

Long-term ecological changes in marine mammals driven by recent warming in northwestern Alaska

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Abstract

Carbon and nitrogen isotopes analyses were performed on marine mammal bone collagen from three archaeological sites (AD 1170–1813) on Cape Espenberg (Kotzebue Sound, northwestern Alaska) as well as modern animals harvested from the same area to examine long-term trends in foraging ecology and sea ice productivity. We observed significant and dramatic changes in ringed seal stable isotope values between the early 19th and early 21st centuries, likely due to changing sea ice productivity and reduced delivery of organic matter to the benthos driven by recent warming in the Arctic. These data highlight the importance of the archaeological record for providing a long-term perspective on environmental variation and interpreting recent changes driven by anthropogenic processes.

KEYWORDS

Arctic, climate change, marine mammals, paleoecology, sea ice, stable isotopes, western Alaska

1 | INTRODUCTION

The Arctic is one of the most undisturbed environments on earth, but is simultaneously believed to be among the most vulnerable to the effects of anthropogenic climate change (Overpeck et al., 1997). Although there has been a surge in research examining the potential effects of climate change on the biosphere, marine ecosystems are understudied relative to their terrestrial counterparts, comprising only a small fraction (ca. 5%) of the literature (Hoegh-Guldberg & Bruno, 2010; Rosenzweig et al., 2008). This is particularly true in the Arctic due to the logistical difficulties of conducting research in the region. The Arctic marine environment is presently in a state of flux, with massive changes occurring to oceanographic processes driven by reductions in sea ice extent and alterations in currents (Shimada et al., 2006; Steele, Ermold, & Zhang, 2008; Stroeve, Holland, Meier, Scambos, & Serreze, 2007; Woodgate, Aagaard, & Weingartner,

2006). These changes have, in turn, already begun to impact the biosphere and in some areas, such as the western North American Arctic, the taxa that have been or are anticipated to be affected are of particular importance to the subsistence economies of northern communities (Grebmeier, 2011).

Kotzebue Sound is an embayment of the southern Chukchi Sea in northwestern Alaska (Figure 1). Sea ice is a prominent feature in the area, which is currently present for 8–9 months of the year (Figure 2). Sea ice is particularly relevant in the context of the marine mammals that would have been and continue to be important subsistence items to the people living in this area (Krupnik, Apangalook, & Apangalook, 2010). The physical structure of the ice is significant for many species for haul-outs, denning areas, and as hunting platforms (Huntington et al., 2013). Moreover, the algae that grow in direct association with the sea ice make major contributions to the productivity of marine ecosystems through delivery of organic matter to the benthos and

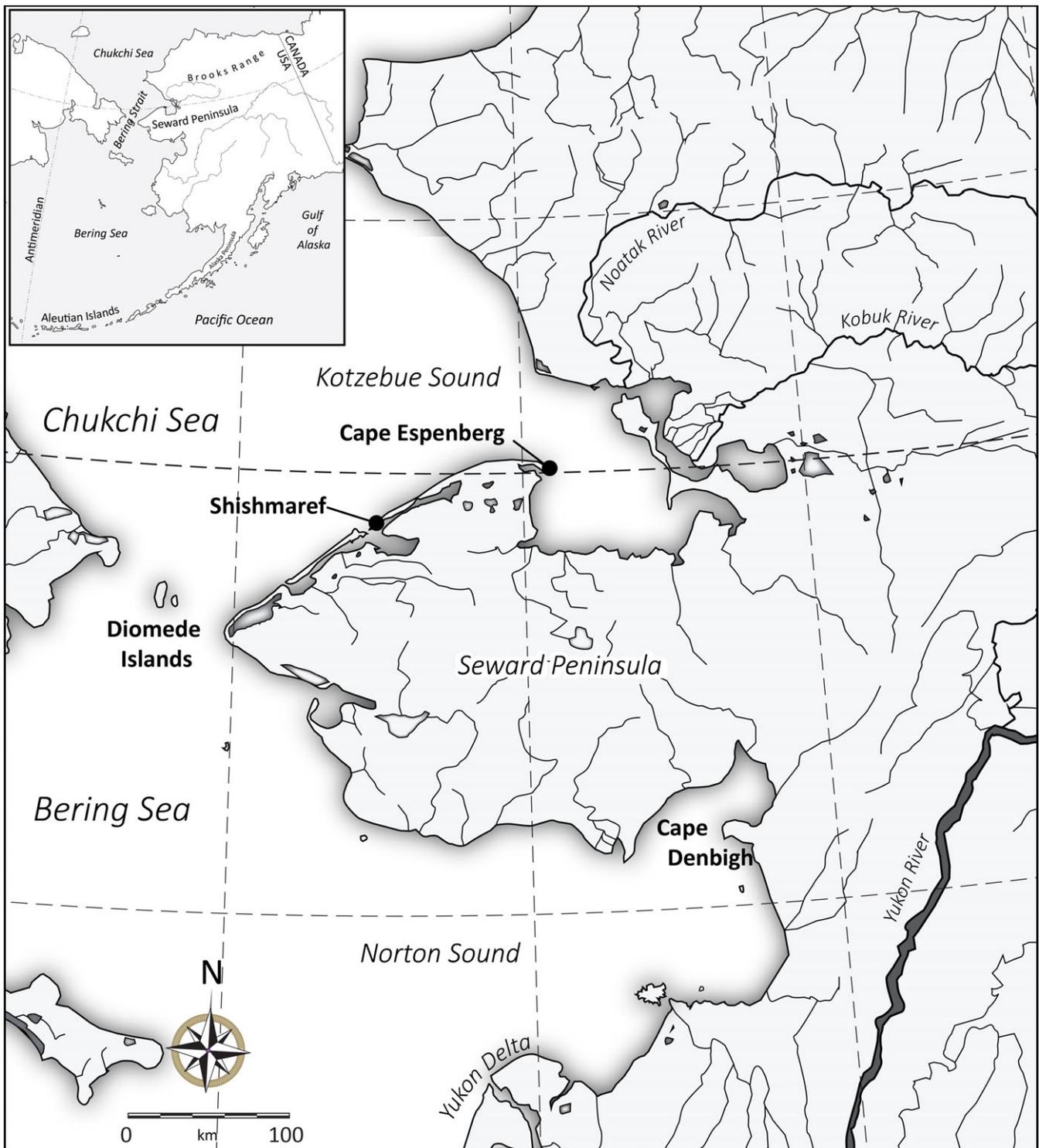


FIGURE 1 Map of the study area with place names mentioned in the text (map prepared by John Darwent)

secondarily through direct grazing (Gradinger, 2009; Kohlbach et al., 2016; Søreide, Leu, Berge, Graeve, & Falk-Petersen, 2010).

The northern Bering Sea/Chukchi Sea region is characterized by high primary productivity, tight benthic–pelagic coupling, and a rich benthic food web (Dunton, Goodall, Schonberg, Grebmeier, & Maidment, 2005; Feder, Jewett, & Blanchard, 2005, 2007; Grebmeier,

Cooper, Feder, & Sirenko, 2006). Notably, and unlike many other regions of the Arctic, grazing by zooplankton is not a major factor, with new production rapidly settling to the sediments, supporting the benthic food web (Grebmeier & McRoy, 1989; Wassmann et al., 2004). There has been a recent shift in the Bering Sea region away from this tight benthic–pelagic coupling, with decreased sea ice,

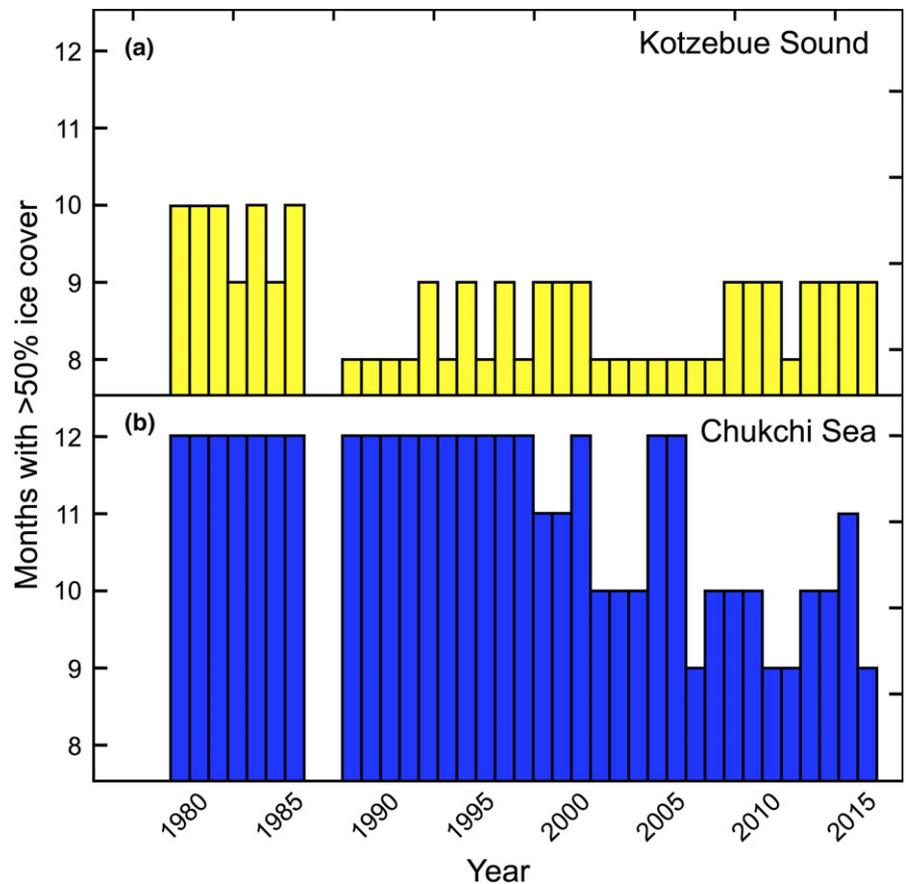


FIGURE 2 Number of months with >50% sea ice cover (based on $25 \times 25 \text{ km}^2$ cells surrounding each area) for (a) Kotzebue Sound (location of the archaeological sites) and (b) the Chukchi Sea ($74^\circ 30.6' \text{N}$ – $159^\circ 58.6' \text{W}$, corresponding to the area studied by de Vernal et al., 2008 on the basis of dinocysts in sediment cores). Sea ice data were extracted from Fetterer, Knowles, Meier, Savoie, and Windnagel (2016). Note that the data for 1987 and 1988 were not accessible

decreased benthic productivity, and an increase in pelagic fishes (Grebmeier, Overland, et al., 2006; Mueter & Litzow, 2008; Overland & Stabeno, 2004).

Traditional ecological knowledge (TEK) indicates that there have been significant recent changes to the thickness of the shorefast ice (decreasing), the overall extent of the sea ice (decreasing), the presence of multiyear sea ice (disappearing or absent), and the timing of ice breakup in the spring (happening earlier) in this region (Huntington, Quakenbush, & Nelson, 2016; Jewett et al., 2009; Krupnik et al., 2010). These observations fit within a broader context of extensive reductions in sea ice thickness and extent that have been recorded throughout the vast majority of the Arctic over the last few decades (Comiso, Parkinson, Gersten, & Stock, 2008; Wang & Overland, 2009), including in the Chukchi Sea and Kotzebue Sound (Figure 2). Aside from the changes that have occurred over the last few decades, sea ice extent has varied in the Arctic at decadal, centennial, and millennial scales throughout the Holocene (de Vernal, Hillaire-Marcel, & Darby, 2005; de Vernal, Hillaire-Marcel, Solignac, Radi, & Rochon, 2008; de Vernal et al., 2013; Vare, Massé, Gregory, Smart, & Belt, 2009). A major trend that has been observed across much of the Arctic is a reduced sea ice extent comparable to the present state around 8 ka, although the opposite has been suggested for the western North American Arctic (de Vernal et al., 2008; Polyak, Belt, Cabedo-Sanz, Yamamoto, & Park, 2016), highlighting the importance of spatial variability. In the western North American Arctic, there has been a trend toward lower sea ice extent over the course of the

Holocene, with cyclical oscillations of temperature and sea ice extent on a 2,500- to 3,000-year period (McKay et al., 2008).

An important implication of our improved understanding of climate variation in the Arctic in recent centuries is that the biosphere has not been at a continuous steady state and has changed significantly over time (Jakobsson, Ingólfsson, Long, & Spielhagen, 2014; Overpeck et al., 1997). Within the context of studies examining the impacts of climate change, a crucial area of uncertainty is our poor understanding of how ecosystems, in the Arctic and more generally, have responded to variation in climate over the long term driven in part by a lack of observations that extend beyond the last few decades (Polyak et al., 2016). Therefore, to examine whether or not changes that are being observed in the biosphere today are in fact unprecedented, we must rely on various proxies of past environmental conditions and biotic responses to changes in those conditions (Smith, Bradley, & Abbott, 2004). The archaeological record offers a unique opportunity to significantly expand the temporal window within which these biotic responses can be examined and provides a long-term historical baseline for modern studies. Numerous other proxy data can be used to infer the state of past marine ecosystems (Briner et al., 2006; de Vernal et al., 2008; Polyak et al., 2010; Smol et al., 2005), but the preservation of large vertebrates in archaeological sites allows the impact of long-term changes at higher trophic levels to be directly assessed.

Unlike other proxy data, such as those derived from marine sediment cores, the distribution of archaeological materials is very

uneven across time. Particular areas may have been more or less suitable for human occupation over the course of hundreds or thousands of years (for environmental or cultural reasons) and therefore relevant materials may be unavailable for analysis (Savelle & Dyke, 2009, 2014; Savelle, Dyke, Whitridge, & Poupart, 2012). The dating of archaeological deposits is relatively imprecise and for Arctic sites with abundant marine mammals, such as those studied here, mostly relies on ^{14}C measurements of associated terrestrial materials; because of the uncertainty of the regional magnitude of the marine reservoir effect, marine mammals are generally not dated directly (Dumond & Griffin, 2002; McGhee & Tuck, 1976; Morrison, 1989). Discrete archaeological features (e.g., houses, midden deposits) may contain decades or more worth of accumulated material with little or no internal vertical stratigraphy. The abundance of particular taxa in archaeological deposits is variable, with some being hyperabundant and others relatively scarce. For example, throughout most of the North American Arctic, ringed seal is ubiquitous and abundant, while other marine mammals (e.g., walrus, harp seal, beluga, narwhal, bowhead whale) vary strongly in abundance across space and time (Darwent, 2001; Moody & Hodgetts, 2013; Savelle & McCartney, 1988). For many species it is therefore difficult, if not impossible, to generate a sample of distinct individuals from a discrete temporal context that would be of sufficient size for the most basic statistical tests. This is true even in the Arctic, where organic preservation tends to be excellent. Nevertheless, the deep time perspective of the archaeological record and the preservation of relatively large quantities of vertebrate tissues provide a unique opportunity to examine long-term environmental variation.

Stable isotope analysis of fauna derived from archaeological sites or natural history collections is a particularly useful tool for studying long-term environmental change (Hobson & Montevecchi, 1991; Moss et al., 2006; Szpak, Orchard, Mckechnie, & Gröcke, 2012; Szpak, Orchard, Salomon, & Gröcke, 2013; Zangrando, Panarello, & Piana, 2014), especially when assessed in light of isotopic studies of modern fauna (Blight, Hobson, Kyser, & Arcese, 2015; Braje et al., 2017; Burton et al., 2001; Guiry, Needs-Howarth, et al., 2016; Misarti, Finney, Maschner, & Wooller, 2009; Vales et al., 2017; Wiley et al., 2013). Carbon and nitrogen isotopes in organic tissues have been used extensively to characterize patterns of habitat use and the foraging ecology of marine consumers (Newsome, Clementz, & Koch, 2010). Tissue carbon isotopic compositions are largely conserved across trophic levels and therefore reflect the ultimate source(s) of primary production (France, 1995). The two most significant sources of production in Arctic waters are pelagic phytoplankton and sea ice algae (Gosselin, Levasseur, Wheeler, Horner, & Booth, 1997). Because of differences in localized water turbidity and its effect on algal cell boundary layer thickness and in turn discrimination against ^{13}C during CO_2 uptake (France, 1995), sea ice algae have $\delta^{13}\text{C}$ values that are 5–12‰ higher than pelagic phytoplankton (France, Loret, Mathews, & Springer, 1998; Hobson, Ambrose, & Renaud, 1995; Søreide, Hop, Carroll, Falk-Petersen, & Hegseth, 2006). Accordingly, the relative importance of pelagic and sympagic production can be approximated on the basis of consumer $\delta^{13}\text{C}$

values (Kohlbach et al., 2016; Tamelander et al., 2006), including marine mammals at high trophic levels (Wang et al., 2016). Additionally, there are gradients in carbon isotope values in particulate organic matter (POM) and consumers between benthic and pelagic habitats, with the latter being characterized by lower $\delta^{13}\text{C}$ values than the former (McConnaughey & Mcroy, 1979). In areas with tight benthic–pelagic coupling, such as the Chukchi Sea, benthic organisms tend to have especially high $\delta^{13}\text{C}$ values relative to pelagic organisms (Dunton, Saupe, Golikov, Schell, & Schonberg, 1989).

Tissue nitrogen isotopic compositions are 3–5‰ higher in consumer tissues relative to prey and therefore largely reflect trophic level (Minagawa & Wada, 1984). Nitrogen isotopic compositions vary at the base of the food web according to types of producers that are present and oceanographic conditions, particularly upwelling and dissolved $[\text{O}_2]$ (Altabet, 2006; Montoya, 2008; Sigman, Karsh, & Casciotti, 2009). Oligotrophic areas with a high proportion of diazotrophic bacteria (such as the colonial cyanobacterium *Trichodesmium*) tend to have lower $\delta^{15}\text{N}$ values throughout the food web than eutrophic areas characterized by strong upwelling of NO_3^- (Dorado, Rooker, Wissel, & Quigg, 2012; Holl et al., 2007). Denitrification occurs in areas with low dissolved $[\text{O}_2]$, producing particularly high $\delta^{15}\text{N}$ values in the residual NO_3^- (Montoya, 2008). Consumers at higher trophic levels record this nutrient- and producer-driven variation in their tissue $\delta^{15}\text{N}$ values (Ruiz-Cooley & Gerrodette, 2012; Wallace, Seminoff, Kilham, Spotila, & Dutton, 2006), typically across spatial scales of 100s or 1,000s of km.

Collagen fingerprinting offers a means with which to overcome taxonomic misidentification based solely on gross morphology (Buckley, Collins, Thomas-Oates, & Wilson, 2009). The method is capable of yielding successful identifications in specimens millions of years old (Rybczynski et al., 2013) and can readily be applied to the analysis of thousands of samples (Buckley, Gu, Shameer, Patel, & Chamberlain, 2016). Although the taxonomic resolution of this technique is largely inferior to DNA-based analyses, genus-level and often species-level identifications (Buckley, Harvey, & Chamberlain, 2017) are typically obtained (note the apparent exception within proboscideans Buckley, Larkin, & Collins, 2011). One of the greatest advantages of collagen fingerprinting is its direct compatibility with other methods, particularly stable isotope analysis, meaning that no additional sample material is destroyed (Harvey, Egerton, Chamberlain, Manning, & Buckley, 2016). Of particular relevance in this case, the differentiation of phocid seals is often difficult on the basis of skeletal morphology and the collagen fingerprinting techniques allows ringed seal (*Pusa hispida*) to be distinguished from coeval phocids (*Phoca vitulina*, *Phoca largha*, *Histiophoca fasciata*, *Erignathus barbatus*) (Buckley et al., 2014). In this study, we present stable isotope and collagen fingerprint data from a set of pinniped remains from three archaeological sites in northwestern Alaska dating between AD 1170 and 1813 along with isotopic measurements from modern subsistence harvested seals from the same region to assess whether there were ecological changes that occurred over the last 900 years with a particular emphasis on benthic–pelagic coupling and sea ice productivity.

2 | MATERIALS AND METHODS

2.1 | Study area

The archaeological sites (KTZ-087, KTZ-088, KTZ-304) from which the samples were obtained are located on Cape Espenberg, situated on the southwest margin of Kotzebue Sound in northwestern Alaska (Darwent, Mason, Hoffecker, & Darwent, 2013; Figure 1). Cape Espenberg has been occupied to some extent for the last 4,500 years (Tremayne, 2015), but the greatest intensity of occupation coincides a few centuries after the initial arrival of Thule culture occupants between AD 900 and AD 1000. They were characterized by a strong maritime adaptation that was particularly well equipped to harvest marine mammals (seals, walrus, and toothed and baleen whales), although the emphasis on particular species varied both spatially and temporally (Darwent, 2011; Savelle & McCartney, 1988). In the Kotzebue Sound area, for example, walrus hunting appears to have been comparatively unimportant in comparison to seal hunting (Darwent & Darwent, 2016; Giddings & Anderson, 1986). Between the earliest Thule settlement of Kotzebue Sound and ca. AD 1450, settlements were characterized by large, multiroom houses organized into relatively large village sites. After AD 1450, however, these larger communities had dispersed, apparently connected with a diversification in subsistence practices and a decline in the emphasis on the hunting of baleen whales (Anderson, 1984; Bockstoce, 1976; Giddings & Anderson, 1986).

2.2 | Sample description

The archaeological pinniped samples were taken from five prehistoric house features located on three distinct beach-ridge formations at Cape Espenberg (Figure 1; Darwent et al., 2013). These dwelling features span 700 years from the arrival of the Thule to just prior to Russian/American contact: (1) Features 12 and 21, Beach Ridge 5, KTZ-304; (2) Features 68A and 68B, Beach Ridge 4, KTZ-087; (3) Feature 33, Beach Ridge 3, KTZ-088. The most abundant element for each species within a given archaeological context (i.e., house feature) was selected to preclude the possibility of taking multiple samples from the same individual. The pinniped samples were not directly radiocarbon dated to avoid issues associated with the marine reservoir effect.

Ages for samples from each archaeological context were estimated based on radiocarbon dates obtained on caribou bone collagen, crowberry seed, and the outermost ring of spruce logs used in house construction, all of which had clear terrestrial carbon isotopic compositions (Table S5). Radiocarbon samples were taken from various units and levels across the house features; all dates were calibrated using OxCAL 4.3 (Bronk Ramsey, 2009) to 2 SDs (94.5%). The radiocarbon dates are both internally comparable, as well as consistent with weighted averages for the beach ridges (Darwent et al., 2013) and the known age of artifact types recovered from within them. For each feature, an age range was estimated using the minimum and maximum calibrated age, and a weighted mean was

calculated using the calibrated mean and standard deviation (i.e., square root of the reciprocal of error). Feature 33, the youngest house feature, yielded radiocarbon dates ranging from AD 1675 to 1942. However, given that this house is situated more than 200 m away from the modern coast on Beach Ridge 3, and the fact that no Russian/American contact period artifacts (e.g., trade beads or metal) were recovered after complete excavation of the well-preserved structure, we are confident that all samples from this feature are late prehistoric in age. Otto von Kotzebue discovered the Sound in 1819, but consistent access to trade goods is limited to after the 1830s. Thus, we conservatively bracket this house feature, and samples collected from it, between AD 1675 and 1850 with a weighted mean of AD 1813.

2.3 | Collagen extraction and purification

Prior to collagen extraction, both the modern and archaeological samples were soaked in 2:1 chloroform:methanol with sonication for 3×20 min to remove lipids (Guiry, Szpak, & Richards, 2016). After lipid extraction, the samples were air-dried for 24–48 hr. Bone samples (278 ± 48 mg) were then demineralized in 0.5 M HCl at 4°C. The demineralized samples were rinsed to neutrality with Type I water, then the insoluble collagen residues were solubilized in 10^{-3} M HCl at 75°C for 48 hr. The resulting solution was filtered using 45–90 μ m mesh filters (Elkay Laboratory Products, Basingstoke, UK) to remove particulate matter and then with 30 kDa molecular weight cut-off ultrafilters (Pall Corporation, Port Washington, NY, USA) to remove low-molecular-weight contaminants (Brown, Nelson, Vogel, & Southon, 1988). The >30 kDa fraction was then freeze-dried.

2.4 | Peptide mass fingerprinting

Approximately 0.5–1.0 mg lyophilized collagen for each sample was resuspended with 50 mM ammonium bicarbonate and heated at 65°C for 1 hr to assist solubilization. Then 0.4 μ g sequencing grade trypsin (Promega, UK) was added and incubated at 37°C overnight to digest the collagen. The peptides were then purified by C18 resin ZipTips (Varian, UK) following manufacturer's protocol into 50% acetonitrile (ACN)/0.1% trifluoroacetic acid (TFA) and evaporated by centrifugal evaporator. After resuspension with 10 μ l 0.1% TFA, 1 μ l was spotted onto a stainless steel matrix-assisted laser desorption ionization (MALDI) target plate and subsequently cocrystallized with 1 μ l α -cyano hydroxycinnamic acid matrix. These were then analyzed using a Bruker Ultraflex II MALDI time-of-flight mass spectrometer with 2,000 laser acquisitions and the fingerprints compared with marine mammal collagen species biomarkers previously published (Buckley et al., 2014).

2.5 | Stable isotope analysis

All collagen samples were analyzed in duplicate using a Vario MICRO cube elemental analyzer coupled to an Isoprime continuous flow

isotope ratio mass spectrometer (CF-EA/IRMS; Elementar, Hanover, Germany). Carbon and nitrogen isotopic compositions were calibrated relative to VPDB and AIR, respectively, using USGS40 and USGS41 (Table S1). Internal accuracy and precision were monitored using a suite of internal standard reference materials (Tables S2 and S3). Using the method presented by Szpak, Metcalfe, and Macdonald (2017), standard uncertainty was determined to be ± 0.18 for $\delta^{13}\text{C}$ and ± 0.27 for $\delta^{15}\text{N}$. A detailed accounting of all elements of the uncertainty calculation is presented in the Supporting Information. Samples were monitored for alteration of the isotopic composition of the collagen by ensuring they met the following criteria: atomic C: N ratio between 2.9 and 3.6 (DeNiro, 1985), wt% collagen (yield) >3.5%, wt% C of extracted collagen >13%, wt% N of extracted collagen >4.8% (Ambrose, 1990; van Klinken, 1999).

2.6 | Data treatment

To compare temporal variation it is first necessary to adjust modern $\delta^{13}\text{C}$ values to account for the changes in atmospheric and oceanic dissolved inorganic carbon (DIC) $\delta^{13}\text{C}$ values that have occurred since the late 19th century (Eide, Olsen, Ninnemann, & Eldevik, 2017; Quay, Tilbrook, & Wong, 1992). To do so, we calculated the Suess effect correction for modern samples ($\Delta^{13}\text{C}_{\text{Suess}}$) using Equation 1 as defined by Hilton et al. (2006):

$$\Delta^{13}\text{C}_{\text{Suess}} = a_{\text{water body}} + e^{(\text{year} - 1850)^b}, \quad (1)$$

where a = the annual rate of $\delta^{13}\text{C}$ decrease for the water body in question and b defines the shape of the exponential curve and is defined by the global decrease in oceanic $\delta^{13}\text{C}$ between 1945 and 1997, determined to be 0.027 by Gruber et al. (1999). The annual rate of decrease for the water body was estimated to be -0.014‰ , following Quay's (1992) estimate for the North Pacific. Although no specific estimate of the decrease in $\delta^{13}\text{C}$ for Kotzebue Sound or the adjacent Chukchi/Bering Sea area is available, polar regions are characterized by relatively small changes in oceanic surface water DIC $\delta^{13}\text{C}$ (Quay, Sonnerup, Westby, Stutsman, & McNichol, 2003) and Quay's estimate of $-0.014\text{‰}/\text{year}$ for the North Pacific may slightly overestimate the magnitude of the local Suess effect, which could serve to decrease the magnitude of any potential differences found between pre- and postindustrial age samples. The $\delta^{13}\text{C}$ values of samples collected in 2000 were adjusted by $+0.80\text{‰}$ and those collected in 2001 were adjusted by $+0.83\text{‰}$, which are comparable but slightly lower than the $\Delta^{13}\text{C}_{\text{Suess}}$ values estimated further south for

the Gulf of Alaska ($+1.1\text{‰}$) by Newsome et al. (2007), as would be expected for this more northerly region. Bauch, Carstens, Wefer, and Thiede (2000) found the local Suess effect for the Arctic Ocean (northern Nansen Basin) to be $+0.9\text{‰}$ based on measurements of forams (*Neogloboquadrina pachyderma*).

Temporal trends in isotopic composition were assessed using only ringed seal isotopic compositions for two reasons. First, the other taxa lacked adequate sample sizes (archaeological, modern, or both) for any meaningful assessment of temporal trends to be conducted. Second, ringed seals have restricted home ranges and should not therefore integrate aspects of multiple environments in their tissue stable isotope compositions (Kelly et al., 2010).

Differences between taxa and time periods were compared using a one-way analysis of variance (ANOVA). Homogeneity of variance was assessed using Levene's test (Levene, 1960). If variance was homoscedastic, Tukey's HSD test was performed (Tukey, 1949); if variance was not homoscedastic, Dunnett's T3 test was performed (Dunnett, 1980). Correlations between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were assessed using Spearman's ρ .

3 | RESULTS

The summarized carbon and nitrogen isotopic compositions of the species sampled are presented in Table 1 and Figure 3; IRMS results for all individual samples are presented in Table S4 along with information on the precise archaeological context of each specimen. The morphological identifications were confirmed using the collagen fingerprinting technique (Fig. S1). There was 100% agreement between the morphological identifications and the collagen fingerprints.

The $\delta^{13}\text{C}$ values did not differ between any of the archaeological taxa ($F_{2,63} = 0.028$, $p = .972$), whereas the $\delta^{15}\text{N}$ values differed significantly among all taxa ($F_{2,63} = 70.61$, $p < .001$), excluding spotted seal as there was only a single sample (Table 2). Walrus occupied the lowest trophic level, with $\delta^{15}\text{N}$ values of $+13.4\text{‰}$ (modern, $n = 1$) and $+13.0\text{‰}$ (archaeological, $n = 4$), consistent with a diet composed predominantly of mollusks. Bearded seals had $\delta^{15}\text{N}$ values of $+16.0 \pm 1.0\text{‰}$ (archaeological, $n = 8$) and $+15.3 \pm 0.1\text{‰}$ (modern, $n = 2$), suggesting that they fed approximately one trophic level higher than walrus. Ringed seals had $\delta^{15}\text{N}$ values of $+18.4 \pm 0.9\text{‰}$ (archaeological, $n = 52$) and $+17.9 \pm 0.5$ (modern, $n = 24$), suggesting strong partitioning of dietary resources between ringed and bearded seals, a pattern that has been observed in this region on the

Species	Modern			Archaeological		
	n	$\delta^{13}\text{C}$ (‰ VPDB)	$\delta^{15}\text{N}$ (‰ AIR)	n	$\delta^{13}\text{C}$ (‰ VPDB)	$\delta^{15}\text{N}$ (‰ AIR)
Walrus	1	-14.8	+13.4	4	-13.3 ± 0.7	+13.0 ± 1.3
Bearded seal	2	-15.6 ± 0.3	+15.3 ± 0.1	8	-13.3 ± 0.5	+16.6 ± 1.0
Ringed seal	25	-15.6 ± 1.0	+17.9 ± 0.5	52	-13.3 ± 0.5	+18.4 ± 0.9
Spotted seal	16	-15.3 ± 0.5	+18.3 ± 0.8	1	-11.8	+20.4

TABLE 1 Summarized carbon and nitrogen isotopic compositions for modern and archaeological marine mammals

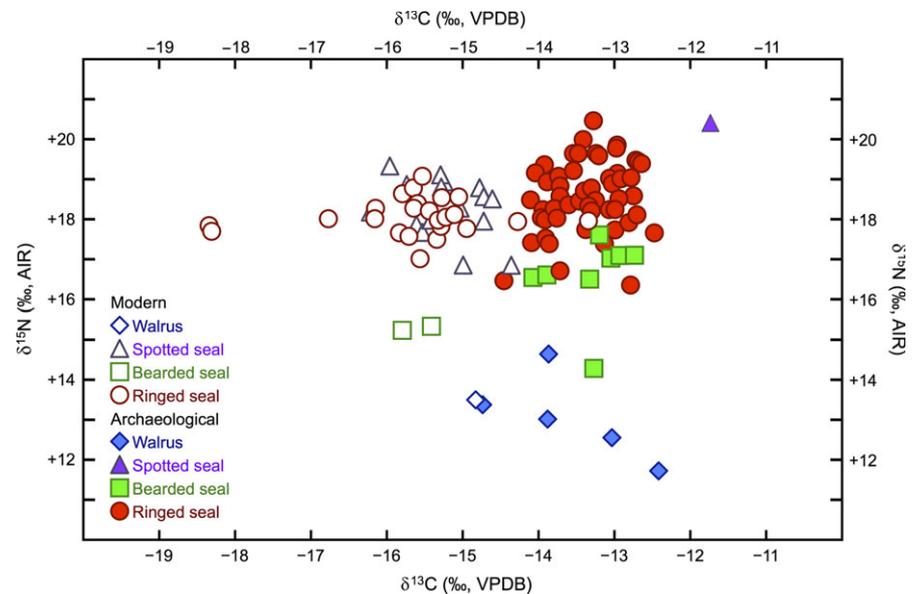


FIGURE 3 Carbon and nitrogen isotopic compositions of modern (open symbols) and archaeological (shaded symbols) fauna. The modern $\delta^{13}\text{C}$ values have not been adjusted to account for the Suess effect for the sake of clarity

TABLE 2 Results of ANOVA post hoc tests (Tukey's HSD) for interspecific differences in the archaeological fauna

	Species	Bearded seal	Ringed seal
$\delta^{13}\text{C}$	Walrus	>0.999	0.992
	Bearded seal	–	0.975
$\delta^{15}\text{N}$	Walrus	<0.001	<0.001
	Bearded seal	–	<0.001

Values in boldface indicate $p < .05$.

basis of blubber fatty acid compositions (Wang et al., 2016). The average $\delta^{13}\text{C}$ values of archaeological bearded and ringed seals were nearly identical ($p = .95$), but the $\delta^{15}\text{N}$ values differed significantly ($p < .001$). Spotted seals had the highest $\delta^{15}\text{N}$ values among all the taxa analyzed, although the archaeological sample consists of only a single individual, and therefore discussion of interspecific variation is necessarily limited to the modern samples. Modern ringed and spotted seals did not differ in terms of their $\delta^{13}\text{C}$ ($p = .25$) or $\delta^{15}\text{N}$ values ($p = .06$).

Temporal variations in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of ringed seal bone collagen are plotted in Figure 4. There were significant differences in both ringed seal bone collagen $\delta^{13}\text{C}$ ($F_{5,75} = 40.01$, $p < .001$) and $\delta^{15}\text{N}$ ($F_{5,75} = 4.27$, $p = .002$) values among the different time periods studied; these differences are summarized in Table 3. Notably, there was a fairly large decline in $\delta^{13}\text{C}$ in the modern relative to the archaeological seals after taking into account adjustments for the Suess effect as discussed previously (Figure 4). The magnitude of this decline was fairly small, but this is to be expected when examining a consumer that feeds somewhere between the third and fourth trophic level and is therefore several steps removed from primary producers. The $\delta^{13}\text{C}$ values of the other taxa for which archaeological and modern samples were available (bearded seal, spotted seal, walrus) were similarly characterized by lower $\delta^{13}\text{C}$ values in the modern relative to archaeological periods,

although the small sample sizes for each of these taxa preclude more detailed assessments. There was a positive correlation between ringed seal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Spearman's $\rho = .33$, $p = .003$). This correlation was reflected by the covariation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values over time (Figure 4).

4 | DISCUSSION

4.1 | Marine mammal diet and ecology

The diets of both ringed seals and bearded seals consist of variable proportions of benthic and pelagic vertebrates and invertebrates. In the Bering/Chukchi Sea region, bearded seals tend to consume more benthic invertebrates and less fish than ringed seals (Lowry, Frost, & Burns, 1980a, 1980b). On the basis of the isotopic data presented for Kotzebue Sound, bearded seals likely consumed a mixture of benthic invertebrates (clams and crabs) and fish, whereas ringed seals focused primarily on higher trophic level prey, particularly saffron cod (*Eleginus gracilis*), shrimp and predatory euphausiids (Lowry et al., 1980a, 1980b). In light of the observation that bearded seals typically consume more benthic prey than ringed seals (Crawford, Quakenbush, & Citta, 2015; Finley & Evans, 1983), the lack of differentiation in $\delta^{13}\text{C}$ between these two species is surprising and does not fit the expected pattern for species utilizing variable quantities of pelagic and benthic prey (McConnaughey & Mcroy, 1979). In studies of modern ecosystems, higher tissue $\delta^{13}\text{C}$ values have been observed in bearded relative to ringed seals in western Hudson Bay (Young, Loseto, & Ferguson, 2010), northern Alaska (Dehn et al., 2007; Hoekstra et al., 2002), and northwestern Alaska (Carroll, Horstmann-Dehn, & Norcross, 2013). Importantly, however, none of these studies found a difference larger than 0.2‰ (typical analytical uncertainty in CF-EA/IRMS measurements) between the mean $\delta^{15}\text{N}$ values of ringed and bearded seals. On the other hand, we observed a difference of +1.8‰ (archaeological) and +2.6‰ (modern) between

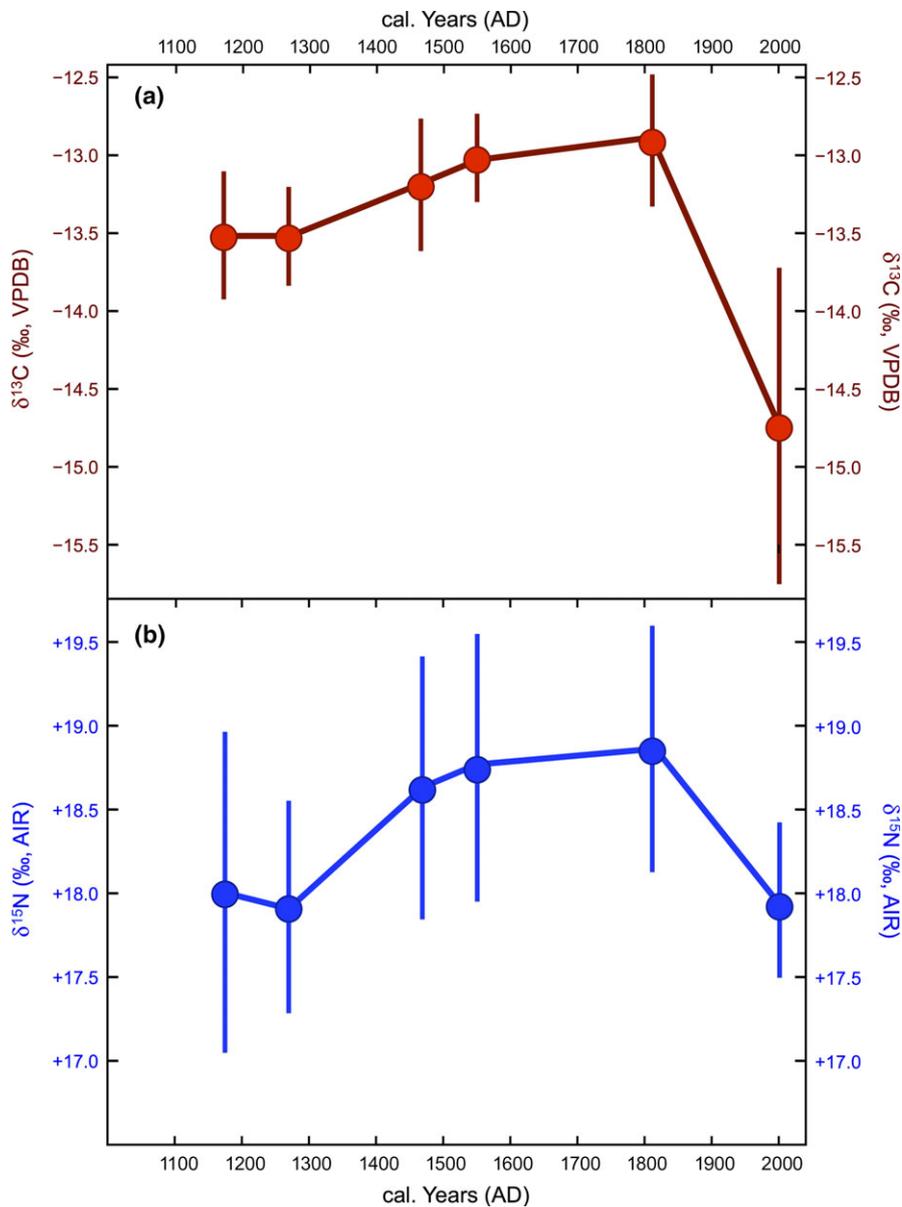


FIGURE 4 Ringed seal carbon (a) and nitrogen (b) isotopic compositions (primary axis) plotted over time. Points represent means for archaeological contexts (house features), vertical lines represent 1 SD

ringed and bearded seals (Table 1). Similarly, in two other studies that examined archaeological bone collagen carbon and nitrogen isotopic compositions of these two species in the Canadian Arctic, there were no differences in $\delta^{13}\text{C}$ values, but mean differences of 3.3‰ (Jaouen, Szpak, & Richards, 2016) and 1.3‰ (Coltrain, Hayes, & O'Rourke, 2004) for $\delta^{15}\text{N}$, with ringed seals having the higher values in both cases. Because there is a small increase in $\delta^{13}\text{C}$ at each trophic level (France & Peters, 1997; Rau et al., 1983), when ringed seals feed at a higher trophic level than bearded seals, this may serve to obscure any differences in $\delta^{13}\text{C}$ related to variable consumption of benthic and pelagic resources.

4.2 | Temporal variation

Ringed seal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values varied in phase with one another over time (Figure 4). The highest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were coincident with cold conditions in the region and extensive sea ice, while

the lowest $\delta^{13}\text{C}$ values were observed in the modern specimens, coincident with relatively reduced sea ice. There are two mechanisms that could be responsible for the temporal trends in ringed seal carbon and nitrogen isotopic compositions, both of which are ultimately causally tied to changing sea ice productivity. First, it is possible that the variations in isotopic compositions reflect differences in the extent to which ringed seals foraged on benthic vs. pelagic resources, with a recent and significant decline in benthic foraging signaled by the low $\delta^{13}\text{C}$ values in the modern samples. A similar explanation for declining $\delta^{13}\text{C}$ values was suggested by Outridge, Hobson, and Savelle (2005) for belugas (*Delphinapterus leucas*) in the central Canadian Arctic Archipelago when contrasting late 19th century and late 20th century individuals. These authors also note that there was no change in ringed seal $\delta^{13}\text{C}$ values in the same area (Somerset Island) between ca. ~AD 1200 and 1970 (unpublished data cited in Outridge et al., 2005).

That the ringed seal $\delta^{15}\text{N}$ values are relatively low when the $\delta^{13}\text{C}$ values are low is consistent with notion of a recent decline in

TABLE 3 Results of ANOVA post hoc tests (Tukey's HSD) for temporal differences in ringed seal bone collagen $\delta^{13}\text{C}_{\text{corr}}$ (modern samples corrected for the Suess effect as described in the text) and $\delta^{15}\text{N}$

	Date (cal years AD)	1170	1466	1548	1813	2000
$\delta^{13}\text{C}_{\text{corr}}$	1170	0.99	0.89	0.35	0.21	<0.001
	1267	–	0.35	0.32	0.32	<0.001
	1466	–	–	0.33	0.33	<0.001
	1548	–	–	–	>0.99	<0.001
	1813	–	–	–	–	<0.001
$\delta^{15}\text{N}$	1170	>0.999	0.42	0.12	0.05	>0.99
	1267	–	0.42	0.15	0.08	0.37
	1466	–	–	0.97	0.99	0.28
	1548	–	–	–	>0.99	0.05
	1813	–	–	–	–	0.02

Values in boldface indicate $p < .05$.

benthic foraging. When POM sinks to the ocean bottom, isotopically light (^{15}N depleted) nitrogen is released due to microbial degradation as the particles sink, producing higher $\delta^{15}\text{N}$ values in organic matter with depth (Saino & Hattori, 1980, 1987). These patterns are, however, more pronounced in the open ocean where greater depths allow for greater ^{15}N enrichment relative to continental shelves and inshore areas. Regardless, benthic food webs tend to be enriched in ^{15}N relative to pelagic food webs (Iken, Bluhm, & Gradinger, 2005). This explanation is also consistent with recent observations in the Bering Sea of a shift from a rich, productive benthos supporting walrus and spectacled eiders to one where pelagic fish species have increased in abundance and benthic productivity has decreased (Dunton et al., 2005; Grebmeier, Overland, et al., 2006; Lovvorn, Grebmeier, Cooper, Bump, & Richman, 2009). The most likely cause for this trend is increased grazing of primary production by zooplankton, ultimately driven by warmer surface water temperatures (Grebmeier, 2011). These changes have been observed south of our study area and have not yet been recorded in the southern Chukchi Sea or Kotzebue Sound. The southern Chukchi Sea, however, has seen a recent shift in the types of pelagic seabirds that are present, with a decline in piscivorous taxa and an increase in planktivorous taxa (Gall, Morgan, Day, & Kuletz, 2017). On the other hand, surveys of epibenthic fauna in the southern Chukchi Sea (Bluhm, Iken, Mincks Hardy, Sirenko, & Holladay, 2009), Norton Sound (Hamazaki, Fair, Watson, & Brennan, 2005), and Kotzebue Sound (Feder et al., 2005) have not documented recent declines in benthic biomass, although these comparisons are on the order of years or decades rather than centuries as is the case in our study.

The second plausible scenario to account for the temporal variation in ringed seal isotopic compositions relates to sea ice productivity. Specifically, the low $\delta^{13}\text{C}$ values observed in the modern samples may reflect a shift toward increased production derived from pelagic phytoplankton relative to sea ice algae, the latter of which have $\delta^{13}\text{C}$ values that may be as much as 12‰ higher than coeval pelagic

phytoplankton (France et al., 1998; Hobson et al., 1995). This scenario fits with the recent and rapid decline of sea ice extent in the region, based on scientific data as well as TEK (Ershova et al., 2015; Krupnik et al., 2010; Steele et al., 2008). The variation in ringed seal $\delta^{13}\text{C}$ values among the archaeological samples may also reflect some temporal variation in sea ice extent. The highest values were recorded in ringed seals from AD 1466, AD 1548, and AD 1813 (Figure 4), which coincides with the Little Ice Age and greater sea extent in other areas of the northern hemisphere (Massé et al., 2008; Vare et al., 2009), although this pattern was not observed by de Vernal et al. (2008) approximately 1,000 km north of our study area in the Chukchi Sea. This period in time saw significant changes in the settlement patterns of the people inhabiting this region, with smaller settlements replacing larger ones, apparently in response to changing climatic conditions and the decline in extended periods of open water conducive to the pursuit of large baleen whales (Anderson, 1984; Bockstoce, 1976). To date, supporting zooarchaeological evidence for a shift in subsistence after the end of the Medieval Climatic Optimum (alternatively Medieval Warm Period) around AD 1400 is lacking, but this may be driven in part by the fact that bones from hunted whales would not have been brought back to settlements (Hoffecker et al., 2012; Stanford, 1976).

That the ringed seal $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values vary in concert with one another cannot be explained by variable contributions of sea ice productivity as sea ice and pelagic POM in the Arctic are not characterized by consistent differences in $\delta^{15}\text{N}$ (Hobson et al., 1995; Sørdeide et al., 2006; Tamelander et al., 2006), although POM associated with sea ice has been observed to be ^{15}N enriched relative to pelagic POM in the Antarctic (Rau, Sullivan, & Gordon, 1991). On the other hand, a shift in ringed seal diet composition related to shifting environmental conditions could produce such a pattern. The relative contribution of high and low trophic level prey may vary according to sea ice extent, which could impact consumer $\delta^{15}\text{N}$ values. Hindell, Lydersen, Hop, and Kovacs (2012) found that the diet of bearded seals in Svalbard varied on an annual scale with greater quantities of fish being consumed when sea ice extent was greatest and larger quantities of benthic invertebrates being consumed when sea ice extent was least. Thus, the recent decrease in sea ice productivity (signaled by the lower ringed seal $\delta^{13}\text{C}$ values) may have initiated a change in ringed seal foraging ecology, with an increased reliance on fish relative to lower trophic level benthic invertebrates.

It is possible that the two explanations outlined above are not mutually exclusive as both can be causally tied to declining sea ice in the region. In the Chukchi Sea, Matsuno, Yamaguchi, Hirawake, and Imai (2011) found that zooplankton biomass (and presumably pelagic grazing) was much higher during years with low sea ice extent relative to years with high sea ice extent. Therefore, it is possible that the low $\delta^{13}\text{C}$ values observed in the modern ringed seals are indicative of decreased delivery of POM to the benthos due to increased zooplankton grazing, decreased productivity of sea ice algae, greater availability of pelagic relative to benthic prey for ringed seals, and weaker benthic–pelagic coupling. The nature of bulk stable isotope data precludes the possibility of a more specific assignment of the precise mechanism driving these patterns.

Compound-specific isotope analysis of individual amino acids offers one potential means of providing greater resolution to these issues. Presently, research in marine environments has focused on comparing $\delta^{15}\text{N}$ measurements of source (reflecting the $\delta^{15}\text{N}$ at the base of the food web) and trophic (reflecting trophic position) amino acids (Chikaraishi et al., 2014) to differentiate changes in consumer trophic position from changes in $\delta^{15}\text{N}$ at the base of the food web (Ostrom et al., 2017; Pomerleau et al., 2017; Ruiz-Cooley, Koch, Fiedler, & McCarthy, 2014). Based on promising studies on marine macroalgae demonstrating distinct amino acid $\delta^{13}\text{C}$ profiles relative to other producers (Larsen et al., 2013), it is possible that these techniques may be able to identify more specific causal factors for temporal variation in bulk isotopic measurements in the Arctic, but much more experimental work focused on characterizing the mechanisms that influence the $\delta^{13}\text{C}$ values of marine producers at various spatial scales is necessary.

In summary, carbon and nitrogen isotope analyses were performed on marine mammals from three archaeological sites in northwestern Alaska as well as modern marine mammals harvested from the same area with taxonomic identifications of the archaeological taxa confirmed using peptide fingerprinting. Ringed seal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values varied in phase with one another over the last 900 years, with a large decline in $\delta^{13}\text{C}$ values between the early-19th century and the early 21st century. The most likely cause of this change relates to declines in sea ice productivity as a result of recent warming in the Arctic and the subsequent decline in ice algae productivity and delivery of organic matter to the benthos, which has in turn influenced the foraging ecology of high trophic level consumers. Given the current temporal trends observed further south in the Bering Sea, it is probable that these changes will intensify in the coming years, with a shift toward more subarctic conditions.

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AUTHOR CONTRIBUTIONS

PS and CMD designed research. PS performed isotopic research. MB performed peptide fingerprinting research. MPR and MB contributed analytical tools. PS wrote the paper with the exception of the

sample description (CMD) and methods/introduction sections for collagen fingerprinting (MB).

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