Pacific walrus diet across 4000 years of changing sea ice conditions

Casey T. Clark[a,b]*, Lara Horstmann[b], Anne de Vernal[c], Anne M. Jensen[d,e], Nicole Misarti[a]

[a]Water and Environmental Research Center, University of Alaska Fairbanks, 1764 Tanana Loop, Fairbanks, Alaska 99775-5860, USA
[b]College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 2150 Koyukuk Drive, Fairbanks, Alaska 99775-7220, USA
[c]Centre de Recherché en Géochimie et Géodynamique (Geotop), Université du Québec à Montréal, P.O. Box 8888, Succursale Centre-Ville, Montréal, Québec H3C 3P8, Canada
[d]UIC Science LLC, P.O. Box 577, Utqiaġvik, Alaska 99723, USA
[e]University of Alaska Museum, University of Alaska Fairbanks, 1962 Yukon Drive, Fairbanks, Alaska 99775, USA
*Corresponding author e-mail address: ctclark@alaska.edu

Abstract

Declining sea ice is expected to change the Arctic's physical and biological systems in ways that are difficult to predict. This study used stable isotope compositions (δ^{13}C and δ^{15}N) of archaeological, historic, and modern Pacific walrus (*Odobenus rosmarus divergens*) bone collagen to investigate the impacts of changing sea ice conditions on walrus diet during the last ~4000 yr. An index of past sea ice conditions was generated using dinocyst-based reconstructions from three locations in the northeastern Chukchi Sea. Archaeological walrus samples were assigned to intervals of high and low sea ice, and δ^{13}C and δ^{15}N were compared across ice states. Mean δ^{13}C and δ^{15}N values were similar for archaeological walruses from intervals of high and low sea ice; however, variability among walruses was greater during low-ice intervals, possibly indicating decreased availability of preferred prey. Overall, sea ice conditions were not a primary driver of changes in walrus diet. The diet of modern walruses was not consistent with archaeological low sea ice intervals. Rather, the low average trophic position of modern walruses (primarily driven by males), with little variability among individuals, suggests that trophic changes to this Arctic ecosystem are still underway or are unprecedented in the last ~4000 yr.

Keywords: Pacific walrus; Sea ice; Arctic; Climate change; Stable isotopes; Historical ecology; Paleoecology; Chukchi Sea; Bering Sea

INTRODUCTION

Recent declines in the extent and thickness of summer sea ice in the Arctic have raised concerns about the future status of ice-dependent and ice-associated species. Predicting the impacts of ice loss on Arctic marine organisms is difficult. All Arctic research to date has been conducted while sea ice cover was relatively high or, in recent decades, during a period of rapid change (Walsh et al., 2017). Little is known about the structure and function of biological systems in the Arctic when sea ice cover is low. Historical ecology has emerged as an important tool for gaining information about past ecosystems (Swetnam et al., 1999; Lotze and Worm, 2009). Rick and Lockwood (2013, pp. 46–47) define historical ecology as "the use of historic and prehistoric data (e.g., paleobiological, archaeological, historical) to understand ancient and modern ecosystems, often with the goal of providing context for contemporary conservation." Studies of historical ecology rely on reconstruction of past conditions using archived or preserved specimens and can therefore capture variability in biological systems across broad time spans (e.g., Dyke and Savelle, 2001; Newsome et al., 2007; Misarti et al., 2009; Alter et al., 2012; Wiley et al., 2013; Sherwood et al., 2014; Ostrom et al., 2017). This approach can provide otherwise unobtainable information about the responses of plants and animals to large-scale changes not observed within the era of modern scientific inquiry. The result is a more complete understanding of natural systems that allows contemporary data to be compared with a variety of historical ecosystem states.

Stable isotope analysis is commonly used in studies of historical ecology, as isotope ratios in preserved hard tissues typically remain unchanged after an animal's death and can be measured in a variety of tissue types (Fry, 2006; Newsome et al., 2010). Stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope compositions are versatile tools for studying animal diet, with δ^{15}N indicating trophic position of the consumer and δ^{13}C the sources of primary production at the base of the food

web (Hobson and Welch, 1992; Goericke and Fry, 1994). Additionally, changes in $\delta^{13}C$ and $\delta^{15}N$ may reflect shifts in baseline isotope ratios and can provide important information about primary production including the type of producers at the base of the food web, rates of production, and nutrient utilization (Fogel and Cifuentes, 1993). Bones are among the few biological structures that are commonly preserved in archaeological assemblages; thus bone collagen is often analyzed for these studies (Hedges et al., 2006). The slow metabolic turnover of bone tissue means that isotope ratios of bone collagen represent a long-term average of animal diet, often encompassing an animal's entire life (Manolagas, 2000). Seasonal and short-term variability are not typically represented, making bone collagen particularly valuable for investigating changes in stable isotope ratios over long time periods.

Arctic marine mammals are ideal candidates for studies of historical ecology, as they have been an important subsistence resource for native peoples in this region for thousands of years, and their discarded remains preserve well in frozen northern soils (Misarti et al., 2009). Pacific walrus (*Odobenus rosmarus divergens*) bones are commonly recovered from archaeological sites in Alaska, and many specimens are available in museum collections. Walruses rely on sea ice as a platform for giving birth, molting, and resting between foraging bouts (Fay, 1982), likely making these animals vulnerable to reduced sea ice coverage associated with Arctic warming (Jay et al., 2011). With the loss of summer sea ice in the Chukchi Sea, the frequency of large, terrestrial walrus haulouts in Alaska has increased, leading to trampling events, increased juvenile mortality, and, presumably, local resource depletion (Garlich-Miller et al., 2011; Jay et al., 2011; MacCracken, 2012). Sea ice also plays an important role in maintaining benthic-pelagic coupling in the Bering and Chukchi Seas, resulting in the export of large amounts of organic carbon to the benthos and supporting rich benthic communities (Grebmeier et al., 2015a; but see Arrigo et al., 2012; Arrigo and van Dijken, 2015). Walruses primarily forage on benthic invertebrates (Fay, 1982; Sheffield and Grebmeier, 2009); therefore, the weakening of benthic-pelagic coupling associated with sea ice loss is expected to reduce availability of preferred walrus prey, possibly driving shifts in walrus diet (Jay et al., 2011; Grebmeier, 2012). Changes in the accessibility of preferred prey could lead to longer, more energetically expensive foraging trips, which may have negative effects at the population level (Jay et al., 2012; Noren et al., 2012, 2016).

Despite concerns about the future of the Pacific walrus population, the effects of ice loss remain largely unknown, and there are some indications that impacts to the health of walruses have so far been minimal. For example, Alaska Native subsistence hunters report that although sea ice conditions have changed and access to walruses has become more difficult, average walrus body condition has not changed in recent years (Huntington et al., 2016). In 2014–2016, hunters from the communities of Gambell and Savoonga, on St. Lawrence Island, Alaska, indicated on biomonitoring data sheets accompanying harvested animals that walruses appeared healthy and were generally in good body condition. In 2017, the U.S. Fish and Wildlife Service (USFWS) came to the decision not to list the Pacific walrus as endangered or threatened under the Endangered Species Act. This decision was based on the conclusion that regional warming and increased use of the Arctic by humans did not pose a serious threat of extinction to the species (MacCracken et al., 2017). The purpose of this study was to investigate how sea ice loss affected Pacific walruses in the past, so that we might better understand how current and future climate change will affect this species. To accomplish this, we measured $\delta^{13}C$ and $\delta^{15}N$ of walrus bone collagen sampled from archaeological assemblages, historical collections, and modern Alaska Native subsistence harvests to assess how changing sea ice conditions over the last ~4000 years affected walrus diet.

METHODS

Sample collection and radiocarbon dating

Pacific walrus bones were identified from archaeological faunal assemblages, historical museum collections, and present-day Alaska Native subsistence harvests (Fig. 1). Bone samples from the 2014–2016 (n = 76) subsistence harvests in the communities of Gambell and Savoonga on St. Lawrence Island, Alaska, were obtained through agreements with Alaska Native subsistence hunters, the Eskimo Walrus Commission, the Alaska Department of Fish and Game, and the USFWS. Bone samples were transferred to the University of Alaska Fairbanks for sample analysis under a letter of authorization from the USFWS to
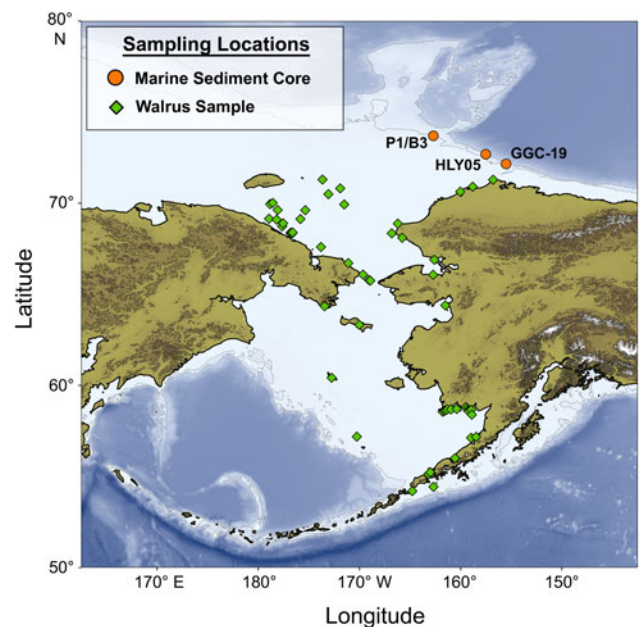

Figure 1. Map of the study area indicating sampling locations of marine sediment cores (P1/B3, GGC-19, and HLY05; orange circles) and walrus specimens (green diamonds).

Dr. L. Horstmann. The North Slope Borough Department of Wildlife Management in Utqiaġvik (formerly Barrow), Alaska, provided additional modern samples collected in 2012, 2014, and 2015 (n = 9; permit #NSB-DWM USFWS MA134907-2). Historical specimens (n = 142) were sampled from collections at the University of Alaska Museum in Fairbanks, Alaska, and spanned the period from 1928 to 2007. Additional historical specimens (n = 18) from the U.S. Museum of Natural History, Smithsonian Institution, Washington, D.C., dated from 1880 to 1973 and were sampled to fill gaps in the chronology (Supplementary Table 1). Only adult and juvenile walruses were included in analyses. Calves and fetuses were removed because of expected differences in $\delta^{13}C$ and $\delta^{15}N$ associated with gestation and nursing (Newsome et al., 2010)

Archaeological specimens (n = 212) were compiled from multiple collections housed at the University of Alaska Museum and UIC Science, Utqiaġvik, Alaska. Samples originated from 12 archaeological sites along the Bering and Chukchi Seas and 2 sites in the North Pacific, on the southern side of the Alaska Peninsula. Timing, methodology, and written documentation of excavations varied widely among sites. Samples used for this study were those that could be identified as belonging to distinct individual walruses and confidently assigned date ranges based on radiocarbon dating and site stratigraphy. Distal limb bones (carpals, tarsals, and phalanges) were excluded from analysis because of the tendency of their stable isotope ratios to be unrepresentative of the rest of the skeleton (Clark et al., 2017). Radiocarbon dating of marine samples is inherently problematic because of complications associated with the marine carbon reservoir (Stuiver et al., 1986). For this reason, the most likely date range of each sample was established using radiocarbon dating of directly associated terrestrial material, where available (mostly caribou [*Rangifer tarandus*] bone collagen; Supplementary Table 2). In instances where directly associated terrestrial dates were not available for a specimen, most likely date ranges for walrus samples were estimated using bracketing terrestrial dates from directly above and below a specimen, information about the provenience of each bone, limiting dates, and temporally diagnostic artifacts (Supplementary Table 3). The 2σ range was used for each radiocarbon date, except where it could be further constrained using additional information such as well-dated stratigraphy and known dates of site occupation. Dating of terrestrial samples was conducted at the University of Georgia Center for Applied Isotope Studies using accelerator mass spectrometry. Archaeological walrus samples used for this study originated from ~4084 to 0 calibrated years before present (cal yr BP).

Pacific walruses exist in a single, mixed population, with little evidence of stock structure (Fay, 1982; Cronin et al., 1994; Scribner et al., 1997; Lindqvist et al., 2009; Shitova et al., 2017; but see Jay et al., 2008; Sonsthagen et al., 2012). Individual walruses move widely across the species' geographic range, foraging as they travel (Fay, 1982; Jay et al., 2012; Beatty et al., 2016). For these reasons, the location at which an animal was harvested was not deemed an important factor for this study. Walruses sampled at any location within the species' geographic range were considered representative of the population as a whole. That said, the annual walrus migration is sex segregated, with females and juveniles following the retreating ice northward into the Chukchi Sea in summer, and males moving to coastal areas of the Bering Sea and Gulf of Anadyr (Fay, 1982). Thus, it is nearly impossible to disentangle sex-related differences in stable isotope ratios (i.e., diet) from geographic variations in baseline stable isotope values between the Bering and Chukchi Seas. To account for the potential impacts of sex/region on the results of this study, the sex ratios and sex-related differences in $\delta^{13}C$ and $\delta^{15}N$ of samples from the historic and modern periods were considered in relation to observed changes in mean isotope ratios between these periods. Sex data were not available for archaeological samples, so the role of sex-related and regional differences could not be quantified. Location of sample collection alone is not a good proxy for sex, as male and female walruses spend much of the year together in the Bering Sea and because the degree of sex-segregation during migration may have changed over time (Fay, 1982; Garlich-Miller et al., 2011).

Bone collagen extraction and stable isotope analysis

Collagen extractions were conducted using the methods described in Misarti et al. (2009), as modified from Matheus (1995). Briefly, ~0.4 g of cortical bone was sampled from walrus bones using handheld cutting tools, submerged in ultrapure water, and placed in a sonic bath for cleaning. Lipids were extracted by soaking the bone in 2:1 chloroform/methanol for 8 hours. The mineral component of the bone was subsequently removed using a mixture of 6N hydrochloric acid (HCl) and ultrapure water. Demineralization was conducted at ~2°C, and the length of time required varied by sample (ranging from 1 to 3 weeks). For archaeological specimens, the demineralized samples were then rinsed to neutral with ultrapure water, soaked in a solution of ultrapure water and 5% potassium hydroxide (KOH) for 8 hours to remove any contamination from soils, and rinsed to neutral again with ultrapure water. For all samples, the organic component of the bone was gelatinized by placing it in 5 mL of ultrapure water, adding 0.05 mL of 3N HCl, and then agitating it at 65°C. The gelatinized product was filtered through a 0.45 μm filter to remove any insoluble particles and noncollagen organic compounds, and freeze-dried for 48 hours to yield purified collagen. A subsample of this collagen (0.2–0.4 mg) was submitted for stable isotope analysis.

Stable carbon and nitrogen isotope ratios of bone collagen samples were analyzed in the Alaska Stable Isotope Facility at the University of Alaska Fairbanks, using a Costech ECS 4010 elemental analyzer and ThermoScientific Conflo IV, interfaced with a ThermoScientific DeltaV mass spectrometer. Stable isotopic compositions were calibrated relative to Vienna Pee Dee belemnite and atmospheric nitrogen gas (air) scales using USGS40 and USGS41 as calibration standards. Results were reported in parts per thousand (‰)

using δ notation. A commercially available peptone standard (No. P-7750 bovine-based protein, Sigma Chemical Company, lot #76f-0300 [$\delta^{13}C$, −15.8‰; $\delta^{15}N$, 7.0‰]) was analyzed as a check standard after every 10 samples to estimate uncertainty. Precision of these analyses was determined to be ±0.2‰ for $\delta^{13}C$ and ±0.2‰ for $\delta^{15}N$, based on repeated measurements of this standard across all analytical runs (n = 144). Measurements were accurate to within less than ±0.01‰ for $\delta^{13}C$ and less than ±0.02‰ for $\delta^{15}N$, based on differences between observed and known values of the check standard. Collagen yield (percent of dry bone weight) and sample composition (weight percent carbon, weight percent nitrogen, and C/N ratio) were assessed to evaluate the quality of the collagen samples (Supplementary Table 4). Only collagen samples with ∼15% nitrogen, ∼45% carbon, and a C/N ratio of ∼3.2 were used for analyses (Tuross et al., 1988; Koch et al., 1994; Hedges et al., 2006; Szpak et al., 2017).

To account for the global decline in $\delta^{13}C$ associated with the combustion of fossil fuels since 1850, known as the Suess effect, a mathematical correction was applied to the $\delta^{13}C$ values of the historic and modern samples. This correction was adapted from Misarti et al. (2009) to provide values specific to the Bering Sea. A Bering Sea correction was used for this study, as walruses spend much of their time in this basin, and because large amounts of Bering seawater carrying nutrients and carbon are advected northward into the Chukchi Sea through the Bering Strait (Grebmeier et al., 2006). Atmospheric CO_2 concentrations from the Mauna Loa Observatory (Keeling et al., 2005) and yearly Bering Sea surface temperature estimates (Huang et al., 2015) from 1854 to 2016 were incorporated into this correction. The mean sea surface temperature for the period from 1854 to 1874 was used to approximate values for the years between 1850 and 1853. Salinity was assumed to remain constant at 32 practical salinity units (Woodgate et al., 2012). Laws et al. (1995, 2002) showed that changes in water temperature, salinity, and aqueous CO_2 concentrations also affect $\delta^{13}C$ discrimination by phytoplankton. Thus, they developed an additional $\delta^{13}C$ correction to account for these changes. The maximum correction factor for the period from AD 1850 to 2016, including both the atmospheric Suess effect and the correction developed by Laws et al. (1995, 2002) for changes in phytoplankton $\delta^{13}C$ discrimination, was 1.4‰ (Supplementary Table 5).

Developing a Chukchi Sea ice index

Estimates of ice cover in the Chukchi Sea over the last ∼4000 yr were compiled using data from marine sediment cores. Dinocyst assemblages from three sites in the northeastern Chukchi Sea (Fig. 1) were used for quantitative sea ice reconstructions (Supplementary Tables 6 and 7). Cores included in this analysis were HLY0501-05 (HLY05; McKay et al., 2008; de Vernal et al., 2013), HLY0205-GGC19 (GGC-19; Farmer et al., 2011), and P1-92-AR-P1/B3 (combined piston/box cores, P1/B3; de Vernal et al., 2005). To improve intercore comparability, age models for

these cores were rerun with the Bacon approach (Blaauw and Christen, 2011) using the rBacon R package, version 2.3.3. The Bacon software used the Marine13 calibration curve (Reimer et al., 2013), and we applied a regional marine reservoir correction (ΔR) of 447 ± 123 based on seven measurements from the Chukchi Sea (McNeely et al., 2006). To generate an index of regional sea ice conditions, data were interpolated along each of the cores to provide yearly sea ice estimates. Cores GGC-19 and P1/B3 spanned the entire study period (4150–0 cal yr BP), whereas HLY05 covered the period from 4150 to 672 cal yr BP. Yearly ice cover data were converted to ice cover anomaly by subtracting the mean ice estimate for each core from the yearly ice estimates along the core. The resulting ice cover anomaly estimates were then scaled by dividing the data from each core by the absolute value of the largest deviation from the average ice condition within that core, such that the maximum or minimum value for each core was 1 or −1. This normalization process removed differences in the magnitude of fluctuations in ice and allowed each core to contribute equally to the ice index. A 101 yr centered moving average was applied to the resulting index, providing an average sea ice anomaly in the Chukchi Sea for the interval extending from 4100 to 50 cal yr BP. Times when this average was greater than 0 were classified as high-ice intervals, and times when it was less than 0 were classified as low-ice intervals. Transitions lasting fewer than 25 yr were not considered to represent a switch between ice states (Supplementary Table 8).

A validation was conducted to test whether sea ice reconstructions from sediment cores in the northeastern Chukchi Sea could provide information about the climate of the broader region. To accomplish this, a sea ice index was generated for 1979–2016, the period of high-resolution satellite passive microwave coverage. Monthly ice cover was calculated for a 1° by 1° area above each core location, and the number of months/year with >50% ice cover was determined for these locations. The methods outlined previously were then used to generate the satellite-era ice index. The correlation between this index and the total annual ice cover in the Chukchi Sea from 1979 to 2016 was investigated using linear regression. Because the annual ice cover data for the Chukchi Sea represent a proportion (thus were bounded by 0 and 1), these data were logit transformed prior to analysis.

Testing for differences through time

Archaeological walrus samples were assigned to high- and low-ice states based on the proportional overlap of their radiocarbon date estimates with intervals of high- and low-ice cover (Supplementary Table 3). Individual walruses were assigned to whichever ice state was more prevalent (>50%) during their estimated radiocarbon date range. A resampling approach was used to examine the potential impacts of improper assignments. For this exercise, each individual was assigned to a high or low sea ice state based on the proportional overlap of that animal's estimated radiocarbon date range and the ice index. Thus, a walrus with an estimated

radiocarbon date range that overlapped with a high-ice interval for 70 yr and a low-ice period for 30 yr was given a 70% probability of being assigned to the high-ice group and a 30% chance of being assigned to the low-ice group. After all animals had been assigned, mean $\delta^{13}C$ and $\delta^{15}N$ values were calculated for high- and low-ice animals. This process was repeated 10,000 times, and the resulting data were used to generate 95% confidence intervals for mean $\delta^{13}C$ and $\delta^{15}N$ of walruses from high and low sea ice states. Time spans covered by the archaeological (4084–0 cal yr BP) and the historic (70 cal yr BP/AD 1880–2007) samples overlapped by ~70 yr, and it is likely that there is some temporal overlap between the most recent archaeological specimens and the oldest historical museum collections; however, the potentially problematic period included only 20 archaeological animals, averaging 28% overlap between their most likely date ranges and the historic period. Removing these animals did not affect the results, so they were included in analyses. Archaeological walruses were assigned to high and low sea ice states using the ice index, whereas historical samples with known collection dates were assigned to the historic period.

Analyses of variance (ANOVAs) were used to test for differences in $\delta^{13}C$ and $\delta^{15}N$ among archaeological walruses from intervals of high and low sea ice, as well as walruses from the historic and modern periods. Shapiro-Wilk normality tests indicated both $\delta^{13}C$ and $\delta^{15}N$ data were nonnormally distributed ($\delta^{13}C$: W = 0.923, $P < 0.001$; $\delta^{15}N$: W = 0.948, $P < 0.001$); however, ANOVAs were used for this analysis because visual examination of the data showed the deviations from normality to be relatively minor, and because ANOVAs are generally robust to nonnormality (Blanca et al., 2017). The $\delta^{13}C$ and $\delta^{15}N$ data from these four time periods had unequal variances, so data were analyzed using White-adjusted one-way ANOVAs, which are robust to heteroscedasticity (White, 1980; Long and Ervin, 2000). Dunnett-Tukey-Kramer (DTK) pairwise multiple comparison tests adjusted for unequal variances and unequal sample sizes were used for post hoc analyses, as this test does not assume equal variances (Dunnett, 1980). Results of the ANOVAs were compared with those of Kruskal-Wallis tests to confirm their robustness (Supplementary File 1). Differences in variability in $\delta^{13}C$ and $\delta^{15}N$ between archaeological walruses from intervals of high and low sea ice cover were examined using Stable Isotope Bayesian Ellipses in R (SIBER, version 2.1.3; Jackson et al., 2011), which are robust to differences in sample size. Modern and historic walruses were not included in comparisons of $\delta^{13}C$ and $\delta^{15}N$ variability, as these animals were collected during much shorter time spans (5 and 127 yr, respectively) and were therefore unlikely to incorporate the same sources of variability expected of the archaeological samples, which spanned thousands of years. Standard ellipse areas corrected for small sample sizes (SEAc) were compared to examine differences in stable isotope variability of archaeological walruses from high and low sea ice intervals. Decadal differences in the $\delta^{13}C$ and $\delta^{15}N$ of male and female walruses from the historic and

modern periods were examined using two-way ANOVAs. Males and females had unequal variances in $\delta^{15}N$, so a White-adjusted ANOVA was used for this comparison. For $\delta^{13}C$, variances were equal across decades and between sexes, so the White adjustment was not applied to the ANOVA. An alpha level of 0.05 was used for all statistical tests.

Known collection dates of historic and modern walruses and more refined sea ice estimates during the last 150 yr allowed for more direct examination of the correlation between sea ice cover and walrus stable isotope ratios. For comparisons with historic and modern walrus samples, yearly September Chukchi Sea ice estimates, expressed as percent ice cover, were extracted from the Scenarios Network for Alaska and Arctic Planning (SNAP) Sea Ice Atlas (http://www.snap.uaf.edu). This data set extends from AD 1850 (100 cal yr BP) to present, with its earliest ice estimates reconstructed from commercial whaling ship logbooks (Mahoney et al., 2011). Linear regressions were used to compare $\delta^{13}C$ and $\delta^{15}N$ with average September sea ice cover during the 16 yr (average estimated age of walruses used in this study based on age estimates from annuli in cementum layers of walrus teeth conducted by Matson's Laboratory LLC, Manhattan, MT; Garlich-Miller et al., 1993) prior to the animal's year of death. September sea ice cover was chosen for these analyses as this month typically represents the annual sea ice minimum and is therefore a sensitive indicator of climate changes.

RESULTS

The sea ice index indicated the presence of eight high-ice and seven low-ice intervals between 4100 and 50 cal yr BP (Fig. 2, Table 1). These high- and low-ice intervals closely matched Heusser et al.'s (1985) reconstruction of air temperature in Southcentral Alaska (Fig. 2). They also aligned well with known climate anomalies such as the Little Ice Age (ca. 500–100 yr; cf. Grove, 1988), Medieval Warm Period (ca. 1150–750 yr; cf. Broecker, 2001), Roman Warm Period (ca. 2500–1600 yr; cf. Wang et al., 2012), and Neoglacial period (ca. 3300–2500 yr; e.g., Porter and Denton, 1967; Matthews and Dresser, 2008; Wang et al., 2012). The satellite-era sea ice index generated using the three core locations had a strong, positive linear relationship with the annual percent ice cover in the Chukchi Sea from 1979 to 2016 ($R^2 = 0.86$, $F_{1,37} = 233.2$, $P < 0.001$; Supplementary Fig. 1).

Assignment of archaeological walruses to high and low sea ice intervals resulted in 124 individuals from high-ice intervals and 88 individuals from low-ice intervals. The resampling approach used to investigate the possible impacts of incorrectly assigning walruses to high or low sea ice intervals demonstrated that improper assignments had little effect on the results of this study (Supplementary Fig. 2). The 95% confidence intervals for the mean $\delta^{13}C$ and $\delta^{15}N$ values from high ($\delta^{13}C$, −12.97‰ to −12.88‰; $\delta^{15}N$, 13.50–13.71‰) and low ($\delta^{13}C$, −13.17‰ to −13.05‰; $\delta^{15}N$, 13.48–13.72‰) sea ice intervals were narrow, indicating
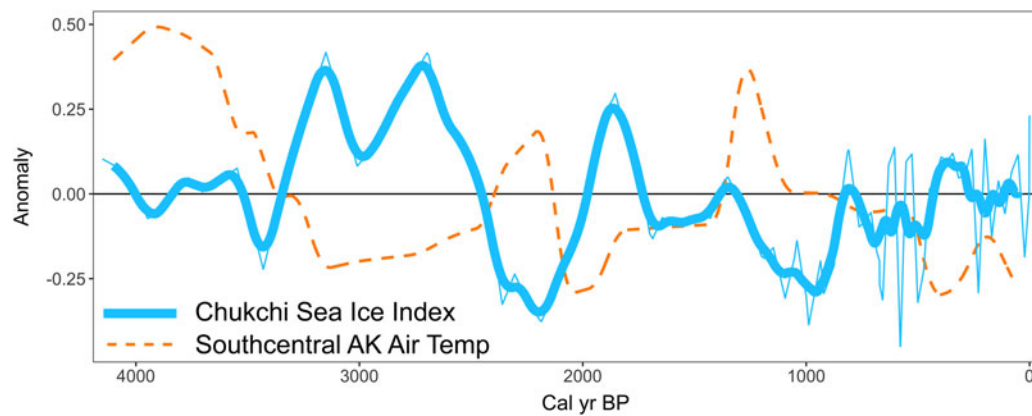
Figure 2. The Chukchi Sea ice index (thin blue line), overlaid by a 101 yr centered moving average (thick blue line), across the study period (4150–0 cal yr BP). For reference, the dashed orange line represents the Southcentral Alaska air temperature anomaly adapted from Heusser et al. (1985). Positive values of the ice index indicate higher than average ice conditions. Negative values indicate lower than average ice conditions.

that improper assignments were unlikely to cause mean $\delta^{13}C$ and $\delta^{15}N$ to shift by more than ~0.1‰ and ~0.2‰, respectively, which is within the range of instrumental error.

The $\delta^{13}C$ and $\delta^{15}N$ values of walrus bone collagen in this study were consistent with published values for modern and archaeological walrus bone collagen in Alaska (Szpak et al., 2018). Results of the White-adjusted ANOVAs indicated significant differences in both $\delta^{13}C$ ($F_{3,453} = 25.56$, $P < 0.001$) and $\delta^{15}N$ ($F_{3,453} = 41.98$, $P < 0.001$) in walruses from high and low sea ice intervals, as well as the historic and modern periods. Post hoc tests revealed differences in $\delta^{13}C$ among all periods except between modern individuals and archaeological walruses from low sea ice intervals, historic walruses and archaeological individuals from high sea ice intervals, and between archaeological walruses from intervals of high and low sea ice (Fig. 3, Table 2). For $\delta^{15}N$, post hoc tests showed significant differences among all groups except archaeological walruses from high and low sea ice intervals (Fig. 3, Table 2). Though the $\delta^{13}C$ differences were significant, they were relatively small (maximum difference = 0.5‰, historic vs. modern walruses). The differences in $\delta^{15}N$ were larger, with those between modern and archaeological walruses from both high and low sea ice intervals exceeding 1.0‰. SIBER demonstrated substantially larger

niche width for archaeological walruses during intervals of low sea ice cover (SEAc = 2.94) as compared with high sea ice intervals (SEAc = 1.39). Ellipses are generated through an iterative, Bayesian process (Jackson et al., 2011), and the proportion of these iterations in which the sizes of the ellipses differed can be used to evaluate the strength and consistency of these differences. In this study, low sea ice ellipses were larger than high sea ice ellipses 100% of the time. Despite the difference in ellipse size, there was 98% ellipse overlap, with the high-ice ellipse existing almost completely within the boundaries of the low-ice ellipse (Fig. 4).

The results of the two-way ANOVA testing the effects of sex and decade on $\delta^{13}C$ indicated that $\delta^{13}C$ differed significantly among decades ($F_{7,208} = 11.56$, $P < 0.001$), but not between sexes ($F_{1,208} = 2.63$, $P = 0.11$). A Tukey's honest significant difference post hoc test revealed that these differences were primarily driven by the 1990s, which were different from all other decades except the 1930s and the 2010s, and by the 2010s, which were different from all other decades except the 1930s and 1990s (Fig. 5, Table 3). The results of the two-way ANOVA testing the effects of sex and decade on $\delta^{15}N$ revealed that both the main effects (sex: $F_{1,201} = 29.71$, $P < 0.001$; decade: $F_{7,201} = 23.99$, $P < 0.001$) and the interaction term (sex × decade: $F_{7,201} = 4.01$, $P < 0.001$) were significant. Because the interaction was significant, the main effects were not examined directly. To examine the simple main effects, the data were divided by sex, and one-way ANOVAs were run to test for differences among decades for males and females. Males had unequal variances among decades for $\delta^{15}N$, so a White-adjusted ANOVA and DTK post hoc test was used. The ANOVA indicated differences in male $\delta^{15}N$ among decades ($F_{7,107} = 26.79$, $P < 0.001$). The post hoc test showed that these differences were driven by the 1930s, which were significantly different from all other decades except the 1990s, and by the 2010s, which in turn were significantly different from all other decades except for the 1980s and 1990s. Female walruses had equal variances in $\delta^{15}N$ among decades, so the White

Table 1. Date ranges (cal yr BP) of low and high sea ice intervals as defined by the Chukchi Sea ice index.

Low Ice Intervals	High Ice Intervals
	4100–4003 cal yr BP
4002–3836 cal yr BP	3835–3521 cal yr BP
3520–3347 cal yr BP	3346–2453 cal yr BP
2452–1979 cal yr BP	1978–1732 cal yr BP
1731–1385 cal yr BP	1384–1312 cal yr BP
1311–828 cal yr BP	827–781 cal yr BP
780–431 cal yr BP	430–270 cal yr BP
269–116 cal yr BP	115–50 cal yr BP

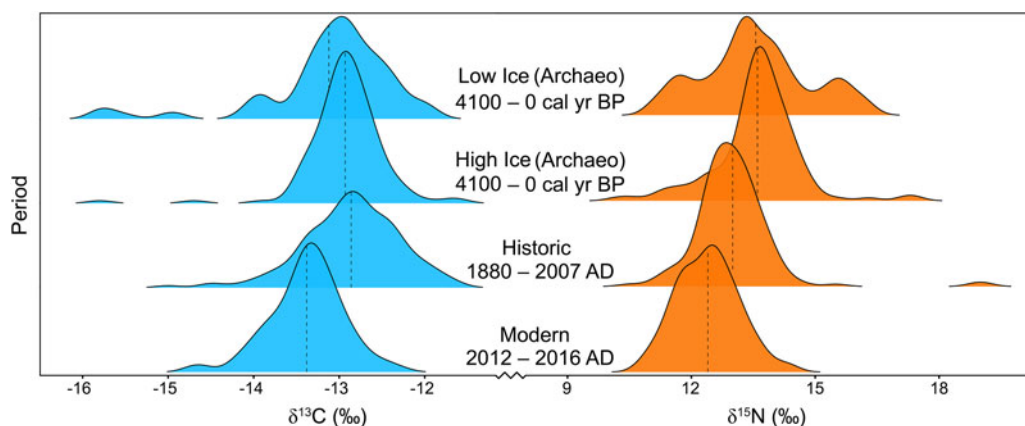**Figure 3.** Walrus bone collagen $\delta^{13}C$ (left, blue) and $\delta^{15}N$ (right, orange) from low-ice (4100–0 cal yr BP), high-ice (4100–0 cal yr BP), historic (AD 1880–2007), and modern (AD 2012–2016) periods. Dashed lines represent means, and shaded areas show the relative frequency and distribution of the data.

adjustment was not applied to the ANOVA. Results of the ANOVA were not significant ($F_{7,94} = 1.97$, $P = 0.07$), indicating that female $\delta^{15}N$ did not differ among decades (Fig. 5, Table 3).

Linear regressions showed positive correlations between $\delta^{13}C$ and September Chukchi Sea ice cover in the 16 yr prior to each animal's year of death for both male and female walruses. In contrast, $\delta^{15}N$ was only correlated with September Chukchi Sea ice cover in male walruses (Fig. 6). The regression parameters between $\delta^{13}C$ and sea ice were nearly identical for male ($y = 0.01x - 13.50$, $R^2 = 0.16$, $F_{1,116} = 21.86$, $P < 0.001$) and female ($y = 0.01x - 13.66$, $R^2 = 0.15$, $F_{1,100} = 17.68$, $P < 0.001$) walruses. Female $\delta^{15}N$ values were not correlated with September Chukchi Sea ice cover ($F_{1,100} = 1.79$, $P = 0.18$), whereas male $\delta^{15}N$ had a positive correlation with sea ice ($y = 0.02x + 11.82$, $R^2 = 0.22$, $F_{1,116} = 32.75$, $P < 0.001$).

DISCUSSION

The Chukchi Sea ice index

The validity of the ice index generated using dinocyst data from three Chukchi Sea sediment cores is supported by an inverse relationship with Heusser et al.'s (1985) palynological reconstruction of air temperature in Southcentral Alaska (Fig. 2). Heusser et al. (1985) indicated that the variability in their air temperature reconstruction likely resulted primarily from changes in the Aleutian Low pressure system, a dominant driver of weather patterns in the North Pacific. The strength and longitudinal position of the Aleutian Low strongly influence Bering Sea ice conditions (Rodionov et al., 2007) and the flow of water through the Bering Strait (Danielson et al., 2014) and thus are directly linked to sea ice extent in the Chukchi Sea. Furthermore, the strong, positive correlation between the satellite-era ice index and the annual percent ice cover in the Chukchi Sea supports the use of these sediment cores as proxies for the broader regional climate (Supplementary Fig. 1). Given the strong links between Chukchi Sea ice cover, the Aleutian Low pressure system, and the Bering Sea climate, it is likely that the ice index is also correlated with environmental conditions (though not necessarily sea ice cover) in the Bering Sea. This supports the assertion that the ice index is an indicator of climatic conditions across Pacific walruses' geographic range and, thus, an appropriate tool for examining the effects of past environmental change on the species.

Table 2. Mean differences in $\delta^{13}C$ and $\delta^{15}N$ in walrus bone collagen among intervals of high sea ice (4100–0 cal yr BP), intervals of low sea ice (4100–0 cal yr BP), and historic (AD 1880–2007) and modern (AD 2012–2016) periods. Bold values indicate significant differences ($P < 0.05$).

	Low ice (archaeological)	High ice (archaeological)	Historic	Modern
$\delta^{13}C$				
Low ice (archaeological)	–	0.2‰	**0.3‰**	0.2‰
High ice (archaeological)		–	0.1‰	**0.4‰**
Historical			–	**0.5‰**
$\delta^{15}N$				
Low ice (archaeological)	–	0.0‰	**0.6‰**	**1.2‰**
High ice (archaeological)		–	**0.6‰**	**1.2‰**
Historical			–	**0.6‰**

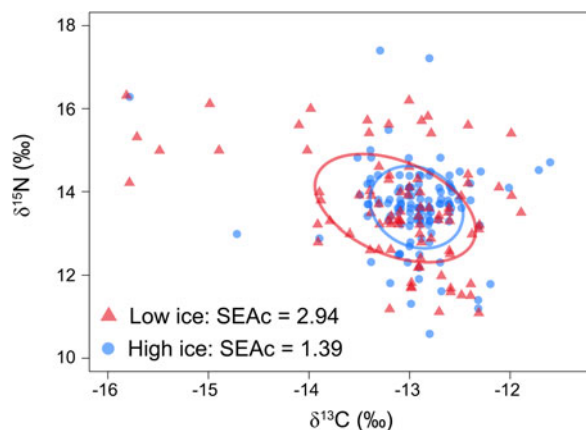**Figure 4.** Scatter plot of $\delta^{13}C$ and $\delta^{15}N$ values of archaeological walrus bone collagen from intervals of high (blue circles) and low (red triangles) sea ice, as defined by the Chukchi Sea ice index. Stable Isotope Bayesian Ellipses in R (SIBER) indicate the niche width of each group, as quantified by the standard ellipse area corrected for small sample sizes (SEAc).

The sea ice index aligns closely with established global climate anomalies during the last ~4000 yr. For example, the Little Ice Age, a cold period extending from ~500 to 100 yr (Grove, 1988), is represented in the ice index as an interval of relatively high sea ice cover between 430 and 270 cal yr BP. Another relatively recent global climate anomaly, the Medieval Warm Period (~1150–750 yr; Broecker, 2001), overlapped substantially with an interval of sustained low sea ice cover in the ice index extending from 1311 to 828 cal yr BP. The expressions of the Little Ice Age and the Medieval Warm Period in the ice index also closely match the timing of these two climate anomalies in North America (Ljungqvist, 2010). The Roman Warm Period extended from ~2300 to 1550 yr in North America (Viau et al., 2006), corresponding with generally lower than average

ice conditions in the index from 2452 to 1385 cal yr BP, though this period was interrupted by a high-ice interval from 1978 to 1732 cal yr BP. Finally, sustained high sea ice conditions from 3346 to 2453 cal yr BP matched the timing of glacial advances associated with the Neoglacial period in North America (Kaufman et al., 2016).

These consistencies with global and hemispheric climate anomalies captured by the ice index are not surprising, as regional variability in the Bering and Chukchi Seas is inherently linked to the processes driving global climate patterns. The atmospheric dynamics of the North Pacific and North Atlantic are directly connected by those of the Arctic. The Arctic Oscillation, an index describing variations in sea level pressure across the Arctic region (Thompson and Wallace, 1998), is strongly correlated with both the North Atlantic Oscillation (Dickson et al., 2000) and Pacific Decadal Oscillation (PDO; Sun and Wang, 2006). The PDO is, in part, determined by the strength and position of the Aleutian Low, which is correlated with major North Atlantic circulation features (Kutzbach, 1970). The changes in Chukchi Sea ice cover during the last ~4000 yr recorded in the ice index are thus a product of these global and hemispheric climate drivers, as modulated by regional and local conditions.

Walrus dietary shifts across broad time scales

Mean $\delta^{13}C$ and $\delta^{15}N$ of walruses that lived during intervals of high and low Chukchi Sea ice cover over the last ~4000 yr were remarkably similar, with differences in isotopic compositions falling within instrumental error (~0.2‰; Table 2). Despite the similarity in the mean isotope values between high- and low-ice conditions, however, the variability in $\delta^{13}C$ and $\delta^{15}N$ was greater for walruses that lived in low sea ice conditions. Though the minimum and maximum values of $\delta^{13}C$ and $\delta^{15}N$ ($\delta^{13}C$, −15.8‰ to −11.9‰; $\delta^{15}N$, 11.1–16.3‰) were similar during low- and high-ice intervals,
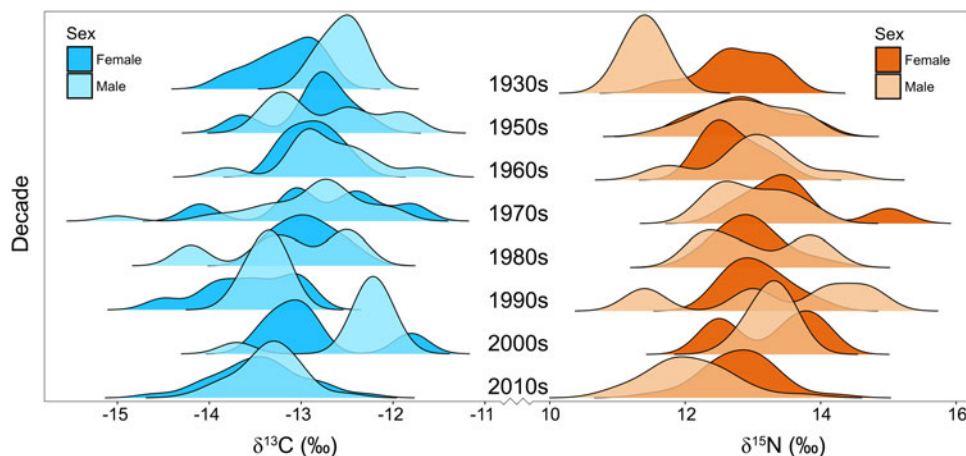

Figure 5. Walrus bone collagen $\delta^{13}C$ (left, blue) and $\delta^{15}N$ (right, orange) from the 1930s, 1950s, 1960s, 1970s, 1980s, 1990s, 2000s, and 2010s. Darker colors represent females, and lighter colors represent males. The shaded areas show the relative frequency and distribution of the data for each decade.

Table 3. Decadal differences in mean bone collagen δ^{13}C for pooled samples of male and female walruses and δ^{15}N split by sex. Bold values indicate significant differences ($P < 0.05$).

	1930s	1950s	1960s	1970s	1980s	1990s	2000s	2010s
Pooled male and female δ^{13}C								
1930s	–	0.2‰	0.2‰	0.1‰	0.0‰	0.5‰	0.5‰	0.4‰
1950s		–	0.0‰	0.1‰	0.2‰	**0.7‰**	0.2‰	**0.6‰**
1960s			–	0.1‰	0.2‰	**0.7‰**	0.2‰	**0.6‰**
1970s				–	0.1‰	**0.6‰**	0.4‰	**0.5‰**
1980s					–	**0.5‰**	0.4‰	**0.4‰**
1990s						–	**1.0‰**	0.1‰
2000s							–	**0.8‰**
2010s								–
Split male and female δ^{15}N				Females				
1930s	–	0.1‰	0.1‰	0.8‰	0.2‰	0.3‰	0.5‰	0.1‰
1950s	**1.5‰**	–	0.2‰	0.7‰	0.1‰	0.2‰	0.4‰	0.1‰
1960s	**1.6‰**	0.1‰	–	0.9‰	0.3‰	0.4‰	0.6‰	0.1‰
1970s	**1.6‰**	0.1‰	0.1‰	–	0.6‰	0.5‰	0.3‰	0.8‰
1980s	**1.6‰**	0.1‰	0.1‰	0.0‰	–	0.1‰	0.3‰	0.2‰
1990s	1.9‰	0.4‰	0.3‰	0.3‰	0.3‰	–	0.2‰	0.3‰
2000s	1.8‰	0.4‰	0.3‰	0.3‰	0.2‰	0.0‰	–	0.5‰
2010s	**0.7‰**	**0.8‰**	**0.9‰**	**0.9‰**	1.0‰	1.2‰	**1.2‰**	–
				Males				

the standard deviations were greater when sea ice cover was low. This resulted in differences in the shapes of the δ^{13}C and δ^{15}N distributions, with most individuals tightly clustered around the mean values during high-ice intervals, in contrast to the broader spread of data during low-ice intervals. Taken together, this information indicates that the walrus population generally occupied the same trophic space (overall range of δ^{13}C and δ^{15}N) during intervals of high and low sea ice; however, diet was more variable among individuals when sea ice cover was low. This can be seen in Figures 2 and 3, which show a tighter distribution in δ^{13}C and δ^{15}N values during high-ice intervals.

There are a variety of possible reasons for the observed differences in walrus δ^{13}C and δ^{15}N variability among high and low sea ice intervals. Perhaps the most likely explanation is a shift in prey abundance that increased intraspecific competition for preferred prey species during low sea ice intervals. Optimal foraging theory (OFT) predicts that when preferred food resources are scarce or absent, individuals will broaden their diet to include resources that were previously unused and/or consume higher proportions of lower-ranked resources (Stephens and Krebs, 1986). Increased diet breadth alone, however, would not necessarily result in differences among the stable isotope ratios of individuals. For variability in δ^{13}C and δ^{15}N among individuals to increase, walruses would need to exhibit some degree of dietary specialization, such that different individuals consumed isotopically distinct diets. This between-individual variation can be driven by numerous factors, including phenotypic differences that allow individuals to better exploit certain types of resources
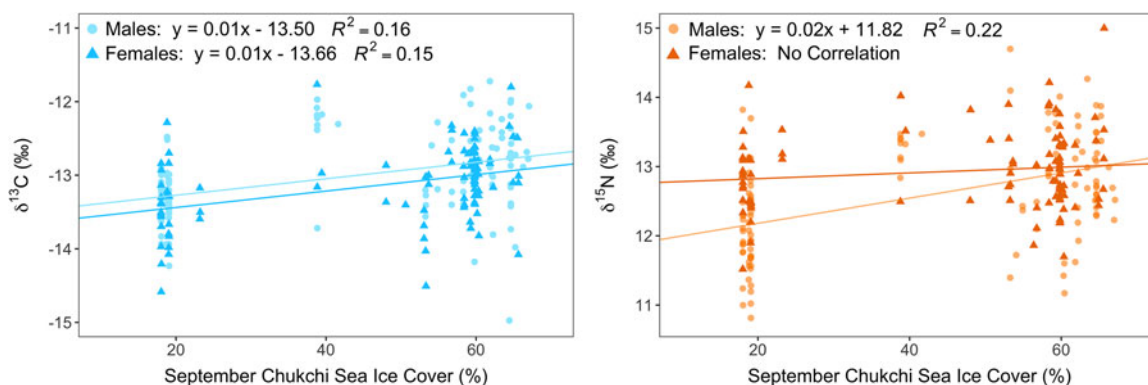

Figure 6. Linear regressions of male (light-colored circles) and female (dark-colored triangles) walrus bone collagen δ^{13}C (left, blue) and δ^{15}N (right, orange) and September Chukchi Sea ice extent. Regression equations and R^2 values are given in the graphs for significant ($P < 0.05$) linear relationships.

(Svanbäck and Bolnick, 2007), different dietary preferences and optimization criteria (Schoener, 1971), and factors such as social hierarchies that differentially affect the abilities of individuals to access resources (Sol et al., 2005). Though it is often considered to be a sign of resource scarcity (Bolnick et al., 2003; Tinker et al., 2008), OFT suggests that increased dietary specialization can result from a decrease in the availability of preferred prey, even when lower-ranked prey items are plentiful (Stephens and Krebs, 1986). For walruses, decreased availability of their preferred benthic bivalve prey because of environmental shifts or increased walrus abundance during previous low sea ice intervals might have led to increased dietary specialization among individuals at these times. Sea ice allows walruses to easily access offshore benthic hot spots, typically rich in benthic bivalves (Grebmeier et al., 2015a); thus, reduced availability of preferred walrus prey during low sea ice intervals may have resulted from a change in the ability of walruses to access these prey resources, rather than a shift in the abundance of benthic invertebrates.

Although it is possible that the observed increase in diet variability among individual walruses in this study resulted from resource stress, this seems unlikely for two reasons. First, though walruses consume a wide variety of prey items even when food resources are plentiful (Fay, 1982; Sheffield and Grebmeier, 2009), if food became severely limiting, it would be expected that their diet would broaden further and that the observed ranges of $\delta^{13}C$ and $\delta^{15}N$ values would increase. However, archaeological walruses from high and low sea ice intervals had similar ranges of $\delta^{13}C$ and $\delta^{15}N$ (Fig. 4). Second, in a situation where food resources were limiting and animals were in a state of chronic nutritional stress, we would expect to see an increase in $\delta^{15}N$ (Hobson et al., 1993), at least for animals experiencing starvation. The $\delta^{15}N$ values of walruses from high and low sea ice intervals were similar and had a slightly lower maximum during low-ice intervals, so chronic nutritional stress is unlikely. It is important to remember when interpreting these results, that $\delta^{13}C$ and $\delta^{15}N$ from bone collagen represent a lifetime average of walrus diet (Manolagas, 2000); thus, for a distinct isotopic signal to be preserved in the collagen, changes in diet would need to last for many years. Marine mammals are highly adapted to extended fasting and can survive on lipid reserves for long periods without having to catabolize muscle proteins (Castellini and Rea, 1992). Given this, it is possible that walruses experienced some degree of resource scarcity and nutritional stress during low-ice intervals; however, it is unlikely that this would leave a detectable signal in bone collagen $\delta^{13}C$ and $\delta^{15}N$.

Mean $\delta^{13}C$ and $\delta^{15}N$ of walruses from the historic and modern periods differed markedly, in contrast to the stable isotope values of archaeological walruses. Most notably, $\delta^{15}N$ was lower in the historic samples than in past intervals of high and low sea ice cover and decreased further in the modern samples, which were significantly distinct from all other periods. These results indicate that the Pacific walrus population is currently occupying a lower average trophic

position than at any point in the last ~135 yr, and possibly even in the last ~4000 yr. Though the mean $\delta^{15}N$ of modern specimens was lower than that of archaeological walruses from either high or low sea ice conditions, the range of modern values fell within the ranges of both ice states (Fig. 3). This indicates that walruses may have occupied a similarly low trophic position at other times in the past. Regardless of whether the diet of modern walruses is unprecedented in the last ~4000 yr, it is clear that walruses harvested in the 2010s had eaten proportionally more lower-trophic-level prey than animals at most other times in the past. These low $\delta^{15}N$ values likely mean that these walruses foraged primarily on benthic bivalves, which are typically primary consumers and have low $\delta^{15}N$ values as compared with other benthic invertebrates (Dehn et al., 2007; Tu et al., 2015). It has been suggested that the proportion of higher-trophic-level prey (e.g., ice seals and seabirds) in walrus diet has increased as a result of Arctic sea ice loss (Seymour et al., 2014b). The results presented here indicate no difference in the average trophic position of the Pacific walrus population between past intervals of high and low sea ice conditions. Instead, they suggest that most modern walruses have decreased their lifetime consumption of higher-trophic-level prey.

Regional and sex-related differences in $\delta^{15}N$ cannot be ruled out as sources of variation in this study. Because male and female walruses spend their summers foraging in different regions (Fay, 1982), the effects of location and sex on walrus stable isotope ratios are difficult to disentangle. The sex ratio of walruses from the modern period (27 females/48 males) was weighted more toward males than that of the historic period (74 females/67 males), whereas the sex ratio of the archaeological samples remains unknown. Sex-related differences in $\delta^{13}C$ observed in this study were small (<0.2‰); however, it is likely that some of the observed differences in $\delta^{15}N$ among time periods in this study resulted from sex-related differences and unequal sex ratios. From the historic to the modern period, mean $\delta^{15}N$ declined by 0.6‰. During this same period, the magnitude of the sex-related difference in $\delta^{15}N$ changed as well. In the historic period, male and female $\delta^{15}N$ values were identical, whereas in the modern period, mean male $\delta^{15}N$ was 0.7‰ lower than that of females. This change, coupled with the difference in the sex ratios between the historic and modern periods, likely accounted for ~0.5‰ of the observed 0.6‰ decline in $\delta^{15}N$ in the modern samples. Presumably, similar changes in the $\delta^{15}N$ offset between males and females and a difference in the sex ratio of the archaeological samples could be responsible for at least some of the observed differences between the archaeological and historic/modern samples. However, the importance of those factors as sources of variation in $\delta^{15}N$ is unknown. Sex information was not available for the archaeological specimens; thus differences in sample sex ratios and changes in the magnitude of sex-related isotopic differences through time could not be estimated. It is important to note that these results do not mean that a change in $\delta^{15}N$ did not occur between these periods. Instead, they indicate that the observed change in

δ^{15}N from the historic to the modern period was driven almost entirely by males. This also means that males were primarily responsible for the apparent shift to a lower average trophic position in the modern period, and that the diet of females remains essentially unchanged.

Dietary shifts may not have been the only factors driving the changes in δ^{15}N observed in this study. Baseline δ^{15}N values are determined primarily by the sources of nitrogen available to primary producers, which may vary through time and space (Fogel and Cifuentes, 1993). Establishing isotopic baselines can be difficult, particularly for historic and archaeological time frames, where directly sampling primary producers is not possible (Casey and Post, 2011). Efforts have been made to infer historical changes in isotopic baselines using preserved animal specimens (e.g., Newsome et al., 2007; Wiley et al., 2013; Szpak et al., 2018). Misarti et al. (2009) examined modern and archaeological stable isotope ratios of bone collagen from Sanak Island in the northwest Gulf of Alaska (one of the sites from which walrus bones were used in this study). These authors found that δ^{15}N values of sea otter (*Enhydra lutris*) bone collagen were significantly lower in modern samples compared with archaeological bone; however, no significant declines in δ^{15}N were observed for Steller sea lions (*Eumatopias jubatus*), harbor seals (*Phoca vitulina*), northern fur seals (*Callorhinus ursinus*), Pacific cod (*Gadus macrocephalus*), or sockeye salmon (*Oncorhynchus nerka*). Unfortunately, such studies have primarily been conducted on higher-trophic-level organisms, and separating dietary changes from baseline shifts remains difficult. Recently, compound-specific stable isotope analysis of amino acids (CSIA-AA) has emerged as a potential solution to this problem. The δ^{15}N values of some amino acids (the so-called source amino acids) do not experience trophic enrichment. Instead, they reflect the δ^{15}N values at the base of the food chain (Chikaraishi et al., 2009; McClelland and Montoya, 2017). Thus, by measuring the δ^{15}N values of these source amino acids in preserved specimens, a long-term baseline can be reconstructed. Misarti et al. (2017) investigated the feasibility of using CSIA-AA on archaeological shell to reconstruct isotopic baselines. Their samples from Sanak Island did not provide evidence for directional baseline shifts in δ^{15}N in the last ~1500 yr. Recent CSIA-AA conducted on polar bear (*Ursus maritimus*) bone collagen from Alaska showed no significant changes in δ^{15}N of source amino acids between archaeological, historic, and modern samples (Horstmann et al., 2017). Though it remains possible that baseline changes in δ^{15}N were responsible for the patterns observed in this study, the results of these studies do not support this hypothesis.

The δ^{13}C values of walruses from the historic and modern periods provided support for the ice state assignments of the archaeological samples. Modern walruses, which lived during an interval of rapidly declining sea ice cover, had δ^{13}C values that were similar to those of walruses from previous low sea ice intervals and different from both the historic walruses and archaeological walruses from intervals of high sea ice. Conversely, δ^{13}C values of walruses from the historic period, an interval of relatively high sea ice cover, were similar to those of animals from previous high sea ice intervals and different from those of modern walruses and animals from previous intervals of low sea ice. Taken together, these results indicate that walrus bone collagen δ^{13}C is changing with sea ice conditions. The exact mechanisms responsible for the observed shifts in δ^{13}C remain unknown. These changes may have resulted from differences in walrus diet during high and low sea ice cover; however, it is perhaps more likely that the correlation between δ^{13}C and sea ice conditions resulted from shifts in baseline δ^{13}C values associated with changing oceanographic conditions and sources of primary production.

Decadal shifts in δ^{13}C and δ^{15}N

Because more information was available for historic and modern samples, including collection year, sex, and estimated age for many animals, we were able to conduct finer-scale investigations of changes in δ^{13}C and δ^{15}N. Additionally, more accurate ice estimates allowed for direct inspection of the correlation between walrus bone collagen stable isotope ratios and Chukchi Sea ice conditions. As with the broader time periods, δ^{15}N exhibited the most substantial differences in the historic and modern samples (Fig. 5). These differences were apparently restricted to male walruses, as female δ^{15}N did not change among decades, whereas males had lower δ^{15}N values in the 1930s and 2010s. Interestingly, there was a shift in the 1920s from a sustained state of high (~75%) September Chukchi Sea ice cover to a state of sustained lower (~60%) September ice cover (Walsh et al., 2017). Given that walrus bone collagen δ^{13}C and δ^{15}N represent a lifetime average (~16 yr in this study, based on age estimates from tooth annuli) of diet and conditions experienced by an animal, it is possible that the changes observed in the 1930s were a response to the shift from a higher to a lower ice state in the 1920s. The samples from the 2010s showed a similar pattern to those from the 1930s; however, it is difficult to say whether these similarities are driven by changing ice conditions or by other factors, such as changing prey availability in male summer habitat, regionally variable baseline shifts, or changes to migratory behavior of male walruses.

Direct examination of the relationship between walrus δ^{15}N values and September Chukchi Sea ice cover supported the results of the decadal comparisons. Female δ^{15}N values were not correlated with September Chukchi Sea ice cover, whereas male δ^{15}N was positively related to ice cover. Though the nature of the relationship between sea ice and δ^{15}N of male walruses remains unclear, it is likely that September Chukchi Sea ice cover did not directly influence the stable isotope ratios of males and, instead, simply acted as a proxy for other changes that have occurred in the male summer habitat. Male walruses typically spend summers in Bristol Bay, Alaska, and along the Russian coastline (Fay, 1982). Chukchi Sea ice cover has declined steadily since the 1980s (Walsh et al., 2017); thus it can be expected that

this measure will be strongly correlated with many other variables associated with changes to regional climate, including Arctic warming and factors associated with the major regime shift that occurred in the North Pacific and Bering Sea in the late 1970s (Ebbesmeyer et al., 1991). This regime shift has been linked to changes in Bering Sea ice cover (Niebauer, 1998), as well as alterations in species compositions and abundances in fish communities, changes to benthic invertebrate community structure on the Bering Sea shelf (Coyle et al., 2007), and a nearly linear increase in the biomass of noncrab benthic invertebrates in Bristol Bay bottom trawls since the early 1980s (Conners et al., 2002). It is these last two factors that are most likely to have led to the decline in $\delta^{15}N$ of male walruses in recent decades, as shifts in the structure of benthic communities and increased abundance of benthic invertebrates likely led male walruses to consume a greater proportion of bivalve prey, thus lowering their average trophic position. The changes in community composition and food web structure attributed to this regime shift may also have been tied to the trend of regional warming that took place at the same time (Grebmeier, 2012). Benthic communities in the Chukchi Sea, though undergoing changes, were comparably stable across the same period (Grebmeier et al., 2015b), perhaps explaining why female $\delta^{15}N$ did not change as sea ice declined. Finally, it has been suggested that the proportion of male walruses accompanying the females and calves on their northward journey has increased as the Arctic climate has warmed (Garlich-Miller et al., 2011). A change in summer migratory destination could lead to a decline in $\delta^{15}N$ for male walruses; however, if this were the case, male $\delta^{15}N$ values would be expected to become more similar to female $\delta^{15}N$ values as sea ice declined. Instead, the opposite is true, and average male $\delta^{15}N$ has diverged from that of females.

Mean decadal $\delta^{13}C$ values did not differ between sexes and remained relatively constant through time, in contrast to $\delta^{15}N$. The exceptions to this general stability in $\delta^{13}C$ were the 1990s and 2010s, which had lower values than other decades (Fig. 5). It is unclear why the first decade of the 2000s had significantly less negative $\delta^{13}C$ values than the 1990s and 2010s. Perhaps the most interesting feature of the historic $\delta^{13}C$ data was not a shift in mean values, but a change in $\delta^{13}C$ variability among decades. Fay et al. (1989) reported that the Pacific walrus population reached and possibly exceeded carrying capacity in the late 1970s and early 1980s. At this time, food resources were apparently limiting, and Alaska Native subsistence hunters reported that animals were generally leaner and age at first reproduction increased. In the present study, the $\delta^{13}C$ values of both male and female walruses from the 1970s exhibited greater variability and a broader distribution than during other decades. This could be interpreted as an indication of increased variation in diet among individuals resulting from increased competition for food resources, as predicted by OFT (Stephens and Krebs, 1986). This, in turn, would support the hypothesis that the greater variability in $\delta^{13}C$ among individuals from intervals of low sea ice was driven by limited access to preferred prey items. However, the apparent variability in the diet of

walruses in the 1970s could also have resulted from the regime shift that caused major changes to regional ecosystems and food webs around 1976/1977 (Ebbesmeyer et al., 1991). In either case, these changes appear in the walrus bone collagen stable isotope ratios earlier than would be expected given the timing of these events, as $\delta^{13}C$ and $\delta^{15}N$ of walruses that lived during the 1970s would be expected to represent an average of diet extending back into the 1960s and, for some individuals, the 1950s. It is worth noting that the walruses from the 2010s had a narrower distribution of $\delta^{13}C$ values, evidence that walrus access to preferred prey items has not been limiting in recent years.

The effects of declining ice algal production on $\delta^{13}C$

The mean $\delta^{13}C$ of modern walruses in this study was significantly lower than that of walruses from the historic period, and from that of archaeological walruses from intervals of high and low sea ice. A decrease in $\delta^{13}C$ values in modern samples was not unexpected. Sea ice algae tend to have less negative $\delta^{13}C$ values than pelagic phytoplankton (e.g., Oxtoby et al., 2016), and, as sea ice declines, the contribution of sea ice algae to total primary production in the region will decrease. As a result, $\delta^{13}C$ values are expected to shift toward more negative (pelagic) values as sea ice in the region continues to decline. This idea was more directly examined by investigating the correlation between September Chukchi sea ice extent and walrus bone collagen $\delta^{13}C$. Though $\delta^{13}C$ of both male and female walruses was positively correlated with ice extent, these relationships were weak (Fig. 6). The slope of the regression lines for both sexes was 0.01, meaning that a shift from 100% to 0% ice cover would result in only 1‰ change in $\delta^{13}C$. Additionally, the correlation between sea ice cover and $\delta^{13}C$ explained only a small portion of the variability in $\delta^{13}C$, indicating that other factors are more important in determining the $\delta^{13}C$ of walrus bone collagen. This is not surprising as many other factors affect $\delta^{13}C$ values, including diet, foraging location, and animal physiology (Newsome et al., 2010).

Climate-driven food web shifts

Finally, it has been suggested that sea ice loss in the Arctic will lead to food webs with a greater number of trophic levels, as warming waters and increased atmospheric CO_2 concentrations cause shifts toward a system dominated by smaller, pelagic phytoplankton species (Li et al., 2009; Kędra et al., 2015). This proportional decline in the larger nanoplankton (average cell diameter = 2–20 μm) and increase in picoplankton (average cell diameter <2 μm) is expected to lead to decreased benthic production, as slower sinking speeds and increased grazing cause a greater proportion of primary production in the region to be consumed or degraded before reaching the seafloor (Wassmann and Reigstad, 2011). The results of this study challenge these hypotheses. A system with longer food webs would be expected to cause walrus $\delta^{15}N$ to increase, as the number of trophic steps between

walrus prey and the system's primary producers increased. Similarly, diminished benthic-pelagic coupling is expected to lead to depauperate benthic systems, which would lead to decreased availability of benthic bivalves, walruses' preferred prey (Sheffield and Grebmeier, 2009), and would likely lead to an increased proportion of higher-trophic-level prey in walrus diet or increased diet variation among individuals, as suggested by Seymour et al. (2014a, 2014b). In this study, we found no difference in mean $\delta^{15}N$ of archaeological walruses from intervals of high and low sea ice cover in the Chukchi Sea, though increased variability in $\delta^{13}C$ and $\delta^{15}N$ during low sea ice intervals may have resulted from changes in prey availability. The only substantial change in $\delta^{15}N$ observed in this study was a decline of ~1.0‰ in modern animals. These results suggest that the number of trophic levels in the food webs leading to walruses in the Bering and Chukchi Seas is not increasing. Instead, the low $\delta^{15}N$ values in modern walruses and the relatively low degree of $\delta^{15}N$ variability among individuals in this time period suggest that walruses are foraging on plentiful, lower-trophic-level prey, a conclusion that is supported by studies of walrus space and resource use in recent years (Jay et al., 2014; Beatty et al., 2016).

CONCLUSIONS

The ~4000 yr index of Chukchi Sea ice conditions presented herein matches well with known climate anomalies and demonstrates that data from multiple sediment cores can be directly combined to provide a more representative estimate of regional climate. Archaeological walrus specimens assigned to high and low sea ice intervals defined by this index indicated that the trophic space occupied by walruses was similar among ice states; however, diet variability among individuals increased during low-ice intervals, possibly resulting from reduced access to preferred prey at those times. Analysis of the historic and modern samples supported the hypothesis that $\delta^{13}C$ values in the Bering and Chukchi Seas have declined as the proportional input of sea ice algae into food webs has decreased; however, results from our walrus data indicate these changes have so far been small. Sea ice conditions were more strongly correlated with $\delta^{15}N$ of male walruses, though Chukchi Sea ice was likely not the factor driving these changes and was instead serving as a proxy for concurrent changes in male walrus summer habitats. Overall, variable sea ice did not appear to be a major driver of change in walrus diet during the last ~4000 years. Perhaps most interestingly, the modern walruses examined for this study were isotopically distinct from archaeological walruses that lived in high and low sea ice intervals, as well as during the last ~135 years, suggesting that changes currently underway in this region are unlike any others that occurred during the study period.

Though the results presented here imply little change in walrus diet with past sea ice loss, the environmental changes currently taking place in the Arctic are occurring at an unprecedented rate. This might mean that previous low sea ice intervals, at least within the last 4000 yr, are not appropriate analogs for the current warming of the Arctic. Additionally, the ongoing changes to the Arctic climate are accompanied by other large-scale perturbations not present during previous intervals of warming (e.g., anthropogenic CO_2 input, increased intensity of human use of the Arctic, and introduction of chemical contaminants into marine ecosystems). It is likely that high atmospheric and aqueous CO_2 concentrations will eventually drive shifts in the physiology of Arctic plants and animals (Kędra et al., 2015). Coupled with the associated ocean acidification, these changes are likely to affect primary producers and benthic invertebrate populations (Fabry et al., 2009). Large-scale removal of great whales and walruses from the Bering and Chukchi Seas in the nineteenth and twentieth centuries, paired with increasing extent and intensity of fisheries in the North Pacific and Bering Sea have substantially altered ecosystems in these regions in ways that are not well understood (e.g., Springer et al., 2003).

It is important to note that the largest changes in $\delta^{13}C$ and $\delta^{15}N$ observed during the ~4000 yr reconstruction of walrus diet presented in this article occurred in the last two decades. Though this is likely attributable, in part, to the relatively short window of time represented by these samples, as compared with the broad archaeological time periods, which average a variety of environmental conditions, these isotopic changes may represent a previously unobserved shift in walrus diet. Given the substantial lag between dietary shifts and their impacts on stable isotope ratios in bone collagen, it is likely that the actual changes in walrus diet are more substantial than those captured in the specimens used for this study. Continued examinations of walrus diet and population health should be employed to track the changes that are currently underway. Future studies using compound-specific stable isotope analysis would be especially valuable for gaining further insight into the more complex aspects of walrus dietary changes and potential baseline shifts through time.

is solely the responsibility of the authors and does not necessarily represent the official views of the National Institutes of Health. The University of Alaska is an AA/EO employer and educational institution and prohibits illegal discrimination against any individual: http://www.alaska.edu/titleIXcompliance/nondiscrimination.

SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at https://doi.org/10.1017/qua.2018.140.

REFERENCES

Alter, S.E., Newsome, S.D., Palumbi, S.R., 2012. Pre-whaling genetic diversity and population ecology in eastern pacific gray whales: insights from ancient DNA and stable isotopes. *PLoS ONE* 7, 1–12.

Arrigo, K.R., Perovich, D.K., Pickart, R.S., Brown, Z.W., van Dijken, G.L., Lowry, K.E., Mills, M.M., *et al.*, 2012. Massive phytoplankton blooms under Arctic sea ice. *Science* 336, 1408–1408.

Arrigo, K.R., van Dijken, G.L., 2015. Continued increases in Arctic Ocean primary production. *Progress in Oceanography* 136, 60–70.

Beatty, W.S., Jay, C.V., Fischbach, A.S., Grebmeier, J.M., Taylor, R.L., Blanchard, A.L., Jewett, S.C., 2016. Space use of a dominant Arctic vertebrate: effects of prey, sea ice, and land on Pacific walrus resource selection. *Biological Conservation* 203, 25–32.

Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. *Bayesian Analysis* 6, 457–474.

Blanca, M.J., Alarcón, R., Arnau, J., Bono, R., Bendayan, R., 2017. Non-normal data: is ANOVA still a valid option? *Psicothema* 29, 552–557.

Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D., Forister, M.L., 2003. The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* 161, 1–28.

Broecker, W.S., 2001. Was the Medieval Warm Period global? *Science* 291, 1497–1499.

Casey, M.M., Post, D.M., 2011. The problem of isotopic baseline: reconstructing the diet and trophic position of fossil animals. *Earth-Science Reviews* 106, 131–148.

Castellini, M.A., Rea, L.D., 1992. The biochemistry of natural fasting at its limits. *Experientia* 48, 575–582.

Chikaraishi, Y., Ogawa, N.O., Kashiyama, Y., Takano, Y., Suga, H., Tomitani, A., Miyashita, H., Kitazato, H., Ohkouchi, N., 2009. Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. *Limnology and Oceanography: Methods* 7, 740–750.

Clark, C.T., Horstmann, L., Misarti, N., 2017. Quantifying variability in stable carbon and nitrogen isotope ratios within the skeletons of marine mammals of the suborder Caniformia. *Journal of Archaeological Science: Reports* 15, 393–400.

Conners, M.E., Hollowed, A.B., Brown, E., 2002. Retrospective analysis of Bering Sea bottom trawl surveys: regime shift and ocean reorganization. *Progress in Oceanography* 55, 209–222.

Coyle, K.O., Konar, B., Blanchard, A., Highsmith, R.C., Carroll, J., Carroll, M., Denisenko, S.G., Sirenko, B.I., 2007. Potential

effects of temperature on the benthic infaunal community on the southeastern Bering Sea shelf: possible impacts of climate change. *Deep-Sea Research Part II: Topical Studies in Oceanography* 54, 2885–2905.

Cronin, M.A., Hills, S., Born, E.W., Patton, J.C., 1994. Mitochondrial DNA variation in Atlantic and Pacific walruses. *Canadian Journal of Zoology* 72, 1035–1043.

Danielson, S.L., Weingartner, T.J., Hedstrom, K.S., Aagaard, K., Woodgate, R., Curchitser, E., Stabeno, P.J., 2014. Coupled wind-forced controls of the Bering-Chukchi shelf circulation and the Bering Strait throughflow: Ekman transport, continental shelf waves, and variations of the Pacific-Arctic sea surface height gradient. *Progress in Oceanography* 125, 40–61.

Dehn, L.A., Sheffield, G.G., Follmann, E.H., Duffy, L.K., Thomas, D.L., O'Hara, T.M., 2007. Feeding ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as determined by stomach contents and stable isotope analysis. *Polar Biology* 30, 167–181.

de Vernal, A., Hillaire-Marcel, C., Darby, D.A., 2005. Variability of sea ice cover in the Chukchi Sea (western Arctic Ocean) during the Holocene. *Paleoceanography* 20, PA4018.

de Vernal, A., Rochon, A., Fréchette, B., Henry, M., Radi, T., Solignac, S., 2013. Reconstructing past sea ice cover of the Northern Hemisphere from dinocyst assemblages: status of the approach. *Quaternary Science Reviews* 79, 122–134.

Dickson, R.R., Osborn, T.J., Hurrell, J.W., Meincke, J., Blindheim, J., Adlandsvik, B., Vinje, T., Alekseev, G., Maslowski, W., 2000. The Arctic Ocean response to the North Atlantic Oscillation. *Journal of Climate* 13, 2671–2696.

Dunnett, C., 1980. Pairwise multiple comparisons in the unequal variance case. *Journal of the American Statistical Association* 75, 796–800.

Dyke, A.S., Savelle, J.M., 2001. Holocene history of the Bering Sea bowhead whale (*Balaena mysticetus*) in its Beaufort Sea summer grounds off southwestern Victoria Island, western Canadian Arctic. *Quaternary Research* 55, 371–379.

Ebbesmeyer, C.C., Cayan, D.R., McLain, D.R., Nichols, F.H., Peterson, D.H., Redmond, K.T., 1991. 1976 Step in the Pacific climate: forty environmental changes between 1968–1975 and 1977–1984. In: Betancourt, J.L., Tharp, V.L. (Eds.), *Proceedings of the Seventh Annual Pacific Climate (PACLIM) Workshop: Asilomar, California – April 1990*. Technical Report 26 of the Interagency Ecological Studies Program for the Sacramento–San Joaquin Estuary. California Department of Water Resources, Sacramento, CA, pp. 115–126.

Fabry, V., McClintock, J., Mathis, J., Grebmeier, J., 2009. Ocean acidification at high latitudes: the bellwether. *Oceanography* 22, 160–171.

Farmer, J.R., Cronin, T.M., De Vernal, A., Dwyer, G.S., Keigwin, L.D., Thunell, R.C., 2011. Western Arctic Ocean temperature variability during the last 8000 years. *Geophysical Research Letters* 38, 4–9.

Fay, F.H. 1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. *North American Fauna* 74, 1–279.

Fay, F.H., Kelly, B.P., Sease, J.L., 1989. Managing the exploitation of Pacific walruses: a tragedy of delayed response and poor communication. *Marine Mammal Science* 5, 1–16.

Fogel, M.L., Cifuentes, L.A., 1993. Isotope fractionation during primary production. In: Engel, M.H., Macko, S.A. (Eds.), *Organic Geochemistry*. Springer, Boston, MA, pp. 73–98.

Fry, B., 2006. *Stable Isotope Ecology*. Springer, New York.

Garlich-Miller, J., MacCracken, J.G., Snyder, J., Meehan, R., Myers, M., Wilder, J.M., Lance, E., Matz, A., 2011. *Status Review of the Pacific Walrus (*Odobenus rosmarus divergens*)*. U.S. Fish and Wildlife Service, Anchorage, AK.

Garlich-Miller, J.L., Stewart, R.E.A., Stewart, B.E., Hiltz, E.A., 1993. Comparison of mandibular with cemental growth-layer counts for ageing Atlantic walrus (*Odobenus rosmarus rosmarus*). *Canadian Journal of Zoology* 71, 163–167.

Goericke, R., Fry, B., 1994. Variations of marine plankton $\delta^{13}C$ with latitude, temperature, and dissolved CO_2 in the world ocean. *Global Biogeochemical Cycles* 8, 85–90.

Grebmeier, J.M., 2012. Shifting patterns of life in the Pacific Arctic and sub-Arctic seas. *Annual Review of Marine Science* 4, 63–78.

Grebmeier, J.M., Bluhm, B.A., Cooper, L.W., Danielson, S.L., Arrigo, K.R., Blanchard, A.L., Clarke, J.T., et al., 2015a. Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic. *Progress in Oceanography* 136, 92–114.

Grebmeier, J.M., Bluhm, B.A., Cooper, L.W., Denisenko, S.G., Iken, K., Kedra, M., Serratos, C., 2015b. Time-series benthic community composition and biomass and associated environmental characteristics in the Chukchi Sea during the RUSALCA 2004–2012 Program. *Oceanography* 28, 116–133.

Grebmeier, J.M., Cooper, L.W., Feder, H.M., Sirenko, B.I., 2006. Ecosystem dynamics of the Pacific-influenced northern Bering and Chukchi Seas in the Amerasian Arctic. *Progress in Oceanography* 71, 331–361.

Grove, J.M., 1988. *The Little Ice Age*. Methuen, London.

Hedges, J.E.M., Stevens, R.E., Koch, P.L., 2006. Isotopes in bones and teeth. In: Leng, M.J. (Ed.), *Isotopes in Palaeoenvironmental Research*. Springer, Dordrecht, the Netherlands, pp. 117–145.

Heusser, C.J., Heusser, L.E., Peteet, D.M., 1985. Late-Quaternary climatic change on the American North Pacific Coast. *Letters to Nature* 315, 485–487.

Hobson, K.A., Alisauskas, R.A.Y.T., Clark, R.G., 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. *Condor* 95, 388–394.

Hobson, K.A., Welch, H.E., 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. *Marine Ecology Progress Series* 84, 9–18.

Horstmann, L., Stimmelmayr, R., McCarthy, M., 2017. Eating seal or hungry like a wolf? Polar bear use of terrestrial resources revealed by compound-specific stable isotopes. In: *22nd Biennial Conference on the Biology of Marine Mammals*, 70. Society for Marine Mammalogy, Lawrence, KS.

Huang, B., Banzon, V.F., Freeman, E., Lawrimore, J., Liu, W., Peterson, T.C., Smith, T.M., Thorne, P.W., Woodruff, S.D., Zhang, H.-M., 2015. Extended reconstructed sea surface temperature version 4 (ERSST.v4). Part I: upgrades and intercomparisons. *Journal of Climate* 28, 911–930.

Huntington, H.P., Quakenbush, L.T., Nelson, M., Huntington, H.P., 2016. Effects of changing sea ice on marine mammals and subsistence hunters in northern Alaska from traditional knowledge interviews. *Biology Letters* 12, 4–7.

Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology* 80, 595–602.

Jay, C.V., Fischbach, A.S., Kochnev, A.A., 2012. Walrus areas of use in the Chukchi Sea during sparse sea ice cover. *Marine Ecology Progress Series* 468, 1–13.

Jay, C.V., Grebmeier, J.M., Fischbach, A.S., McDonald, T.L., Cooper, L.W., Hornsby, F., 2014. Pacific walrus (*Odobenus rosmarus divergens*) resource selection in the northern Bering Sea. *PLoS ONE* 9, e93035.

Jay, C.V., Marcot, B.G., Douglas, D.C., 2011. Projected status of the Pacific walrus (*Odobenus rosmarus divergens*) in the twenty-first century. *Polar Biology* 34, 1065–1084.

Jay, C.V., Outridge, P.M., Garlich-Miller, J.L., 2008. Indication of two Pacific walrus stocks from whole tooth elemental analysis. *Polar Biology* 31, 933–943.

Kaufman, D.S., Axford, Y.L., Henderson, A.C.G., McKay, N.P., Oswald, W.W., Saenger, C., Anderson, R.S., et al., 2016. Holocene climate changes in eastern Beringia (NW North America) – a systematic review of multi-proxy evidence. *Quaternary Science Reviews* 147, 312–339.

Kędra, M., Moritz, C., Choy, E.S., David, C., Degen, R., Duerksen, S., Ellingsen, I., et al., 2015. Status and trends in the structure of Arctic benthic food webs. *Polar Research* 34, 1–23.

Keeling, C.D., Piper, S.C., Bacastow, R.B., Wahlen, M., Whorf, T.P., Heimann, M., Meijer, H.A., 2005. Atmospheric CO_2 and $^{13}CO_2$ exchange with the terrestrial biosphere and oceans from 1978 to 2000: observations and carbon cycle implications. In: Baldwin, I.T., Caldwell, M.M., Heldmaier, G., Jackson, R.B., Lange, O.L., Mooney, H.A., Schulze, E.-D., et al. (Eds.), *A History of Atmospheric CO_2 and Its Effects on Plants, Animals, and Ecosystems*. Springer, New York, pp. 83–113.

Koch, P.L., Fogel, M.L., Tuross, N., 1994. Tracing the diets of fossil animals using stable isotopes. In: Lajtha, K., Michener, B. (Eds.), *Stable Isotopes in Ecology and Environmental Science*. Blackwell Scientific, Boston, MA, pp. 63–92.

Kutzbach, J.E., 1970. Large-scale features of monthly mean Northern Hemisphere anomaly maps of sea-level pressure. *Monthly Weather Review* 98, 708–716.

Laws, E.A., Popp, B.N., Bidigare, J.R.R., Kennicutt, M.C., Macko, S.A., 1995. Dependence of phytoplankton carbon isotopic composition on growth rate and $[CO_2]_{aq}$: theoretical considerations and experimental results. *Geochimica et Cosmochimica Acta* 59, 1131–1138.

Laws, E.A., Popp, B.N., Cassas, N., Tanimoto, J., 2002. 13C discrimination patterns in oceanic phytoplankton: likely influence of CO_2 concentrating mechanisms, and implications for palaeoreconstructions. *Functional Plant Biology* 29, 323–333.

Li, W.K.W., McLaughlin, F.A., Lovejoy, C., Carmack, E.C., 2009. Smallest algae thrive as the Arctic Ocean freshens. *Science* 326, 539.

Lindqvist, C., Bachmann, L., Andersen, L.W., Born, E.W., Arnason, U., Kovacs, K.M., Lydersen, D., Abramov, A.V., Wiig, Ø., 2009. The Laptev Sea walrus *Odobenus rosmarus laptevi*: an enigma revisited. *Zoologica Scripta* 38, 113–127.

Ljungqvist, F.C., 2010. A regional approach to the Medieval Warm Period and the Little Ice Age. In: Simard, S., Austin, M. (Eds.), *Climate Change and Variability*. Sciyo, Rijek, Croatia, pp. 1–26.

Long, J.S., Ervin, L.H., 2000. Using heteroscedasticity consistent standard errors in the linear regression model. *American Statistician* 54, 217–224.

Lotze, H.K., Worm, B., 2009. Historical baselines for large marine animals. *Trends in Ecology and Evolution* 24, 254–262.

MacCracken, J.G., 2012. Pacific Walrus and climate change: observations and predictions. *Ecology and Evolution* 2, 2072–2090.

MacCracken, J.G., Beatty, W.S., Garlich-Miller, J.L., Kissling, M.L., Snyder, J.A., 2017. *Final Species Status Assessment for the Pacific Walrus.* U.S. Fish and Wildlife, Anchorage, AK.

Mahoney, A.R., Bockstoce, J.R., Botkin, D.B., Eicken, H., Nisbet, R.A., 2011. Sea-ice distribution in the Bering and Chukchi seas: information from historical whaleships' logbooks and journals. *Arctic* 64, 465–477.

Manolagas, S.C., 2000. Birth and death of bone cells: basic regulatory mechanisms and implications for the pathogenesis and treatment of osteoporosis. *Endocrine Reviews* 21, 115–137.

Matheus, P.E., 1995. Diet and co-ecology of Pleistocene short-faced bears and brown bears in eastern Beringia. *Quaternary Research* 44, 447–453.

Matthews, J.A., Dresser, P.Q., 2008. Holocene glacier variation chronology of the Smørstabbtindan massif, Jotunheimen, southern Norway, and the recognition of century- to millennial-scale European Neoglacial Events. *Holocene* 18, 181–201.

McClelland, J.W., Montoya, J.P., 2017. Trophic relationships and the nitrogen isotopic composition of amino acids in plankton. *Ecology* 83, 2173–2180.

McKay, J.L., de Vernal, A., Hillaire-Marcel, C., Not, C., Polyak, L., Darby, D., 2008. Holocene fluctuations in Arctic sea-ice cover: dinocyst-based reconstructions for the eastern Chukchi Sea. *Canadian Journal of Earth Sciences* 45, 1377–1397.

McNeely, R., Dyke, A.S., Southon, J.R., 2006. Canadian Marine Reservoir Ages, Preliminary Data Assessment. Open File 5094. *Geological Survey of Canada*, Calgary, AB, Canada.

Misarti, N., Finney, B., Maschner, H., Wooller, M.J., 2009. Changes in northeast Pacific marine ecosystems over the last 4500 years: evidence from stable isotope analysis of bone collagen from archeological middens. *Holocene* 19, 1139–1151.

Misarti, N., Gier, E., Finney, B., Barnes, K., McCarthy, M., 2017. Compound-specific amino acid $\delta^{15}N$ values in archaeological shell: assessing diagenetic integrity and potential for isotopic baseline reconstruction. *Rapid Communications in Mass Spectrometry* 31, 1881–1891.

Newsome, S.D., Clementz, M.T., Koch, P.L., 2010. Using stable isotope biogeochemistry to study marine mammal ecology. *Marine Mammal Science* 26, 509–572.

Newsome, S.D., Etnier, M.A., Kurle, C.M., Waldbauer, J.R., Chamberlain, C.P., Koch, P.L., 2007. Historic decline in primary productivity in western Gulf of Alaska and eastern Bering Sea: isotopic analysis of northern fur seal teeth. *Marine Ecology Progress Series* 332, 211–224.

Niebauer, H.J., 1998. Variability in Bering Sea ice cover as affected by a regime shift in the North Pacific in the period 1947–1996. *Journal of Geophysical Research: Oceans* 103, 27717–27737.

Noren, S.R., Udevitz, M.S., Jay, C.V., 2012. Bioenergetics model for estimating food requirements of female Pacific walruses *Odobenus rosmarus divergens. Marine Ecology Progress Series* 460, 261–275.

Noren, S.R., Udevitz, M.S., Jay, C.V., 2016. Sex-specific energetics of Pacific walruses (*Odobenus rosmarus divergens*) during the nursing interval. *Physiological and Biochemical Zoology* 89, 93–109.

Ostrom, P.H., Wiley, A.E., James, H.F., Rossman, S., Walker, W.A., Zipkin, E.F., Chikaraishi, Y., 2017. Broad-scale trophic shift in the pelagic North Pacific revealed by an oceanic seabird. *Proceedings of the Royal Society B: Biological Sciences* 284, 20162436.

Oxtoby, L.E., Mathis, J.T., Juranek, L.W., Wooller, M.J., 2016. Estimating stable carbon isotope values of microphytobenthos

in the Arctic for application to food web studies. *Polar Biology* 39, 473–483.

Porter, S.C., Denton, G.H., 1967. Chronology of neoglaciation in the North American Cordillera. *American Journal of Science* 265, 177–210.

Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Buck, C.E., *et al*., 2013. Intcal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon* 55, 1869–1887.

Rick, T.C., Lockwood, R., 2013. Integrating paleobiology, archeology, and history to inform biological conservation. *Conservation Biology* 27, 45–54.

Rodionov, S.N., Bond, N.A., Overland, J.E., 2007. The Aleutian Low, storm tracks, and winter climate variability in the Bering Sea. *Deep Sea Research Part II: Topical Studies in Oceanography* 54, 2560–2577.

Schoener, T.W., 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2, 369–404.

Scribner, K.T., Hills, S., Fain, S.R., Cronin, M.A., 1997. Population genetics studies of the walrus (Odobenus rosmarus): a summary and interpretation of results and research needed. In: Dizon, A.E., Chivers, S.J., Perrin, W.F. (Eds.), *Molecular Genetics of Marine Mammals*. Society for Marine Mammalogy, Lawrence, KS, pp. 173–184.

Seymour, J., Horstmann-Dehn, L., Wooller, M.J., 2014a. Interannual variability in the proportional contribution of higher trophic levels to the diet of Pacific walruses. *Polar Biology* 37, 597–609.

Seymour, J., Horstmann-Dehn, L., Wooller, M.J., 2014b. Proportion of higher trophic-level prey in the diet of Pacific walruses (*Odobenus rosmarus divergens*). *Polar Biology* 37, 941–952.

Sheffield, G., Grebmeier, J.M., 2009. Pacific walrus (*Odobenus rosmarus divergens*): differential prey digestion and diet. *Marine Mammal Science* 25, 761–777.

Sherwood, O.A., Guilderson, T.P., Batista, F.C., Schiff, J.T., McCarthy, M.D., 2014. Increasing subtropical North Pacific Ocean nitrogen fixation since the Little Ice Age. *Nature* 505, 78–81.

Shitova, M.V., Kochnev, A.A., Dolnikova, O.G., Kryukova, N.V., Malinina, T.V., Pereverzev, A.A., 2017. Genetic diversity of the Pacific walrus (*Odobenus rosmarus divergens*) in the western part of the Chukchi Sea. *Russian Journal of Genetics* 53, 242–251.

Sol, D., Elie, M., Marcoux, M., Chrostovsky, E., Porcher, C., Lefebvre, L., 2005. Ecological mechanisms of a resource polymorphism in Zenaida Doves of Barbados. *Ecology* 86, 2397–2407.

Sonsthagen, S.A., Jay, C.V., Fischbach, A.S., Sage, G.K., Talbot, S.L., 2012. Spatial genetic structure and asymmetrical gene flow within the Pacific walrus. *Journal of Mammalogy* 93, 1512–1524.

Springer, A.M., Estes, J.A., van Vliet, G.B., Williams, T.M., Doak, D.F., Danner, E.M., Forney, K.A., Pfister, B., 2003. Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences of the United States of America* 100, 12223–12228.

Stephens, D.W., Krebs, J.R., 1986. *Foraging Theory*. Princeton University Press, Princeton, NJ.

Stuiver, M., Pearson, G.W., Braziunas, T., 1986. Radiocarbon age calibration of marine samples back to 9000 cal yr BP. *Radiocarbon* 28, 980–1021.

Sun, J., Wang, H., 2006. Relationship between Arctic Oscillation and Pacific Decadal Oscillation on decadal timescale. *Chinese Science Bulletin* 51, 75–79.

Svanbäck, R., Bolnick, D.I., 2007. Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society B: Biological Sciences* 274, 839–844.

Swetnam, T.W., Allen, C.D., Betancourt, J.L., Applications, E., Nov, N., 1999. Applied historical ecology: using the past to manage for the future. *Ecological Applications* 9, 1189–1206.

Szpak, P., Buckley, M., Darwent, C.M., Richards, M.P., 2018. Long-term ecological changes in marine mammals driven by recent warming in northwestern Alaska. *Global Change Biology* 24, 490–503.

Szpak, P., Metcalfe, J.Z., Macdonald, R.A., 2017. Best practices for calibrating and reporting stable isotope measurements in archaeology. *Journal of Archaeological Science: Reports* 13, 609–616.

Thompson, D.W.J., Wallace, J.M., 1998. The Arctic Oscillation signature in the wintertime geopotential height and temperature fields. *Geophysical Research Letters* 25, 1297–1300.

Tinker, M.T., Bentall, G., Estes, J.A., 2008. Food limitation leads to behavioral diversification and dietary specialization in sea otters. *Proceedings of the National Academy of Sciences of the United States of America* 105, 560–565.

Tu, K.L., Blanchard, A.L., Iken, K., Horstmann-Dehn, L., 2015. Small-scale spatial variability in benthic food webs in the northeastern Chukchi Sea. *Marine Ecology Progress Series* 528, 19–37.

Tuross, N., Fogel, M.L., Hare, P.E., 1988. Variability in the preservation of the isotopic composition of collagen from fossil bone. *Geochimica et Cosmochimica Acta* 52, 929–935.

Viau, A. E., Gajewski, K., Sawada, M. C., & Fines, P. (2006). Millennial-scale temperature variations in North America during the Holocene. *Journal of Geophysical Research: Atmospheres*, 111(D9).

Walsh, J.E., Fetterer, F., Scott Stewart, J., Chapman, W.L., 2017. A database for depicting Arctic sea ice variations back to 1850. *Geographical Review* 107, 89–107.

Wang, T., Surge, D., Mithen, S., 2012. Seasonal temperature variability of the Neoglacial (3300-2500 BP) and Roman Warm Period (2500-1600 BP) reconstructed from oxygen isotope ratios of limpet shells (*Patella vulgata*), northwest Scotland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 317–318, 104–113.

Wassmann, P., Reigstad, M., 2011. Future Arctic Ocean seasonal ice zones and implications for pelagic-benthic coupling. *Oceanography* 24, 220–231.

White, H., 1980. A heteroskedasticity-consistent covariance matrix estimator and a direct test for heteroskedasticity. *Econometrica* 48, 817–838.

Wiley, A.E., Ostrom, P.H., Welch, A.J., Fleischer, R.C., Gandhi, H., Southon, J.R., Stafford, T.W., Jr., *et al*., 2013. Millennial-scale isotope records from a wide-ranging predator show evidence of recent human impact to oceanic food webs. *Proceedings of the National Academy of Sciences of the United States of America* 110, 8972–8977.

Woodgate, R.A., Weingartner, T.J., Lindsay, R., 2012. Observed increases in Bering Strait oceanic fluxes from the Pacific to the Arctic from 2001 to 2011 and their impacts on the Arctic Ocean water column. *Geophysical Research Letters* 39, 2–7.