

Unprecedented shift in Canadian High Arctic polar bear food web unsettles four millennia of stability

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ABSTRACT

Stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope analysis was conducted on modern and archaeological polar bear bone collagen from the Canadian Arctic Archipelago to investigate potential changes in polar bear foraging ecology over four-millennia. Polar bear $\delta^{13}\text{C}$ values showed a significant decline in the modern samples relative to all archaeological time-bins, indicating a disruption in the sources of production that support the food web, occurring after the Industrial Revolution. The trophic structure, indicated through $\delta^{15}\text{N}$, remained unaltered throughout all time periods. The lower $\delta^{13}\text{C}$ observed in the modern samples indicates a change in the relative importance of pelagic (supported by open-water phytoplankton) over sympagic (supported by sea ice-associated algae) primary production. The consistency in polar bear $\delta^{13}\text{C}$ through the late Holocene includes climatic shifts such as the Medieval Warm Period (MWP, A.D. 950–1250) and the early stages of the Little Ice Age (LIA, A.D. 1300–1850). These findings suggest that polar bears inhabit a food web that is more pelagic and less sympagic today than it was through the Late Holocene. We suggest that modern, anthropogenic warming has already affected food web structure in the Canadian Arctic Archipelago when modern data are contextualized with a deep time perspective.

1. Introduction

Polar bears (*Ursus maritimus*) are apex predators in a food web situated in a rapidly changing environment. Increasing global temperatures are causing precipitous circumpolar reduction in sea ice extent, with the magnitude of the effects in the Canadian Arctic Archipelago (CAA) increasing over the last two decades (Howell et al., 2016; IPCC, 2019; Noël et al., 2018). Sea ice is an important feature of Arctic marine ecosystems, both as a physical habitat for marine mammals and as a substrate for primary production in the form of sea ice algae that bloom prior to pelagic phytoplankton (Leu et al., 2015). The landfast ice of the Canadian Arctic Archipelago hosts one of the most productive sea ice algae populations in the Arctic, driven largely by the input of nutrient rich waters from the Pacific Ocean (Leu et al., 2015).

The observed and predicted impacts of climate change to the marine Arctic food web are plentiful and complex. An increased number of ice-free days has been correlated with decreasing $\delta^{13}\text{C}$ values in organic and inorganic carbon in the Arctic caused by changes in the composition of primary production (De La Vega et al., 2019; Johnson et al., 2019).

These changes have impacted the food web through decreased benthic coupling and increased consumption of pelagic production (Mueter et al., 2021). With increasing warming, models predict detrimental losses of energy-dense ice-associated zooplankton, an essential component of the food web for many Arctic species (Mueter et al., 2021). When low ice years are experienced, species reliant on sympagic production have been observed to fall back on less nutritious food sources, and breeding success is negatively impacted (e.g. Cusset et al., 2019). Diminished sea ice also alters movement patterns and increases exposure to toxins, especially mercury (Dietz et al., 2021). Warmer waters alter currents throughout the Arctic facilitating the introduction of Boreal and Pacific species, increasing competition with endemic species and destabilizing regional food web (Kortsch et al., 2015; Polyakov et al., 2020). Anomalous advection currents make the regional impacts of climate change difficult to estimate in advance (Polyakov et al., 2020).

Specialist, endemic predators like polar bears are expected to face significant impacts from a changing Arctic. Recent reduction in multi-year sea ice has resulted in a regime of thinner, seasonal sea ice, and

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models of sea ice loss project the potential for ice-free Arctic summers by the end of the century, or likely sooner (Overland et al., 2019). Sea ice is required by polar bears for hunting their sea ice-obligate primary prey, ringed seals (*Pusa hispida*) (Laidre et al., 2008, 2022; Hamilton et al., 2017). When the sea ice breaks up in the summer, the bears enter a fasting period. The fasting period can be successfully endured for between 100 d for females with cubs, to more than 200 d for solitary males and females, provided they have adequate body mass at the onset of the fast (Molnár et al., 2020). Longer fasting periods, resulting from a greater number of sea ice-free days have already impacted the viability of the Western Hudson Bay subpopulation and are expected to impact all subpopulations, apart from the Queen Elizabeth Islands subpopulation, by the end of this century (Molnár et al., 2020).

The ringed seal soft tissues consumed by polar bears during the spring hunt reflect the sea ice associated environment. Compound specific stable isotope analysis (Kunisch et al., 2021) and sea ice-specific isoprenoid lipid biomarker IP₂₅ (Brown et al., 2018) confirm the importance of sympagic primary production for polar bears and their prey. Through bulk stable isotope analysis, sources of primary production can be distinguished through predictable differences in their $\delta^{13}\text{C}$ values. In the Arctic, sympagic (sea-ice associated) algae have $\delta^{13}\text{C}$ values 4–12 ‰ higher than pelagic (open-water) phytoplankton, making the two sources of primary production isotopically distinguishable (France et al., 1998; Søreide et al., 2006). There is little trophic enrichment of carbon isotopes in bone collagen, making $\delta^{13}\text{C}$ a reliable indicator of the relative importance of primary producers (DeNiro and Epstein, 1978; Fry and Sherr, 1989). Stable nitrogen isotope compositions ($\delta^{15}\text{N}$) undergo a predictable increase averaging approximately 3.4 ‰ with each trophic level (Post, 2002), providing a useful indicator of trophic structure.

With documented disruption to the Arctic cryosphere, evidence of the negative effects of diminishing sea ice are accumulating for polar bears (Rode et al., 2022; Florko et al., 2021; Maduna et al., 2021; Molnár et al., 2020). The Earth’s climate has never been static, however, and polar bears have endured past periods of warming and cooling. It is useful to contextualize the current crisis with the past to assess the magnitude of the impacts of anthropogenic warming relative to past

climate disruptions (e.g., the Medieval Warm Period). As an area with an extensive polynya, Lancaster Sound offers seasonal accessibility to both archaeologists and ecologists, which has allowed for the collection of samples spanning 4000 years. Here, we compared the stable isotope compositions of modern (1998–2007 CE) and ancient polar bear bone collagen (>500 BP) from the Lancaster Sound subpopulation (Fig. 1) to assess the impacts on the polar bear’s food web ecology resulting from recent and past climate instability. Specifically, we ask: 1. Is there evidence of alteration of the trophic structure or source of primary production in the Lancaster Sound food web at any period in the past 4000 years? 2. How do periods of past climate change compare to recent anthropogenic climate change with respect to the sources of primary production supporting the Lancaster Sound food web?

2. Materials and methods

Ancient bone samples were collected from 35 polar bears from 10 archaeological sites (Supplement S2) in the region inhabited by the Lancaster Sound polar bear subpopulation (Fig. 1). The archaeological samples came from pre-Dorset (N = 10; 4000–2800 BP), Dorset (N = 15; 1500–700 BP), and Thule (N = 10; 700–500 BP) sites, and consisted of several different anatomical elements but each element represented a distinct individual (Table 1; Supplement S2). The archaeological samples could not be sexed or aged. Modern bone samples (N = 11; 1998–2007 CE) were obtained from individuals harvested

Table 1
Mean polar bear bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the four different time-bins.

Time Period	Date Range	n Samples	$\delta^{13}\text{C}$ mean \pm 1 SD	$\delta^{15}\text{N}$ mean \pm 1 SD
Modern	1998–2007 CE	11	- 13.93 \pm 0.17	+ 21.86 \pm 0.68
Thule	700–500 BP	10	- 13.30 \pm 0.39	+ 22.03 \pm 0.73
Dorset	1500–700 BP	15	- 13.56 \pm 0.41	+ 22.28 \pm 1.29
Pre Dorset	4000–2800 BP	10	- 13.36 \pm 0.39	+ 22.48 \pm 0.99

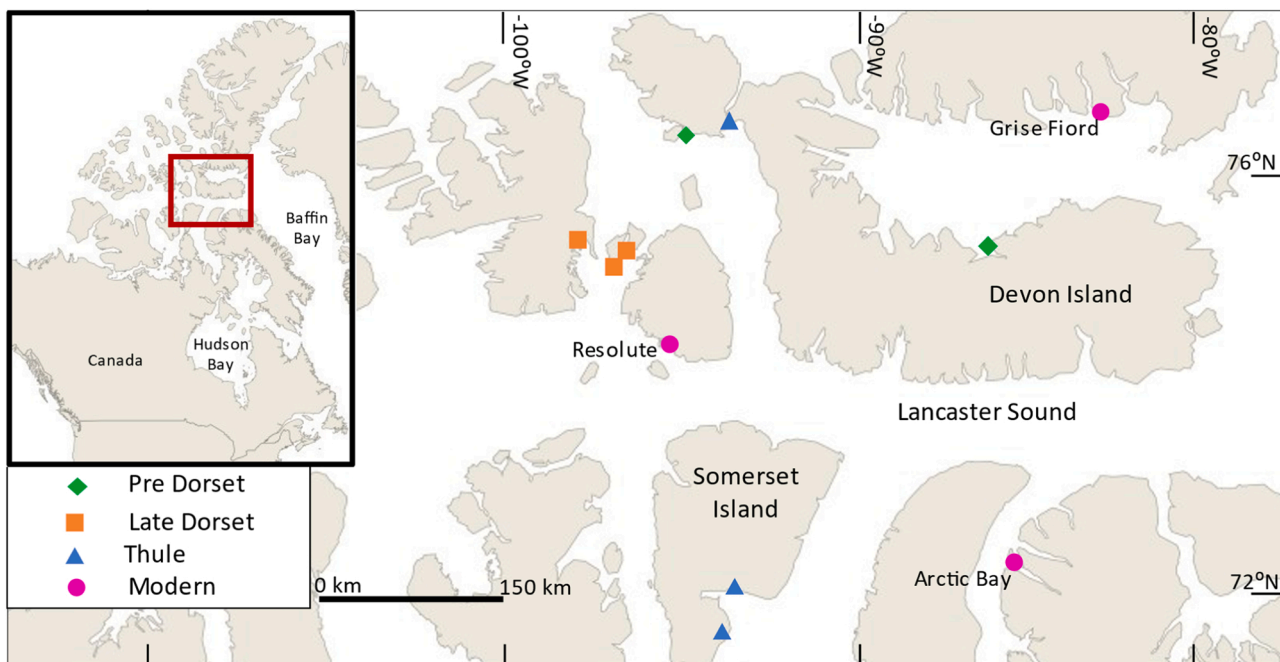


Fig. 1. Map of the Lancaster Sound region showing the locations of the archaeological and modern sample acquisition sites: pre Dorset (green triangle), late Dorset (orange square), Thule (blue triangle), and modern (pink circle). Modern samples were collected within a 150 km radius of the communities indicated by the pink circles on the map. (Inset) Map showing the location of the Lancaster Sound polar bear subpopulation (red box) relative to the entire Canadian Arctic.

within a 150 km radius of the communities of Ikpiarjuk (Arctic Bay), Ajuittuq (Grise Fiord), and Qausuittuq (Resolute) between 1998 and 2007 (Supplement S3). The modern samples consisted of polar bear bacula, collected as a mandatory sample by subsistence hunters (Sonne et al., 2015). The modern samples were, therefore, male and ranged in age from three to 8-years-old (Sonne et al., 2015).

For the archaeological specimens, chunks of bone weighing ~200 mg were sampled using an NSK dental drill equipped with a diamond-tipped cutting wheel. Samples were demineralized in 16 × 100 mm glass culture tubes with 0.5 M HCl at room temperature. After the samples were demineralized, they were rinsed three times with Type I water (resistivity >18.2 MΩ·cm). The samples were treated with 0.1 M NaOH to remove humic contaminants from bones that exhibited a dark coloration. After 30 min, the NaOH was removed, and samples were rinsed twice with Type I water. The samples were then placed in a solution of 0.01 M HCl and placed in a dry bath at 75°C for 36 h, to solubilize the collagen. The collagen was extracted from the modern specimens using the same protocol with the following exceptions. First, powdered bone was removed from the samples using a Dremel equipped with a rotary burr. Because modern bone contains significant quantities of lipids whereas ancient bone does not, the samples were first treated with 2:1 chloroform:methanol under sonication for 1 h. The powdered samples were demineralized in 0.5 M HCl for 4 h. Demineralization in HCl does not alter the stable carbon or nitrogen isotopic composition of the bone collagen (Wilson and Szpak, 2022).

The solution containing the solubilized collagen was then transferred into pre-weighed 4 ml glass vials and freeze-dried. Collagen samples (0.45–0.55 mg) were weighed into tin capsules for analysis with a EuroEA 3000 (Euro Vector SpA) Elemental Analyzer coupled to a Nu Horizon (Nu Instruments) continuous flow isotope ratio mass spectrometer at the Water Quality Centre at Trent University. Ten percent of samples were analyzed in duplicate to assess homogeneity. Analytical sessions were calibrated using international standards USGS40, USGS41a and USGS66. Accuracy and precision were assessed with in-house check standards: SRM-1 (caribou bone collagen), SRM-2 (walrus bone collagen), and SRM-14 (polar bear bone collagen), the known isotopic compositions of which are given in supplement S1 (Tables S1.1 and S1.2). The standard uncertainty across analytical sessions was calculated to be ± 0.13 ‰ for δ¹³C and ± 0.24 ‰ for δ¹⁵N.

3. Data treatment

Modern bone samples may be particularly prone to contamination with lipids under certain circumstances (Guiry and Szpak, 2020). Despite lipid extraction with a commonly used protocol, we observed a correlation between the atomic C:N ratios and the δ¹³C values of the collagen even though our highest C:N ratio was 3.30 (Supplement S3). This observation is consistent with increasing quantities of residual lipids causing lower δ¹³C values as C:N ratios rise. No additional collagen from the modern specimens was available for further chemical pretreatment after the initial analyses. We therefore applied a mathematical correction to the modern bone collagen δ¹³C values (e.g., Post et al., 2007) using the following equation:

$$\delta^{13}\text{C}_{\text{lipid corrected}} = \delta^{13}\text{C}_{\text{measured}} + (10.122) * (\text{C:N}_{\text{measured}} - \text{C:N}_{\text{expected}}) \quad (1)$$

δ¹³C_{measured} and C:N_{measured} are the isotopic and elemental compositions determined for the sample prior to any adjustments. We used an expected C:N ratio for mammalian bone collagen of 3.23 (Guiry and Szpak, 2020) and 10.122 represents the slope of the regression line when plotting our modern C:N_{measured} and δ¹³C_{measured} (Supplement S1, Fig. S1.1).

When comparing the δ¹³C values of modern and ancient samples, it is important to correct for the global decrease in δ¹³C of atmospheric and oceanic CO₂ since the beginning of the industrial revolution (the Suess Effect; Eide et al., 2017; Francey et al., 1999). The magnitude of this

effect on ocean surface water is lower than for the atmosphere and decreases with latitude (Sonnerup et al., 2000). A correction was calculated using Eq. (2) (Hilton et al., 2006):

$$\Delta^{13}\text{C}_{\text{Suess}} = (\alpha_{\text{water body}}) * e^{(y-1850)} \quad (2)$$

where α is the annual rate of decrease in δ¹³C specific to the water body (we used a value of 0.014 ‰ for the Northwest Atlantic (Mellon, 2018)), y is the year of sample harvest and b is the global oceanic decrease in δ¹³C (0.027 ‰; Gruber et al., 1999).

The carbon isotopic compositions of the modern samples have undergone correction through Eqs. (1) and (2) and the revised carbon isotope values are denoted δ¹³C_{corr}. Both of these corrections have been applied to account for confounding causes of low δ¹³C values in modern samples to avoid an exaggeration of any differences between modern and ancient samples since both of these adjustments increase the δ¹³C values of the modern samples (Fig. S1). Statistical comparisons were made using Past 4.03 (Hammer, 2020). On the basis of Shapiro-Wilk, the isotopic compositions for carbon and nitrogen of the four time-bins were assessed to have normal distributions. Differences in polar bear isotopic compositions between periods were assessed using Welch's t-tests, with confidence set at 95%. Construction of niche size and overlap comparisons were conducted using SIBER for Rstudio 4.3.0 using standard ellipses corrected for small sample sizes (Jackson et al., 2011).

4. Results

The isotopic and elemental compositions of the modern and ancient polar bear samples are presented in full in the [supplementary information](#) (S2 and S3) and summarized in Table 1. Based on the atomic C:N ratios, the archaeological samples were assessed to be well preserved and uncontaminated (DeNiro, 1985). The atomic C:N ratios of the modern samples fall within a very narrow range and after being corrected for lipid contamination comply with the most conservative quality control criteria established by Guiry and Szpak (2020) for modern bone collagen. The δ¹³C_{corr} values of the modern samples was significantly lower than the δ¹³C values of each of the ancient time periods (modern/Pre-Dorset p = 0.001, modern/Dorset p = 0.005, modern/Thule p = <0.001) (Table S1.3, Fig. 2A). There were no significant differences in δ¹³C values observed among any of the ancient time periods (Table S1.3). There was no significant difference in δ¹⁵N values among any of the time periods (Table S1.3, Fig. 2B). Polar bear bone collagen associated with the Dorset and Thule cultures preceding and including the MWP (respectively) did not produce significantly different isotopic compositions (Table S1.3, Table 1).

Niche sizes were calculated for each time-bin using standard ellipse areas corrected for small sample size and are reported in per mille squared (Table S1.4). The modern time-bin yielded the smallest isotopic niche size (0.4 ‰²), likely due to the limited number of years represented (9 years) relative to the centuries represented by the samples in the other time-bins. The Dorset time-bin yielded the largest niche size (1.7 ‰²) and also contains the largest number of samples of the four time-bins. Thule and Pre Dorset polar bears had niche sizes of 0.9 ‰² and 0.7 ‰² respectively. Most likely niche overlap was calculated as both a proportion, and is reported in percent overlap and quantified in units of per mille squared (Table 2, Fig. S1.2).

5. Discussion

The comparison of modern and archaeological polar bear bone collagen isotopic compositions indicates that there has been a recent shift in the Lancaster Sound food web, with modern polar bears presenting significantly lower δ¹³C values than ancient bears from any period. The lower δ¹³C values of the modern polar bears indicates a change in the source of primary production in the food web, specifically less consumption of sympagic production (with higher δ¹³C values) and

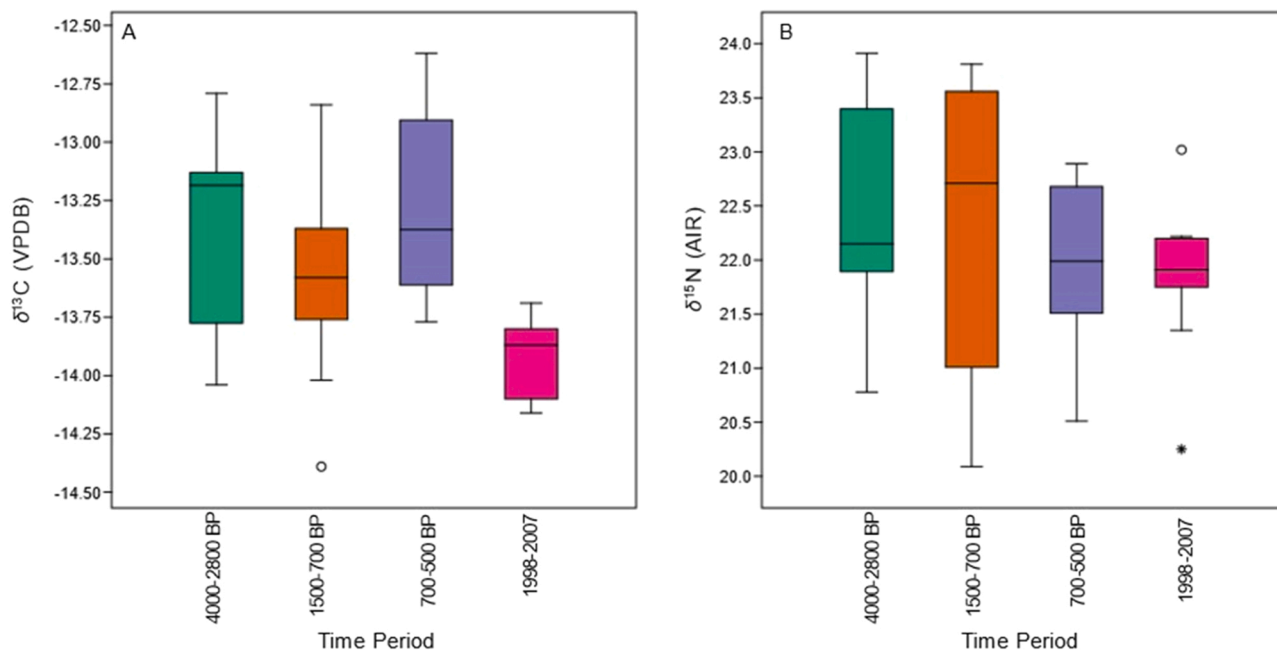


Fig. 2. (A) Boxplot of polar bear bone collagen $\delta^{13}\text{C}$ values. The modern $\delta^{13}\text{C}$ values have been corrected for lipid contamination and the Suess Effect as described in the text. (B) Boxplot of polar bear bone collagen $\delta^{15}\text{N}$ values. Boxes indicated the interquartile (Q1-Q3) range. Horizontal bars within the boxes indicate medians. Error bars indicate the range excluding outliers. Circles indicate outliers.

Table 2

Most likely overlap of the standard ellipse for each time-bin. Shaded cells are proportion of overlap as a percent, unshaded cells report the area $\%^{2}$.

	Modern	Thule	Dorset	Pre Dorset
Modern	NA	0%	5%	0%
Thule	0.0 $\%^{2}$	NA	25%	23%
Dorset	0.1 $\%^{2}$	0.7 $\%^{2}$	NA	23%
Pre Dorset	0.0 $\%^{2}$	0.4 $\%^{2}$	0.6 $\%^{2}$	NA

a pivot toward greater consumption within the pelagic system. The difference persists after correction for the confounding factors of change to $\delta^{13}\text{C}$ values through CO_2 produced by industrialization and endogenous lipid contamination. Both the CO_2 produced by burning fossil fuels and lipids contaminating modern collagen shift the $\delta^{13}\text{C}$ values of modern samples lower and may be misinterpreted as more dramatic changes in polar bear diet or local ecological conditions without these adjustments. The differences observed here between modern and ancient samples are, therefore, conservative. The fact that a decrease in the $\delta^{13}\text{C}$ values is still apparent for the modern bears, after accounting for these other factors, suggests a real environmental shift. Reconstruction of isotopic niche overlap of the four time periods demonstrates the significance of the shift in the source of primary production. Due to the change in $\delta^{13}\text{C}$ values, the modern isotopic niche has only a 5 % likely overlap with the Dorset isotopic niche and zero likely overlap with the pre-Dorset and Thule isotopic niches, while the three archaeological isotopic niches overlap with one another 23–25%. The $\delta^{15}\text{N}$ values of the modern isotopic niche is well matched with the $\delta^{15}\text{N}$ values of the isotopic niche for the Thule time period and is within the more extensive ranges of $\delta^{15}\text{N}$ values of the pre-Dorset and Dorset.

Analogous observations of shifting primary production have been made for modern and historic belugas (*Delphinapterus leucas*) in the Canadian High Arctic, with the interpretation of greater importance of pelagic production reaching higher trophic levels more recently (Desforges et al., 2021; Outridge et al., 2005); a similar observation has been made in narwhals from northwest Greenland (Dietz et al., 2021). This interpretation is consistent with research on the quality and extent of sea ice in the Canadian Arctic Archipelago which indicates that seasonal

consolidation in Lancaster Sound is increasingly incomplete, frequently consisting of mobile pack ice in open water throughout the winter (Haas and Howell, 2015). Assessment of the timing of autumn freeze-up and summer thaw indicated that from 1979 to 2014 the number of ice-free days has increased by an average of 1.08 d/yr (Regehr et al., 2016).

The lack of diversity in sex (all male) and age (all adult) for the modern samples is a potential source of bias. Though ringed seal blubber makes up the majority of polar bear diets, there is plasticity to consume alternative diets and sex-based differences in diet have been observed (Rode et al., 2022; Boucher et al., 2019; Johnson et al., 2019; Thiemann et al., 2011; Thiemann et al., 2008). Using quantitative fatty acid signatures, Thiemann et al. (2008) studied polar bears across ten Canadian subpopulations and found that sex and age resulted in differential polar bear foraging in some but not all regions of the Arctic. In some cases, larger, older males had the most diverse diets relative to females and younger males, an observation that was supported by Johnson et al. (2019). This pattern was not observed in Lancaster Sound, Baffin Bay, and Gulf of Boothia, where there was no indication of differential foraging by age. Additionally, bears from Lancaster Sound, Baffin Bay, and Davis Strait were not characterized by any differences in prey consumption according to sex. In Western Hudson Bay there is evidence of individual specializations on alternate food sources, particularly bearded seal, especially among adult male polar bears (Thiemann et al., 2011). Significant consumption of bearded seal would result in higher $\delta^{13}\text{C}$ values and lower $\delta^{15}\text{N}$ values, relative to a diet predominated by ringed seal (Fig. 3). Females and juvenile polar bears are more likely to be stranded on land when sea ice is low and may turn to the consumption of alternate species (beluga whales, bearded seals, bowhead whales) or scavenging on lower energy tissues like muscle instead of the preferred blubber (Rode et al., 2022; Boucher et al., 2019). These alternative prey sources, consumed in significant quantities, would shift polar bear tissue $\delta^{13}\text{C}$ values higher and $\delta^{15}\text{N}$ values lower, relative to a diet that is principally composed of ringed seal blubber. It is, therefore, unlikely that the biased sex/age distribution of our modern samples is the source of the differences in $\delta^{13}\text{C}$ values between the ancient and modern populations, but we cannot rule out the possibility that sex-based differences in diet may have existed in the past for the Lancaster Sound population that do not exist in today's population. In the

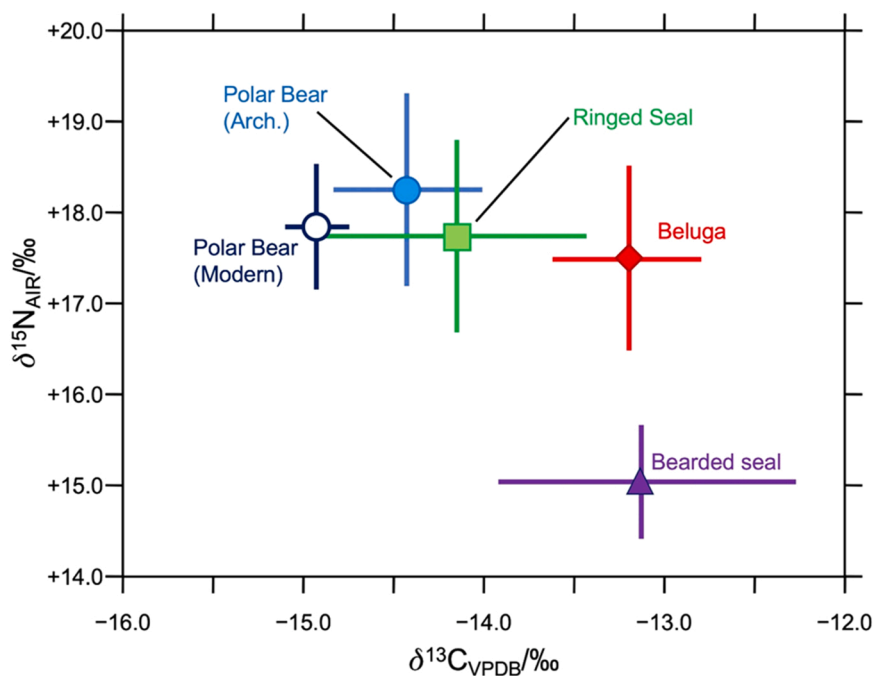


Fig. 3. Stable isotopic compositions of modern (open circles) and ancient (filled circles) polar bears relative to isotopic compositions of the bone collagen of potential ancient prey. Bearded seal isotopic compositions (filled triangle) are derived from Late Dorset individuals (Jaouen et al., 2016). Beluga isotopic compositions (filled diamond) are from 19th century individuals from Somerset Island (Szpak et al., 2020). Ringed seal isotopic compositions (filled square) are from Thule individuals from Somerset Island (Szpak et al., 2019). Modern and ancient polar bear $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values have been adjusted by -1.0 and -4 ‰, respectively, to account for the differences in bone collagen isotopic compositions between predator and prey (Bocherens and Drucker, 2003).

future, sexing of the ancient polar bear remains via ancient DNA, combined with stable isotope analysis could be used to test this hypothesis (e.g., Szpak et al., 2020).

Under a scenario of increasing pelagic resource consumption, the magnitude of a shift in polar bear bone collagen $\delta^{13}\text{C}$ should be relatively small since sympagic and pelagic primary producers often differ by only a few per mille (France et al., 1998). A more pronounced decline in $\delta^{13}\text{C}$ values observed by McKinney et al. (2013) for East Greenland polar bear adipose sampled between 1985 and 2010 suggest an increasing reliance on pelagic prey over this short period (fewer ringed seals and more harp or hooded seals in the diet). This study, however, did not account for the Suess Effect so the magnitude of change may actually be more subtle or even non-existent. The fact that the isotopic data in our study were derived from bone collagen, which remodels at a very slow rate in mammals with its isotopic composition representing dietary intake over years (Hedges et al., 2007), means that short term temporal variation is more likely to have been dampened. The subtle temporal change that we observe in $\delta^{13}\text{C}$ values likely reflects real and sustained shifts in the source of primary production for the Lancaster Sound food web.

There was no significant change in $\delta^{15}\text{N}$ values over time indicating consistency in the trophic position of the bears through the Late Holocene and into the modern era. This is significant because it decreases the probability that polar bear $\delta^{13}\text{C}$ values have declined due to a change in prey taxonomic composition. On the basis of quantitative fatty acid signature analysis, ringed seal, bearded seal, and beluga whale were interpreted to be the most important prey for Lancaster Sound polar bears (Thiemann et al., 2008). Relative to ringed seals, beluga whales in this region have comparable $\delta^{15}\text{N}$ values but higher $\delta^{13}\text{C}$ values (Szpak et al., 2019, 2020) while bearded seals have higher $\delta^{13}\text{C}$ values and lower $\delta^{15}\text{N}$ values relative to ringed seals (Jaouen et al., 2016). Neither species has the requisite lower $\delta^{13}\text{C}$ values relative to ringed seals to explain the decline in polar bear $\delta^{13}\text{C}$ values in recent years (Fig. 3). Moreover, the stability in polar bear $\delta^{15}\text{N}$ values across time is inconsistent with any appreciable variation in the importance of bearded seal in the diet since this would result in stronger temporal variation. The most likely explanation is a downward shift in the $\delta^{13}\text{C}$ values throughout the food web caused by changes at the level of the abundance of sympagic and pelagic primary producers (Mueter et al., 2021;

Johnson et al., 2019). While we do not have modern ringed seal $\delta^{13}\text{C}$ data to speak directly to this hypothesis, Outridge et al. (2009) analyzed the $\delta^{13}\text{C}$ values in ringed seal teeth from the 1300 s, late 1800 s, and 2002 and found the 2002 ringed seal $\delta^{13}\text{C}$ values were ~ 2 ‰ lower than those from either the 1300s or late 1800s. Outridge et al. (2005) also found much lower (~ 4 ‰) $\delta^{13}\text{C}$ values in beluga teeth from Somerset Island in the 1990s relative to the late 1800s. Neither of these studies extracted lipids from the samples, nor did they correct for the Suess Effect so the actual magnitude of changes in $\delta^{13}\text{C}$ values that they observed may be very similar to those observed here for polar bears. Nevertheless, the observation of a decline in tissue $\delta^{13}\text{C}$ values for other high trophic level predators (including polar bear prey) in this environment support the hypothesis that a shift at the base of the food web is responsible for this pattern.

The studies discussed above were able to detect temporal shifts between two or three discrete points in time within the last 700 years (Outridge et al., 2005; Outridge et al., 2009). The polar bear data presented here extends this temporal framework four thousand years into the past. Notably, the modern polar bear $\delta^{13}\text{C}$ values are on average more than 0.5 ‰ lower than the ancient samples. Each of the ancient time-bins presents individuals with $\delta^{13}\text{C}$ values higher than -13 ‰ while the modern time-bin does not contain any individuals with similarly high values. This implies that, while there may have been similar shifts in polar bear diets in the past, none of these seem to be of the magnitude that has been observed today. A very important caveat, however, stems from the derivation of the ancient samples from archaeological sites, meaning they represent bears that were hunted by humans, and were not evenly distributed across time. Based on extensive radiocarbon surveys (Savelle and Dyke, 2014; Savelle and Dyke, 2009; Savelle et al., 2012), large areas of the Canadian Arctic underwent massive demographic shifts with prolonged periods of abandonment. This is an important consideration because regional abandonments, potentially driven by unusual climatic conditions, would result in an absence of archaeological sites and consequently an absence of polar bear remains available to sample through these periods. We may, therefore, be missing important periods of climatic instability that were potentially unfavorable for both polar bear and human populations. Such a scenario is not inconceivable given that both polar bears and many of the human populations in the Canadian High Arctic relied to a

great extent on ringed seals for subsistence (Darwent, 2001). Nevertheless, the stable carbon isotope compositions of Lancaster Sound polar bears from the 21st century are notably lower than any period for which we have data in the past four thousand years.

The significance of the modern shift in carbon isotopes can be illustrated by comparison within the ancient data set, between samples that precede the MWP (associated with Late Dorset archaeological sites) and samples dating to the MWP (associated with Classic Thule sites). If this past climate disruption was impactful to the food web, we would anticipate lower $\delta^{13}\text{C}$ values during the MWP relative to the period immediately preceding it. We found no significant difference in the polar bear bone collagen $\delta^{13}\text{C}$ values, suggesting relative stability in the importance of pelagic and sympagic primary production immediately before and during the MWP. Decreased sea ice cover and the ability to pursue bowhead whales (*Balaena mysticetus*) has been discussed as an important environmental driver of the expansion of the Classic Thule eastwards across the Canadian Arctic (McGhee, 1969/1970). Even if there were other non-environmental variables (e.g., demographic or social factors) wholly or partly driving the migration, other proxies for climatic conditions in the region suggest generally warmer conditions (Fisher et al., 1998; Thomas et al., 2010). Our data demonstrate that these relatively warm conditions did not result in a change in the isotopic composition of polar bear bone collagen and suggest that any changes in sea ice productivity during this time were subtle enough not to be reflected in the isotopic composition of polar bear tissues. The modern polar bear isotopic compositions are significantly lower than at any time in the past, suggesting an unusual environmental shift has taken place. The polar bear food web is derived in greater proportion from pelagic productivity now than at any past period for which an archaeological record exists in the region.

6. Conclusion

This study compared the stable carbon and nitrogen isotopic compositions of modern and ancient polar bears from the Lancaster Sound subpopulation, as a method to assess the impacts of periods of climate instability on the Arctic marine food web. We found that 1. There is no evidence of alteration of the trophic structure or source of primary production in the food web in the past 4000 years, prior to current anthropogenic warming. 2. The magnitude of impact to the Lancaster Sound food web resulting from modern climate warming is visible in the $\delta^{13}\text{C}$ values of the modern polar bear samples, indicating an increase in the importance of pelagic primary production that was not observable through the MWP.

Due to their reliance on the functional ecosystem provided by sea ice, both polar bears and their preferred prey are vulnerable to declining sea ice extent through limitations to movement, reduced accessibility to hunting opportunities and subsequent impacts on breeding success (Molnár et al., 2020; Hamilton et al., 2016). While the Lancaster Sound food web appears relatively unperturbed by past climate fluctuations, the speed and magnitude of change currently underway in the Arctic has already had demonstrable impacts to the source of production at the base of the food web. By contextualizing the modern food web relative to observations of the same region over four millennia, the data presented in this study represent a unique illustration of the effects of past and present warming on the marine food web in the Canadian Arctic Archipelago.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

All data has been made available in the Supplemental Information.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ancene.2023.100397.

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