of caribou, for example in Quinhagak where a lack of snow has resulted in fewer caribou in the area in recent years (Warren Jones, pers. comm. 2016). The modern caribou herd in this area are the Mulchatna, whose range includes the community of Quinhagak and the area immediately surrounding the Nunalleq archaeological site. The Mulchatna are a migratory herd of mountain caribou (*Rangifer tarandus*

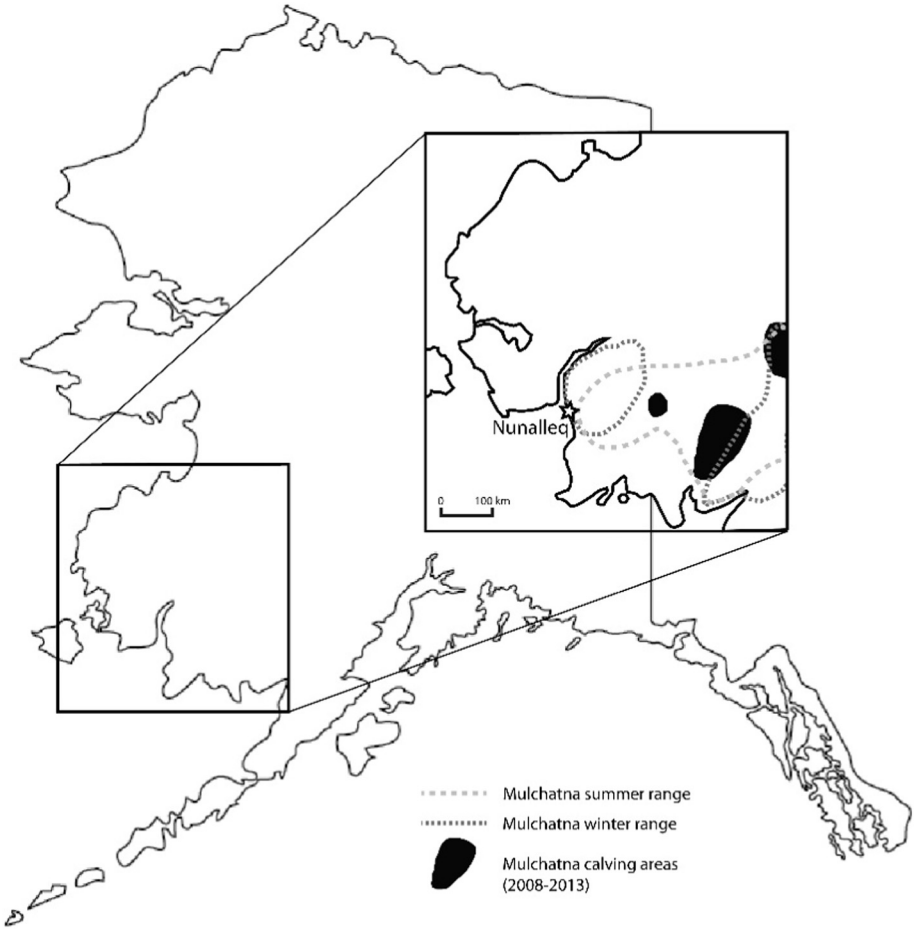

Fig. 3. Map of modern day Mulchatna caribou herd seasonal ranges and movements, with location of the Nunalleq site shown.
(Source: adapted from image provided by Alaska Department of Fish and Game c/o Dominic Demma).

caribou) that undertake seasonal movements of up to 240 km (150 miles) over a range encompassing approximately 103,000 km^2 (approximately 40,000 m^2) (Division of Wildlife Conservation, Alaska Department of Fish, and Game, 2016; and see Fig. 3). The area in which the herd currently calve is within their broader summer range, although split into two main areas. Both the summer range and the calving grounds incorporate areas of older lithology (including Mesozoic sedimentary and volcanic rock, and Paleozoic sedimentary, metamorphic, and igneous rock; see Beikman, 1980), with median bedrock values exceeding 0.709 and > 0.711 in the higher ground often favoured by mountain caribou during calving (Bataille et al., 2014: 6, Fig. 3B; and see Figs. 2 and 3 (this paper)).

4. Materials and methods

Second (M2) and third (M3) molars were extracted from four archaeological caribou hemi-mandibles (individuals NUN- 1, -2, -3, -4, which correspond to bioarchaeological site sample identifiers B-248-534, - 539, -541 and -540, respectively) and selected for strontium and oxygen (carbonate) isotope analysis. The material presented here come from two different phases of occupation at the site; the earlier phase III (NUN-1, 2, 3) and the later phase II (NUN-4). It should be noted that although material from the site has been radiocarbon dated, and stratigraphic relationships between these two phases are established, a more precise chronological model for the site has yet to be determined which currently limits diachronic investigations. Based on dental eruption and wear patterns it is estimated that these four individuals were aged between 2 and 3 years at death, with crown heights averaging between 10.3–15.5 mm (M2) and 10.6–15.7 mm (M3). No studies relating *Rangifer* tooth growth and development exist at present, however studies of other deer species can be used to gauge an estimation of the time period represented by a complete and unworn molar tooth (e.g. Brown and Chapman, 1991a, 1991b). It is estimated that *Rangifer* M2 and M3 teeth form sequentially with a M2 forming between < 3.5 and 9 months and a M3 between 9 and < 18 months (Brown and Chapman, 1991a). This estimation has been confirmed by previous sequential oxygen and strontium isotope studies of M2 and M3 enamel in modern caribou, although, in practice, periods represented in caribou/reindeer molars are slightly reduced due to wear that removes some enamel containing a few months of isotope data at the crown, so that the time period represented is thought to be approximately 1 year (Britton et al., 2009; Britton, 2010). While these modern studies have highlighted correlations between intra-tooth strontium and oxygen isotope profiles in *Rangifer* molars and changes in these isotope systems and migratory behaviours, it should be noted that uncertainties do surround the phasing and periodicity of mineralisation in *Rangifer* enamel and thus their intra-tooth isotopic profiles. For example, it cannot be unequivocally assumed that the strontium and oxygen isotopic signals are incorporated into tooth enamel synchronously. While this does not limit current applications (given that most methods of intra-tooth sampling tend to target multiple growth layers, somewhat homogenising isotopic 'signals' from neighbouring portions of enamel), further experimental studies would be needed in order to investigate this, and other aspects of *Rangifer* tooth development and mineralisation, in order to facilitate the resolution achievable in incremental enamel isotope studies were more fine-grained sampling approaches employed (e.g. laser ablation).

4.1. Sampling

Molars were extracted from the bone using a stainless-steel circular saw, brush-cleaned with deionised (DI) water, and then left to dry overnight. Whole teeth were then mechanically abraded using a tungsten carbide burr (NTI-Kahla, Germany) to remove surficial enamel and any adhering material, ultrasonicated in DI water, and dried. Intra-tooth sampling was performed using flexible, stainless steel diamond-coated superfine circular bits (NTI-Kahla, Germany), with drill bits cleaned between each sample using a weak nitric acid (< 0.3 M) to dissolve any adhering enamel, rinsed with DI water, ultrasonicated for 5 minutes in DI water and left to dry before re-use.

Enamel from the buccal face of the anterior loph of each tooth was selected for sampling, following the method detailed in Britton et al. (2009). After cutting and cleaning, enamel faces were measured, marked, and cut as horizontal sequential samples (perpendicular to the occlusal surface) at ~1.5 mm intervals. Sections were given sequential numerical sample assignments, starting from the enamel-root junction (ERJ) to the occlusal surface (M2-E1, M2-E2, M2-E3, etc.), and sections were split longitudinally, with ~5 mg of enamel reserved for each isotope analyses. A sample of (root) dentine was retained for bulk strontium isotope analysis.

4.2. Strontium

Strontium was extracted using the method from Deniel and Pin (2001) with modifications outlined in Copeland et al. (2008), at the clean laboratory facility, Department of Archaeology, Memorial University, Newfoundland (Canada). Clean enamel samples (~5 mg) were rinsed once with ~200 µl of ultra-pure acetone and left to dry completely. Samples were then dissolved in closed 3 ml Savillex vials (Minnetonka, MN, USA) with 1.5 ml 8 M HNO_3 (single distilled Reagent grade, Sigma Aldrich) at 70 °C. After samples were fully digested 0.5 ml HNO_3 was removed to determine Sr concentration. The remaining solution (1 ml) was loaded into pre-conditioned micro columns (after Charlier et al., 2006) containing Sr-spec resin (EiChrom, Darian, Il, USA). After three successive washes using 1 ml of 8 M HNO_3, strontium was eluted from the resin in 2 ml deionized water and then acidified with the addition of 75 µl of 8 M HNO_3, ready for analysis of $^{87}Sr/^{86}Sr$ ratios using a Neptune Multi-Collector Inductively Coupled Plasma Mass Spectrometer (MC-ICP-MS, Thermo Fisher Scientific, Bremen, Germany). A 200 ppb solution of Sr isotope standard SRM 987 (strontium carbonate dissolved in 0.3 N HNO_3, National Institute of Standards and Technology, Gaithersburg, MD, USA) was analysed between every five samples for quality control purposes. Using the average $^{87}Sr/^{86}Sr$ value for all the SRM 987 collected in the analytical session, all data was externally corrected to the SRM 987 value of $^{87}Sr/^{86}Sr = 0.710240$ (Johnson and Fridrich, 1990). The facility's long-term average for SRM 987 from 2014–2016 was 0.710268 ± 0.000028 (2SD, $n = 338$).

4.3. Oxygen

Enamel was prepared for carbonate oxygen isotope analysis following the methods outlined in Koch et al. (1997), with modifications detailed in Britton et al. (2009: 1166). Samples were powdered using an agate pestle and agitated in 30% H_2O_2(40 µl/1 mg) at room temperature for 24 hours. Samples were then rinsed five times with DI water and dried for 48 hours at 40 °C. Samples were measured for carbonate oxygen isotope ratios at Johannes Gutenberg Universität Mainz, Germany and Iso-Analytical Ltd., Sandbach, Cheshire, UK. In Mainz, ~1 mg aliquots of the dried pre-treated powders were analysed using a Thermo Gasbench II coupled via a Conflo II to a ThermoFinnigan MAT 253 gas mass spectrometer. At Iso-Analytical Ltd. sample sizes were larger (3.8 mg to 8.4 mg), and weighed into vials that were then flushed with 99·995% helium. Phosphoric acid was then added to vials and left overnight to react to allow for complete conversion of carbonate to CO_2. The CO_2 gas was analysed using CF-IRMS (Europa Scientific 20-20 IRMS). In both laboratories, values were normalised to in-house and international standards (NBS-18, NBS-19, Carrara Marble), and analytical error for $\delta^{18}O_{CO3}$ measurements was ± 0.2 ‰ (1 SD) and ± 0.1 ‰ (1 SD) (or better) at Iso-Analytical Ltd. and Mainz respectively, based on repeat analyses of those standards. This analytical error was also confirmed by the repeated analysis of an internal enamel reference material (horse tooth enamel) in analytical runs. All $\delta^{18}O_{CO3}$ values are reported here relative to the international reference material VSMOW.

5. Results and discussion

The results of the isotopic measurements are summarised in Table 1. Sequential strontium and oxygen isotope data from the four individuals are presented in Figs. 4 and 5, respectively. The values have been plotted aligning the most recently formed parts of each tooth (i.e. M2-E1, M3-E1) to allow inter-individual comparison. 'Anchoring' and plotting the data from the ERJ in this way ensures cross comparability and is a common approach in incremental studies when using variable sampling increments (e.g. Balasse et al., 2012; Buchan et al., 2016) or fixed ones (e.g. Britton et al., 2009, 2011; this study). Fig. 6a–d show the individual strontium and oxygen isotope profiles from each of the individuals, allowing a direct comparison of the intra- and inter-tooth $^{87}Sr/^{86}Sr$ and $\delta^{18}O_{CO3}$ trends.

The total isotopic range for all intra-tooth data from all individuals is 0.7057 to 0.7069 ($^{87}Sr/^{86}Sr$), with the lowest individual mean of 0.7062 ± 0.0003 (1SD, $n = 14$) and highest individual mean of 0.7067 ± 0.0001 (1SD, $n = 12$), and from 17.4 ‰ to 21.6‰, with a lowest individual mean of 18.2 ‰ ± 0.7(1SD, $n = 11$) and highest individual mean of 20.4 ± 0.6‰ (1SD, $n = 10$) ($\delta^{18}O_{CO3\ VSMOW}$). The strontium isotope values determined from the dentine ($n = 8$) are higher than the values measured in the enamel. These values ranged from 0.7064 to 0.7077, with a mean of 0.7071 ± 0.0004 (1SD). Given the coastal location of the site, it is possible that seawater strontium (as sea spray) has influenced the depositional environment and thus the dentine values (Whipkey et al., 2000).

5.1. Sequential strontium isotope data

The strontium isotope profiles for all four individuals display the same overall, cyclical trend from lower values to higher to lower again, suggesting some seasonal movement (Fig. 4). All individuals demonstrate intra-tooth $^{87}Sr/^{86}Sr$ variation in the third or fourth decimal place and display a similar trend in their $^{87}Sr/^{86}Sr$, from lower values in the earliest forming parts (0.7063 ± 0.0002, 1SD, at point M2-E6) to more elevated values (0.7067 ± 0.0002, 1SD, at point M2-E1) and a return to lower values (0.7062 ± 0.0004, 1SD, at point M3-E1) over a time period thought to represent approximately one year of life (Britton et al., 2009).

The relatively low intra-tooth variation/range of values for individuals NUN-1 and NUN-2 (0.7061 to 0.7065 and 0.7066 to 0.7068, respectively) suggests minimal movement over young, relatively isotopically homogenous lithologies. The intra-tooth strontium isotope profiles of NUN-3 and NUN-4 demonstrate slightly more variation, with values ranging from 0.7063 to 0.7071 in NUN-3 and 0.7057 to 0.7065 in NUN-4 across all sections taken in both teeth, perhaps suggesting movement over slightly more isotopically- (i.e. geologically) varied terrain. However, inter-individual variation is like that determined in modern herds (Britton et al., 2009), suggesting similar migration-histories. Indeed, the inter-individual similarities in all four caribou in the earliest forming parts of the M2 (e.g. ± 0.0002 at point M2-6) indicate spatial proximity in the first few months of life. This would likely correspond with the latter phases of infancy on and around the calving grounds and summer range of these individuals, as has been observed in experimental studies on caribou from modern caribou herds of known movement (Britton et al., 2009; Britton, 2010). Further similarities in

Table 1
Summary of isotopic results ($\delta^{18}O_{CO3\ VSMOW}$ and $^{87}Sr/^{86}Sr$) from sequentially-sampled enamel (E) of second and third molars of four caribou from Nunalleq. Sections were given numerical assignments commencing from the enamel-root junction (ERJ) to the occlusal surface. Also presented are the bulk dentinal (D) $^{87}Sr/^{86}Sr$ data for each individual.

Individual	Sample	$\delta^{18}O_{CO3\ VSMOW}$	$^{87}Sr/^{86}Sr$	Individual	Sample	$\delta^{18}O_{CO3\ VSMOW}$	$^{87}Sr/^{86}Sr$
NUN-1	M2-E9	No data	0.7061	NUN-2	M2-E6	No data	0.7066
(*B-248-534*)	M2-E8	No data	0.7061	(*B-248-539*)	M2-E5	19.6	0.7066
	M2-E7	19.8	0.7061		M2-E4	18.9	0.7066
	M2-E6	19.6	0.7061		M2-E3	19.3	0.7067
	M2-E5	18.6	0.7061		M2-E2	18.4	0.7067
	M2-E4	18.7	0.7063		M2-E1	18.5	0.7068
	M2-E3	18.5	0.7064		M3-E6	18.5	0.7069
	M2-E2	17.6	0.7063		M3-E5	18.7	0.7069
	M2-E1	No data	0.7064		M3-E4	19.0	0.7068
	M3-E10	17.9	0.7065		M3-E3	19.2	0.7068
	M3-E9	17.8	0.7065		M3-E2	19.4	0.7067
	M3-E8	17.6	0.7065		M3-E1	No data	0.7066
	M3-E7	17.7	0.7065		M2-D	No data	0.7073
	M3-E6	18.1	0.7065		M3-D	No data	0.7069
	M3-E5	18.8	0.7064				
	M3-E4	19.6	0.7064				
	M3-E3	20.0	0.7064				
	M3-E2	20.6	0.7063				
	M3-E1	20.5	0.7062				
	M2-D	No data	0.7077				
	M3-D	No data	0.7076				
NUN-3	M2-E7	21.63	0.7064	NUN-4	M2-E7	17.8	0.7062
(*B-248-541*)	M2-E6	20.78	0.7064	(*B-248-540*)	M2-E6	17.7	0.7062
	M2-E5	20.44	0.7064		M2-E5	17.6	0.7063
	M2-E4	20.09	0.7066		M2-E4	17.4	0.7064
	M2-E3	19.97	0.7067		M2-E3	17.6	0.7066
	M2-E2	19.58	0.7068		M2-E2	17.8	0.7066
	M2-E1	No data	0.7069		M2-E1	No data	0.7065
	M3-E6	19.81	0.7071		M3-E7	18.4	0.7064
	M3-E5	19.91	0.7070		M3-E6	19.0	0.7062
	M3-E4	20.17	0.7068		M3-E5	19.1	0.7061
	M3-E3	21.02	0.7066		M3-E4	19.0	0.7060
	M3-E2	20.94	0.7065		M3-E3	18.7	0.7059
	M3-E1	No data	0.7063		M3-E2	18.9	0.7058
	M2-D	No data	0.7064		M3-E1	No data	0.7057
	M3-D	No data	0.7068		M2-D	No data	0.7073
					M3-D	No data	0.7069

later-forming portions of both teeth further demonstrate this likely spatial proximity throughout much of the first year of life and indicate that these four animals were moving over similar lithologies, likely within the same broad geographical area. In all individuals, the $^{87}Sr/^{86}Sr$ closest to that of the mean 'local' value, as indicated by dentine values (0.7071 ± 0.0004, 1SD, n = 8), occur in the latest-forming parts of the M2 and earliest forming parts of the M3. This may indicate these caribou were near Nunalleq during this period, perhaps giving the inhabitants of Nunalleq their hunting opportunity. This hypothesis is not without merit; zooarchaeological analysis of the age at death of caribou from Nunalleq point to the likelihood of a winter hunt, although hunts may have occurred at other times of the year too (McManus-Fry, 2015). The caribou 'search and harvest areas' (hunting areas) used by the inhabitants of Quinhagak today are approximately between 60 (north and southwards) and 120 (eastwards) km (37 and 75 miles) away, so it could be likely that the traditional hunting

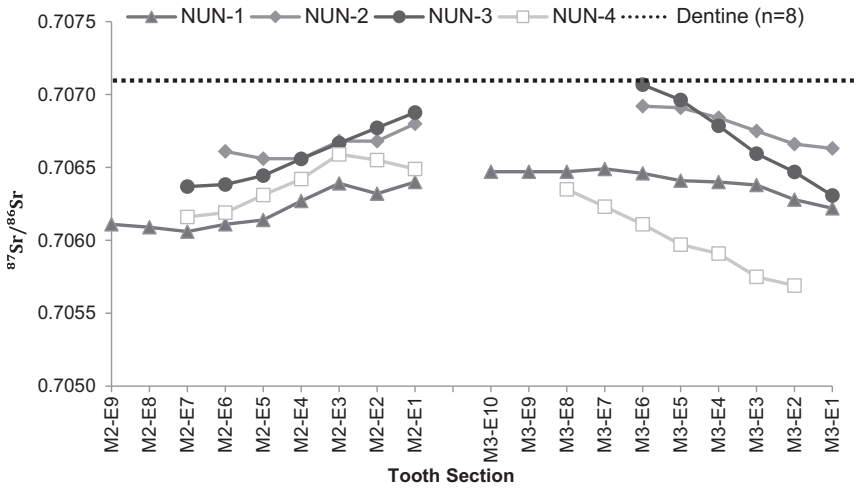

Fig. 4. Plot of all strontium isotope data ($^{87}Sr/^{86}Sr$) from intra-tooth sections from M2 and M3 enamel of each of the four Nunalleq caribou. Closed symbols are Phase III individuals (triangle = NUN-1, diamond = NUN-2, circle = NUN-3) and open symbols are the Phase II individual (square = NUN-4). The mean dentinal value (0.7071 ± 0.0004 1SD; n = 8) is represented by the dashed line. Analytical error is within the symbol markers.

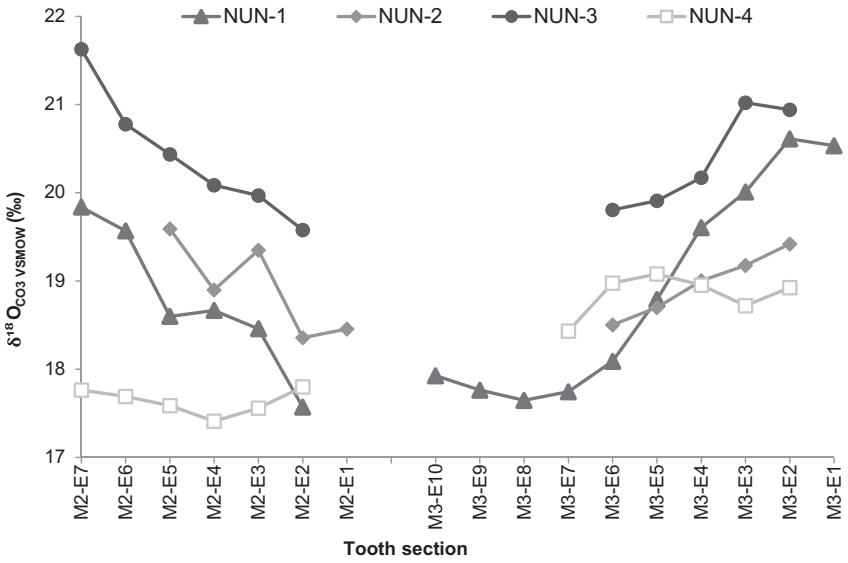

Fig. 5. Plot of all $\delta^{18}O_{CO3}$ data from intra-tooth sections from enamel from second and third molars of four caribou from Nunalleq. Closed symbols are Phase III individuals (triangle = NUN-1, diamond = NUN-2, circle = NUN-3) and open symbols are the Phase II individual (square = NUN-4).

grounds were of a similar distance away from the site of Nunalleq (Simon, 2016: 57).

The $^{87}Sr/^{86}Sr$ from all individuals are within the range of expected values for the area surrounding the site, which is predicted to be between 0.705 and 0.707 based on a predicted geospatial model for $^{87}Sr/^{86}Sr$ in Alaskan rocks (Bataille et al., 2014: 6, Fig. 3B), and are also similar to the $^{87}Sr/^{86}Sr$ of dentine measured from the site (presumed to reflect locally bioavailable Sr), which range from 0.7064 to 0.7077, with a mean of 0.7071 ± 0.0004 (1SD, n = 8; see Table 1). Given that the present-day Mulchatna Herd in this region calve and spend the summer months in areas which incorporate older lithologies (with expected higher $^{87}Sr/^{86}Sr$; see Figs. 2 and 3, and Bataille et al., 2014: 6: Fig. 3B), it seems unlikely that the Nunalleq caribou utilised the same calving grounds and broader summer range as the Mulchatna caribou use today. This is especially interesting given that calving ground location in particular is thought to be quite stable (Ferguson and Elkie, 2004; Russell et al., 1993). Given the more lithologically varied terrain encompassed in the total range of the Mulchatna herd today, it is unlikely that the geographical range used by the Nunalleq caribou was the same as modern populations in the region or perhaps only incorporated part of what is used today. Given the lack of bioavailability data for the broader region, and the relative homogeneity of lithology to the northeast of the site, the precise location of the calving and summer range areas used by these archaeological caribou cannot be determined. It can

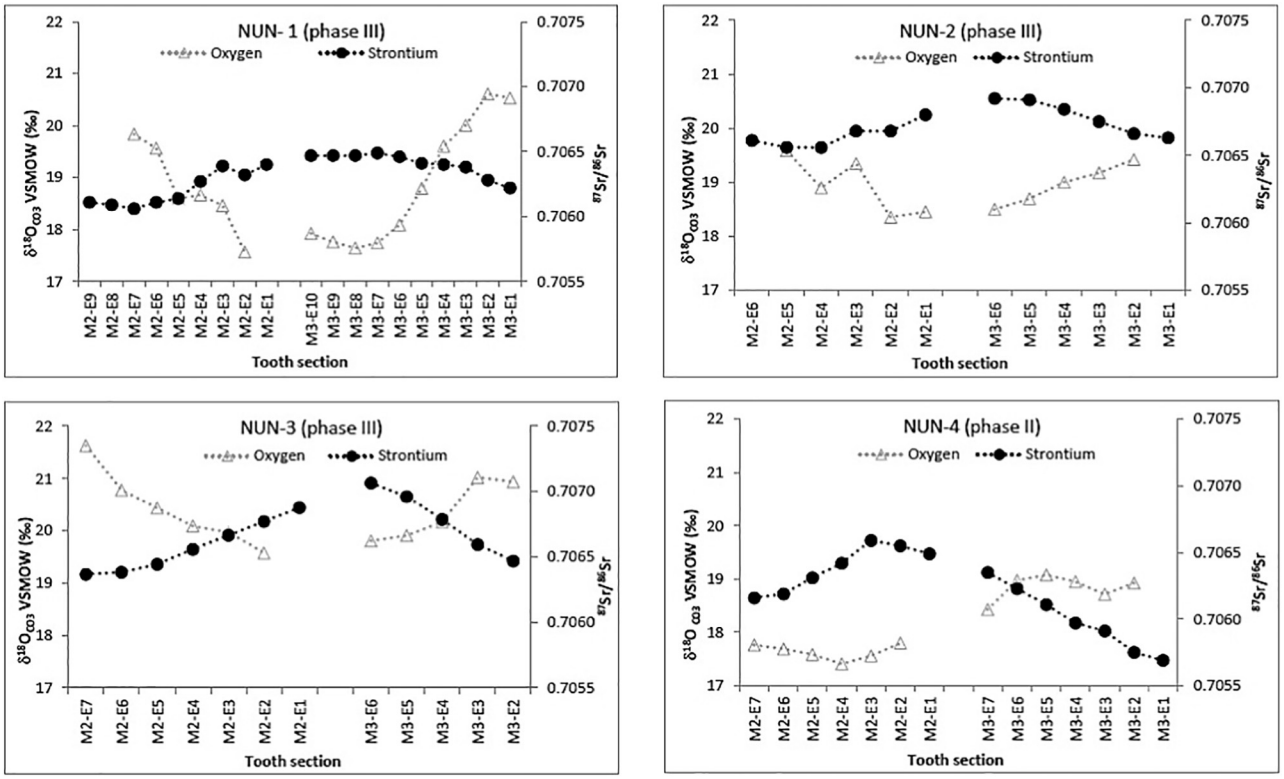

Fig. 6. Plots a–d demonstrate intra-tooth isotope values of $^{87}Sr/^{86}Sr$ (solid circles) and $\delta^{18}O_{CO3}$ (open triangles) for M2 and M3s of each of the caribou analysed. Plot a, b and c represent the phase III individuals NUN-1, -2 and -3, respectively. Plot d represents the phase II individual NUN-4. Analytical error for strontium measurements is within the symbol markers.

be noted that there is a large swathe of Quaternary lithology (sedimentary) extending northwards from Nunalleq to the Norton Sound area. Beyond this are areas of older rock (e.g. Mesozoic sedimentary rock, Upper Paleozoic metamorphic and igneous rock; see Fig. 2). It is perhaps likely then that these caribou were born in, and ranged throughout, this relatively 'penned-in' area of Quaternary lithology.

Recent large shifts in the calving areas used by the Mulchatna herd have been observed during annual survey work and are thought to have resulted from increased predation, short-term weather affects as well as longer-term climate change (Dominic Demma, pers. comm. 2016). Similar abandonments and shifts in calving areas have been observed for other caribou herds in Canada and Alaska (e.g. Abraham et al., 2012; Cameron et al., 1992). In Greenland, an association has also been demonstrated between caribou population size and climate change, and it has been shown that caribou herds undergo 'boom-bust' cycles, with herd sizes expanding and contracting enormously in a relatively periodic fashion and in relation to climatic shifts in relatively recent history (Meldgaard, 1986: 59–64). Similar population fluctuations, albeit not regular cycles, in caribou herds have been observed in Alaska (e.g. Bergerud et al., 1984; Skoog, 1968) and Canada (e.g. Couturier et al., 1990) and more recent studies, using long-term satellite and radio-collar observation, have identified similar trends in caribou herd population-size peaks and troughs (e.g. Abraham et al., 2012; Hegel and Russell, 2013; Ruttan, 2012). The reasons for these, apparently cyclical, fluctuations in herd numbers, and the trigger behind such extreme 'boom-bust' cycles, may be (local and global) climatic variations, forage availability and changes in predation risks (Gunn, 2003; Meldgaard, 1986; McNeil et al., 2005; Weladji et al., 2002). The relationship between fluctuations in overall herd size and range use in past caribou populations requires further research, although how past herd sizes could be determined remains unclear. Additionally, further investigation into the implications of such changes in caribou behaviours for contemporary human groups would be of great interest both to archaeologists and present-day Indigenous communities. Future work, including the integration of these isotopic data with site-specific diachronic human stable isotope palaeodietary data, more detailed zooarchaeological analyses and material culture changes (particularly of hunting implements), will undoubtedly prove illuminating. The integration of ethno-historical accounts and oral histories into such studies would also prove valuable.

It is also possible that, rather than documenting the *changing* behaviour of the Mulchatna, the strontium data from Nunalleq instead evidence the behaviour of another (now extinct) population of caribou. Indeed, there was a historically-documented population of caribou (Bering Sea Coast Herds) that were abundant along the lowland areas of the Bering Sea coast until the early 1900s when they disappeared entirely (Murie, 1935, after Nelson, 1888). Although not a distinct herd, these caribou appear to have undertaken a general north-south migration from the Norton Sound area to Kuskokwim Bay (Murie, 1935: 61). Such a migratory route would have incorporated the vicinity of the site.

5.2. Sequential oxygen isotope data

Oxygen isotope compositions for the four individuals also display a similar trend through time, from higher $\delta^{18}O_{CO3}$ values, to lower values, before a return to higher $\delta^{18}O_{CO3}$ values again (Fig. 5). These fluctuations in $\delta^{18}O_{CO3}$ values are likely a result of seasonal variations in temperature during the period of tooth growth. The higher $\delta^{18}O_{CO3}$ isotope values correspond to summer, the lower values to winter.

Intra-tooth oxygen values in individuals NUN-1 and NUN-2 are similar in terms of overall trend and measured values. These values vary from 19.1 ± 0.7 ‰ (1SD) at point M2-5 to 18.0 ± 0.6 ‰ (1SD) at point M2-E2 to 20.0 ± 0.8‰ (1SD) at point M3-E2. This indicates that, after being born in the same season (albeit very likely across different years), the $\delta^{18}O_{CO3}$ values of water ingested during the first year of life (either directly, or via plants consumed) was similar for these different animals. The same trend is also visible in individual NUN-3; however, the measured values are slightly higher. This could be due to intra or inter-annual climatic variations, or even due to differences in feeding behaviours and the water physiology of plants consumed.

These three animals, from phase III, demonstrate greater intra-tooth variation (0.4–1.0‰) than inter-tooth variation (i.e. means for M2 and M3 measurements are similar in the same animal). The intra-tooth values fluctuate in both teeth, with summer peaks and winter troughs, demonstrating the seasonality of birth and the period of tooth development. Measurements in the later-forming parts of the M2 and the earliest forming parts of the M3 are similar across all three individuals; NUN-1 (17.6‰ and 17.9‰ at points M2-E2 and M3-E10 respectively), NUN-2 (18.5‰ at points M2-E1 and M3-E6), NUN-3 (19.6‰ and 19.8‰ at points M2-E2 and M3-E6 respectively).

Individual NUN-4 displays a slightly different trend in $\delta^{18}O_{CO3}$ values. The values vary from 17.8‰ at M2-E7, to 17.4‰ at M2-E4, to 18.9‰ at M3-E2. These absolute values, especially within the M2, are lower (~1.3–2.8‰) compared to the other three individuals' values at equivalent points in tooth development. Given that the $^{87}Sr/^{86}Sr$ in the M2 from this same individual indicates spatial proximity with the other three individuals at/around the time of birth, it is perhaps likely that the difference in absolute values represent a difference in seasonal (spring/summer) temperatures between these phases/time periods. However, NUN-4 also shows little intra-tooth variation (0.6‰) but more inter-tooth variation (~1.2‰), which may reflect a substantial shift in location or environment between the period of M2 and M3 formation, and perhaps suggests this individual – while traversing similar lithological units to the other individuals studied – may have undertaken a seasonal migratory behaviour of a different nature from the other individuals (e.g. varying in distance, north-south directionality, and/or altitude).

5.3. Inter-individual variability in $^{87}Sr/^{86}Sr$ and $\delta^{18}O_{CO3}$

Particularly in $\delta^{18}O_{CO3}$, individual NUN-4 demonstrates a different isotopic profile compared to the other three caribou (see Fig. 6a–d). The intra-tooth variation in $\delta^{18}O_{CO3}$ for NUN-1, 2 and 3 – in combination with the $^{87}Sr/^{86}Sr$ variation – suggests seasonal movement but over a restricted range. Conversely, the lower $\delta^{18}O_{CO3}$ intra-tooth variation observed in NUN-4 is more comparable to modern migratory caribou undertaking north-south trajectory migrations (Britton et al., 2009). It is possible therefore that this animal was undertaking more significant seasonal movements compared to the three caribou from Phase III. The lack of intra-tooth $\delta^{18}O_{CO3}$ variation is also perhaps representative of this caribou being a long-distance thermo-stress migrant since the observed 'dampening' in the intra-tooth oxygen isotope values is likely further influenced by rapid, seasonal migrations (Britton et al., 2009). An alternative hypothesis which would similarly explain the greater attenuation in $\delta^{18}O_{CO3}$ intra-tooth values is that this caribou was born at a higher elevation and ranged altitudinally, since this type of mobility can also serve to reduce the annual amplitude of isotopic variation resulting in 'dampened' values (Tornero et al., 2016, 2017). Indeed, the nearby Kuskokwim and Kilbuck mountain ranges are known to have been used by caribou herds both in the historical past and in more recent times (Simon, 2016). Additionally, it is possible that this individual was of a different sex compared to the other three. Sexual segregation and differences in habitat use have been observed in other modern caribou herds (e.g. Jakimchuk et al., 1987), which could potentially result in possible differences in the timing, scope, or distance travelled during migrations.

This observed inter-individual variability, particularly in $\delta^{18}O_{CO3}$, may point to between-phase, and thus between time period, differences in the isotopic profiles (and perhaps the climate and/or ranging behaviours) of these caribou although, with only a single individual from phase II, estimation of behavioural differences of caribou between the

two occupation phases cannot be further elaborated upon. Strontium and oxygen isotope measurements from individuals from the modern herd in the region today would aid in better understanding intra-group isotopic variability across this broader area, although unfortunately none were available for this study.

6. Conclusions

This study has provided the first isotopic evidence for caribou seasonal movements in pre-contact Alaska, and in this region during the Little Ice Age. Here intra-tooth $^{87}Sr/^{86}Sr$ and $\delta^{18}O_{CO3}$ data from caribou bioapatite from the site of Nunalleq indicate that these four animals were undertaking seasonal migrations, albeit perhaps limited in nature. In all individuals, the $^{87}Sr/^{86}Sr$ closest to the locally bioavailable $^{87}Sr/^{86}Sr$ occur in winter and may indicate these caribou were near Nunalleq during this period, perhaps giving the inhabitants of Nunalleq their hunting opportunity. Possible inter-individual differences in $\delta^{18}O_{CO3}$ have been discussed, which may be related to differences in climate and/or ranging behaviours between phases of site occupation. Further work to establish the nature of the change in climate during the site's occupation is ongoing and may provide the opportunity to correlate any climatic or environmental shifts with the possible changes in behaviour observed here. The comparison of the $^{87}Sr/^{86}Sr$ data from all archaeological individuals with values expected for modern caribou in the region (given the known locations of the local present-day herd's range) may indicate a shift in the location of calving grounds/summer range, and possibly the size of overall range, between the 15th to 17th century AD and the present day. The reasons for this apparent shift can only be speculated upon, however, it may be that the period of relatively rapid climatic warming which has occurred in this region since the end of the Little Ice Age may have played a part. Additionally, it is possible that these Nunalleq caribou represent members of an extinct population that historically roamed along the Bering Sea coast. The analysis of additional *Rangifer* remains from historical, pre-contact and prehistoric contexts in the region and more broadly across the circumpolar North is clearly needed to better investigate the impact of climate change on caribou/reindeer range use and ecological behaviours. Ideally, however, this should be coupled with the analysis of modern environmental samples as part of broader bioavailability studies and with the experimental analysis of modern animals, analysed alongside accompanying telemetry and satellite survey information.

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