



Variation in marine mammal sulfur stable isotope compositions ($\delta^{34}\text{S}$) is driven by sources of primary production, not trophic position

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ABSTRACT: The homogeneous isotopic composition of marine sulfate ($\delta^{34}\text{S} \cong +21\text{‰}$) leads to the expectation of an oceanic isoscape exhibiting little variation in $\delta^{34}\text{S}$ values. Nevertheless, instances of variation in $\delta^{34}\text{S}$ values have been identified in Arctic marine ecosystems that require clarification to explain the mechanisms driving unexpectedly low values. Walrus are frequently characterized by low $\delta^{34}\text{S}$ values compared to other marine mammals, but it is unclear if these values are a function of the low trophic position of walrus or of a specialized foraging niche. Here we examined the 2 potential drivers of differences in sulfur isotopes at the species level: trophic position and foraging ecology. By analysing archaeological samples of walrus, ringed seal and polar bear from archaeological sites at 3 discrete locations in the Canadian Arctic (Smith Sound, Ellesmere Island; Lancaster Sound, Devon Island; and northwest Hudson Bay), we clarified and confirmed that in collagen-to-collagen comparisons, differences in $\delta^{34}\text{S}$ values are not driven by trophic discrimination factors. Bacterial influences on the sulfur cycle, particularly symbiotic relationships between chemosynthetic bacteria and invertebrates in the benthos, may be a cause of the low $\delta^{34}\text{S}$ values in walrus and likely represent an often-overlooked contribution of primary production to the shelf food web.

KEY WORDS: $\delta^{34}\text{S}$ · Trophic discrimination · Trophic effect · Marine · Arctic · Chemosynthesis · Primary production

1. INTRODUCTION

Improved and more widely available instrumentation has led to a recent rapid increase in the analysis of stable sulfur isotopes ($\delta^{34}\text{S}$) by ecologists and archaeologists (Nehlich 2015, Raoult et al. 2024). Yet, the fundamentals that underpin variation in $\delta^{34}\text{S}$ values need greater exploration and elucidation, especially when variations are small, as is the case within marine environments (Raoult et al. 2024, Reaves et al. 2025). Here, we explore the potential of trophic discrimination or foraging ecology to drive differences in $\delta^{34}\text{S}$ values between species.

Based on isotopically homogeneous marine sulfate ($\cong \delta^{34}\text{S} + 21\text{‰}$) (Rees et al. 1978) and small discrimination against ^{34}S associated with uptake and assimilation of sulfate by phytoplankton (1–2‰) (Peterson & Fry 1987), it is predicted that consumers in marine

ecosystems will be characterized by $\delta^{34}\text{S}$ values within a narrow range, consistent with photosynthetic primary production. Marine consumers typically have tissue $\delta^{34}\text{S}$ values ranging from +15 to +20‰ (Gaston et al. 2004, Gosnell et al. 2017, Dance et al. 2018), yet specific environments, especially nearshore, benthic and seagrass habitats, are associated with lower consumer $\delta^{34}\text{S}$ values relative to consumers in pelagic habitats (Barros et al. 2010, Guiry et al. 2021a, Lamb et al. 2023). When the specific interactions between bacteria in anoxic sediments and rooted plants are not present or are not incorporated into the food web, this nearshore/offshore gradient is not observable in $\delta^{34}\text{S}$ values (Reaves et al. 2025). The expected range of $\delta^{34}\text{S}$ values (+15 to +20‰) comes from analysis of a range of tissues and aggregations of tissues from whole organisms (Table 1). Bone collagen $\delta^{34}\text{S}$ values are sometimes lower than the expected range, which may

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Table 1. Published literature examining trophic discrimination factors (TDFs) for $\delta^{34}\text{S}$

Consumer species	Consumer tissue analysed	Diet	TDF $\Delta^{34}\text{S}$ (‰)	Notes	Reference
Gypsy moth	Whole (likely pooled)	Potential primary producers	+1.4		Peterson & Howarth (1987)
Leaf hopper	Whole (likely pooled)	<i>Spartina</i>	-1.1	Researchers considered leaf hoppers to be close to the mean for <i>Spartina</i>	Peterson & Howarth (1987)
Iberian swine	Liver tissue	Acorn with shell	+0.65 to -0.35	Results differed with preparation protocol	González-Martin et al. (2001)
Iberian swine	Liver tissue	Principal components of commercial diet	-0.49 to -1.69	Results differed with preparation protocol. Entire diet not captured within these main components	González-Martin et al. (2001)
Buckeye butterfly	Whole organism	Artificial diet	+1.8 ± 0.36	In aggregate, this study found that $\Delta^{34}\text{S}$ was dependent on protein sufficiency	McCutchan et al. (2003)
		Canker-root	-0.7 ± 0.57	with mean results for high protein diets being +2.0 ± 0.65‰ and the mean for low protein diets being -0.5 ± 0.56‰	
		Plantago	+6.9 ± 1.19		
Buckeye pupae	Whole organism	Canker-root	-1.5 ± 0.32		McCutchan et al. (2003)
		Plantago	+7.3 ± 0.67		
Tent caterpillar	Whole organism	Choke cherry tree	-0.4 ± 0.02		McCutchan et al. (2003)
Tiger moth caterpillar	Whole organism (pooled)	Cottonwood tree	-3.2		McCutchan et al. (2003)
Aphids	Whole organism (pooled)	Thai dragon pepper plant	-0.5		McCutchan et al. (2003)
Rainbow trout	Muscle	Trout chow	+4.0 ± 0.09		McCutchan et al. (2003)
Brook trout	Muscle	Trout chow	+1.6 ± 0.36		McCutchan et al. (2003)
Horse	Tail hair	Plant diet (C ₃ vs. C ₄)	-1 when dietary protein is sufficient; +4 when dietary protein is potentially insufficient	This study also found that the $\Delta^{34}\text{S}$ was dependent on protein sufficiency	Richards et al. (2003)
Mouse	Whole blood	Control diet	-1.6 ± 0.3	Control diet (wheat and corn),	Arneson & MacAvoy (2005)
		Experimental diet 1	-0.9 ± 0.4	Experimental diet 1 (beet sucrose, casein, soybean oil),	
		Experimental diet 2	+0.3 ± 0.4	Experimental diet 2 (cane sucrose, fish meal, soybean oil)	
Mouse	Liver	Control diet	-2.1 ± 0.1		Arneson & MacAvoy (2005)
		Experimental diet 1	-0.9 ± 0.4		
		Experimental diet 2	+0.3 ± 0.4		
Mouse	Skeletal muscle	Control diet	-1.5 ± 0.5		Arneson & MacAvoy (2005)
		Experimental diet 1	-1.1 ± 0.4		
		Experimental diet 2	+0.1 ± 0.2		
Mouse	Heart	Control diet	-1.9 ± 0.3		Arneson & MacAvoy (2005)
		Experimental diet 1	-0.1 ± 0.2		
		Experimental diet 2	+0.6 ± 0.2		

Table continued on next page

Table 1 (continued)

Consumer species	Consumer tissue analysed	Diet	TDF $\Delta^{34}\text{S}$ (‰)	Notes	Reference
Mouse	Brain	Control diet Experimental diet 1 Experimental diet 2	-1.2 ± 0.6 -2.1 ± 0.5 +0.1 ± 0.3		Arneson & MacAvoy (2005)
Ox	Muscle	Controlled diet consisting of hay and feed concentrate	+0.6	Study found that bulk samples of animals had no TDF but isolated tissues discriminated ^{34}S differently, based on tissue metabolism	Tanz & Schmidt (2010)
Ox	Collagen (cartilage)	Controlled diet consisting of hay and feed concentrate	-1.7		Tanz & Schmidt (2010)
	Collagen (bone)	Controlled diet consisting of hay and feed concentrate	-0.5		Tanz & Schmidt (2010)
Ox	Hoof/horn keratin	Controlled diet consisting of hay and feed concentrate	+0.8 to +2.3		Tanz & Schmidt (2010)
Ox	Hair keratin	Controlled diet consisting of hay and feed concentrate	+3.3		Tanz & Schmidt (2010)
Goat (infant)	Muscle	Mother's milk	+0.2		Tanz & Schmidt (2010)
Goat (infant)	Collagen (bone)	Mother's milk	+0.7		Tanz & Schmidt (2010)
Goat (infant)	Collagen (cartilage)	Mother's milk and infant goat collagen (cartilage)	-1.8		Tanz & Schmidt (2010)
Pigs (sows, piglets, adolescent pigs)	Collagen (bone)	Controlled 20% protein diet	-1.5 ± 0.8		Tanz & Schmidt (2010)
	Muscle	Controlled 20% protein diet	-1.0 ± 0.6	Controlled feeding study analysing sows, piglets and adolescent pigs. Results were consistent across demographics. Results did not vary with protein source	Webb et al. (2017)
Pigs (sows, piglets, adolescent pigs)	Liver	Controlled 20% protein diet	-1.2 ± 0.4	Pigs were fed 1 of 5 controlled diets which varied the admixture of terrestrial and marine sources. All diets were nutritionally equivalent with a consistent 20% protein contribution. The amount of marine source in the diet did not affect the $\Delta^{34}\text{S}$	Webb et al. (2017)
Pigs (piglets)	Hair	Controlled 20% protein diet	+1.2 ± 0.3		Webb et al. (2017)
Pigs (adolescent pigs)	Faeces	Controlled 20% protein diet	+0.7 ± 0.8		Webb et al. (2017)
Pigs (sows)	Milk	Controlled 20% protein diet	-0.8 ± 1.0		Webb et al. (2017)
Fox	Collagen (bone)	Subfossil accumulation of bone from both predator and likely prey	~0	-0.54 to +0.03 which is approximately the analytical error of the study (±0.4)	Krajcarz et al. (2019)

simply relate to the amino acid composition of bone collagen compared to tissues containing other sulfur-bearing amino acids (Webb et al. 2017, Szpak & Buckley 2020).

In terms of sulfur isotopes, the analysis of isolated bone collagen is tantamount to a compound-specific analysis in that methionine is the only amino acid contributing sulfur. Tissues like hair, claw and muscle are complicated by sulfur contributions from other amino acids (cysteine, taurine) which undergo different routing and synthesis processes (Nehlich 2015). In a well-controlled study by Webb et al. (2017), bone collagen had consistently lower $\delta^{34}\text{S}$ values than tissues that contained both methionine and cysteine (e.g. hair) (Webb et al. 2017). Clearly, teasing apart the mechanisms of $\delta^{34}\text{S}$ variation is complex.

Szpak & Buckley (2020) examined archaeological samples of ringed seal *Pusa hispida* and walrus *Odobenus rosmarus* across the high Arctic from Alaska to Greenland. They observed a statistically significant difference in $\delta^{34}\text{S}$ values between the species (mean $+14.0 \pm 1.0\%$ for walruses, $+14.8 \pm 0.8\%$ for ringed seals). While the difference was small (averaging less than 1.0%), it occurred regularly at sites across the Arctic. These low $\delta^{34}\text{S}$ values and species-specific variation were interpreted by Szpak & Buckley (2020) as resulting from specialized benthic foraging by walruses. This study still prompted a mechanistic question: Do walruses often produce lower $\delta^{34}\text{S}$ values than ringed seals as a function of lower trophic position or because of their foraging specialization?

1.1. Sulfur and trophic position

Taken in aggregate, the literature describing a trophic discrimination factor (TDF) for $\delta^{34}\text{S}$ is unclear. Studies that have examined the offsets between diet and consumer tissues found $\Delta^{34}\text{S}$ ($\delta^{34}\text{S}_{\text{consumer}} - \delta^{34}\text{S}_{\text{diet}}$) being both negative and positive, depending on the tissues being compared (Table 1). A TDF around 0% for $\delta^{34}\text{S}$ values is reasonable to expect when making collagen-to-collagen comparisons between predator and prey species, which is a common analysis when examining ancient ecosystems (Bocherens & Drucker 2003, McCutchan et al. 2003, Krajcarz et al. 2019). Since methionine, the only sulfur-bearing amino acid in collagen, is essential, it should transfer from diet to consumer without fractionation (Nehlich 2015). Nevertheless, small-scale variations in $\delta^{34}\text{S}$ values, such as those observed between ringed seal and walrus, can be difficult to explain, and more investigation of possible TDFs is necessary (Raoult et al. 2019). A recent meta-

analysis of the literature dealing with sulfur isotopes (Raoult et al. 2024) suggests a small TDF of $-0.4 \pm 1.7\%$, which may be influenced by taxon as well as the $\delta^{34}\text{S}$ of the diet, particularly when the diet is principally marine. This review also noted a subtle correlation between $\Delta^{34}\text{S}$ and $\delta^{34}\text{S}$. Although the mechanism driving this relationship has not been identified, it likely stems from differences between the amino acid compositions of the diet and the tissue being analysed (Webb et al. 2017). The results of a controlled feeding study conducted by Webb et al. (2017) revealed a correlation in the offset between diet and collagen when the $\delta^{34}\text{S}$ values of the diet increased. This finding was most influenced by the diet with the greatest contribution of marine fish.

Mechanisms that influence stable nitrogen isotope ($\delta^{15}\text{N}$) and stable carbon isotope ($\delta^{13}\text{C}$) values are much better understood and we can interpret our $\delta^{34}\text{S}$ values alongside these other isotope systems to better understand why $\delta^{34}\text{S}$ values vary. For example, $\delta^{15}\text{N}$ has a well-characterized increase associated with trophic position in collagen_{prey} to collagen_{consumer} comparisons, averaging approximately $3.4\text{--}4\%$ (Post 2002, Bocherens & Drucker 2003, Krajcarz et al. 2025). Therefore, if variation in $\delta^{34}\text{S}$ values is driven by trophic position, we would expect a positive correlation between $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$ within a given study area. The baseline $\delta^{15}\text{N}$ of primary production is variable by location in the Arctic, with no clear relationship to the relative importance of sympagic vs. pelagic algae or phytoplankton (Iken et al. 2005, Pineault et al. 2013). Within a given area, pelagic phytoplankton tends to span a wider range of $\delta^{15}\text{N}$ values relative to sympagic algae but with considerable overlap between the 2 (Iken et al. 2005, Pineault et al. 2013). In addition to $\delta^{15}\text{N}$ values derived from photosynthetic primary producers, there is also occasional potential for chemosynthetic contributions around cold seeps and thermal vents which have been associated with unusually low $\delta^{15}\text{N}$ values (Levin & Michener 2002). We do not have baseline $\delta^{15}\text{N}$ values for the archaeological systems investigated in this study, which may differ from modern baselines; however, differences between species at each location are observable and species can be assessed relative to one another.

1.2. Sulfur variability in the Arctic marine environment

If a trophic level effect cannot explain interspecific differences in $\delta^{34}\text{S}$, an environmental explanation is appropriate. Environmental differences can be investi-

gated through an association with $\delta^{13}\text{C}$. Dissimilatory sulfate reduction by benthic bacteria discriminates strongly against ^{34}S , resulting in fractionations between -30 and -70% (Peterson & Fry 1987). The resulting sulfides are reoxidised through further bacterial interactions but retain a lower $\delta^{34}\text{S}$ signature. The uptake of re-oxidised sulfate (with relatively low $\delta^{34}\text{S}$ values) by benthic primary producers is incorporated at higher trophic levels (Guiry et al. 2021a,b, 2025). This type of benthic production coincides with relatively high $\delta^{13}\text{C}$ values due to thicker cellular boundary layers resulting from lower aquatic turbulence in benthic, sympagic and near-shore systems, relative to open water primary producers (Fry 1981, Hobson 1993, France 1995). Alternatively, low $\delta^{34}\text{S}$ and/or low $\delta^{13}\text{C}$ values derived from consumer tissues (e.g. muscle, soft tissue and whole organism in the case of micro-fauna) in association with specific environments around cold seeps and thermal vents have been observed in equatorial regions as well as the Arctic (Yamanaka et al. 2000, Higgs et al. 2016, Åström et al. 2022). This positive correlation results from the uptake of chemosynthetic primary production resulting from symbiotic relationships between invertebrates and bacteria, wherein the lighter isotope of both elements is preferentially incorporated and may be seen through a positive correlation between low $\delta^{34}\text{S}$ and low $\delta^{13}\text{C}$ values (Higgs et al. 2016, Åström et al. 2022).

In the investigation of $\delta^{34}\text{S}$ in the Arctic marine system, we can think of primary production as stemming from either photosynthetic producers, specifically ice algae, phytoplankton and rooted vegetation, or occasional contribution of chemosynthetic production originating through symbiotic relationships between bacteria and host bivalves around cold seeps and thermal vents. Photosynthetic producers are likely to contribute $\delta^{34}\text{S}$ values consistent with marine sulfate and thus provide corresponding values to consumers, with the exception of contribution from rooted plants (e.g. in seagrass beds or mangrove forests) which may result in lower $\delta^{34}\text{S}$ values in nearshore relative to offshore environments (Fry et al. 1982, Barros et al. 2010, Pellerin et al. 2015). The nearshore/offshore gradient corresponds with a similar effect seen in $\delta^{13}\text{C}$ values, with nearshore, benthic and sympagic production being 4–12‰ higher in $\delta^{13}\text{C}$ relative to pelagic producers (France et al. 1998, Søreide et al. 2006). While algae and phytoplankton usually have $\delta^{34}\text{S}$ values consistent with marine sulfate, rooted plants may have lower $\delta^{34}\text{S}$ values resulting from microbial activities in anoxic sediments (Fenchel & Riedl 1970, Fry et al. 1982). Bacterial reduction and reoxidation of sulfate and sulfur intermediaries have been interpreted

to impart benthic marine consumers with lower $\delta^{34}\text{S}$ values relative to more pelagic consumers in the same area (Higgs et al. 2016, Szpak & Buckley 2020). When the appropriate conditions are absent, however, this gradient is not established (Reaves et al. 2025). Food web contributions of chemosynthetic primary production should be observed through a pattern of unexpectedly low $\delta^{34}\text{S}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values relative to consumers exclusively utilising the photosynthetic food web.

1.3. Ecology of the sampled species

Polar bears *Ursus maritimus* are apex predators, typically positioned between the fourth and fifth trophic levels (Trites 2019). These bears are specialized ice-obligate hunters and partition their hunting largely to the spring, when they can forage for ringed seal mothers and pups (Laidre et al. 2008, 2022, Hamilton et al. 2017, Petherick et al. 2021). As such, polar bears typically reflect ice association and winter/early spring seasonality through their $\delta^{13}\text{C}$ values (Brown et al. 2018, Routledge et al. 2023). To a lesser extent, polar bears will hunt and may become specialist predators of bearded seals *Erignathus barbatus* and may also fall back on less preferred marine mammal prey such as beluga *Delphinapterus leucas* and opportunistic scavenging of bowhead whale *Balaena mysticetus* carcasses (Thiemann et al. 2011, Boucher et al. 2019, Rode et al. 2023).

Ringed seals are the primary prey of polar bears in much of the Canadian Arctic (Thiemann et al. 2008) and approximately occupy the fourth trophic position (Trites 2019). They forage flexibly, deriving much of their energy from small to medium-sized fish, with emphasis on polar cod *Boreogadus saida*, as well as a selection of crustaceans (amphipods, decapods and mysids) (Reeves 1998, Ross et al. 2022). Ringed seals are ice-associated during the denning period and rely on a more pelagic (open water) food web during the summer, making their resource exploitation ecologically varied (Tamelander et al. 2006, Thiemann et al. 2007, Brown et al. 2018, Kunisch et al. 2021).

Walrus are usually primary carnivores, with a trophic position of typically 3–3.5 (Trites 2019). They are highly specialized benthic feeders, and their anatomy is adapted to consuming bivalves through suction (Fay 1982). Clams are the dominant prey, with an individual walrus consuming about 6000 clams d^{-1} (Ray et al. 2006). Clams are filter feeders and will opportunistically ingest particulate organic matter (POM) from the water column but may also form symbiotic rela-

tionships with bacteria around hydrothermal vents, incorporating some chemosynthetic production (Yamanaka et al. 2000, Dubilier et al. 2008, Higgs et al. 2016).

To clarify the potential of trophic position or environmental conditions to drive differences in marine mammal bone collagen $\delta^{34}\text{S}$ values, we conducted stable isotope analysis ($\delta^{34}\text{S}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of the bone collagen of 3 species: the food web apex predator, polar bear; a mid-level (trophic level ~ 4) predator, ringed seal; and a benthic specialized bivalve consumer, walrus (trophic level ~ 3). These species are distinct in their foraging ecologies, with polar bears being sympagic specialist hunters, ringed seals being flexible, ice-associated and pelagic hunters, and walrus being specialist benthic bivalve consumers. All 3 species were sampled from archaeological assemblages at each of 3 discrete regions in the Canadian Arctic (northwest Hudson Bay, Devon Island, and Ellesmere Island) (Fig. 1). Since methionine is the only essential, sulfur-bearing amino acid contained in bone collagen (Guiry & Szpak 2020), we did not expect to find an effect of trophic position on the $\delta^{34}\text{S}$ value of the tissue. We predicted that significant differences in the $\delta^{34}\text{S}$ values of bone collagen would be driven by environmental factors reflecting distinguishable differences in the resource base of the food webs in which these species feed.

2. MATERIALS AND METHODS

Polar bears, ringed seals and walrus were deliberately chosen as representative mammalian predators with distinct trophic positions and foraging ecologies. Three study areas were selected where environmental and behavioural differences may be discernable.

New $\delta^{34}\text{S}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses ($n = 45$) in combination with some previously published walrus and ringed seal stable isotope data from Ellesmere Island (walrus $n = 8$, ringed seals $n = 9$; Szpak & Buckley 2020) are presented for ancient bone collagen collected from 4 archaeological sites in northwest Hudson Bay (KkJg-1), Devon Island on Lancaster Sound (RbJr-1, 4, RbJu-1), and Ellesmere Island, associated with Smith Sound (SfFk-4) (Fig. 1). The 2 sites on Devon Island are located approximately 15 km from one another. All samples date to the Late Holocene, spanning 3800 to 325 cal BP. Included in the study are 62 individual samples from 3 marine mammal species: polar bear, $n = 28$; ringed seal, $n = 17$; and walrus, $n = 17$. To ensure that the same individual was not sampled twice, for each discrete context (e.g. house feature at a site), samples were selected from the same non-repeating skeletal element, typically cortical tissue from long bones.

Bone chunks, weighing ~ 200 mg, were cut from each element using an NSK dental drill equipped

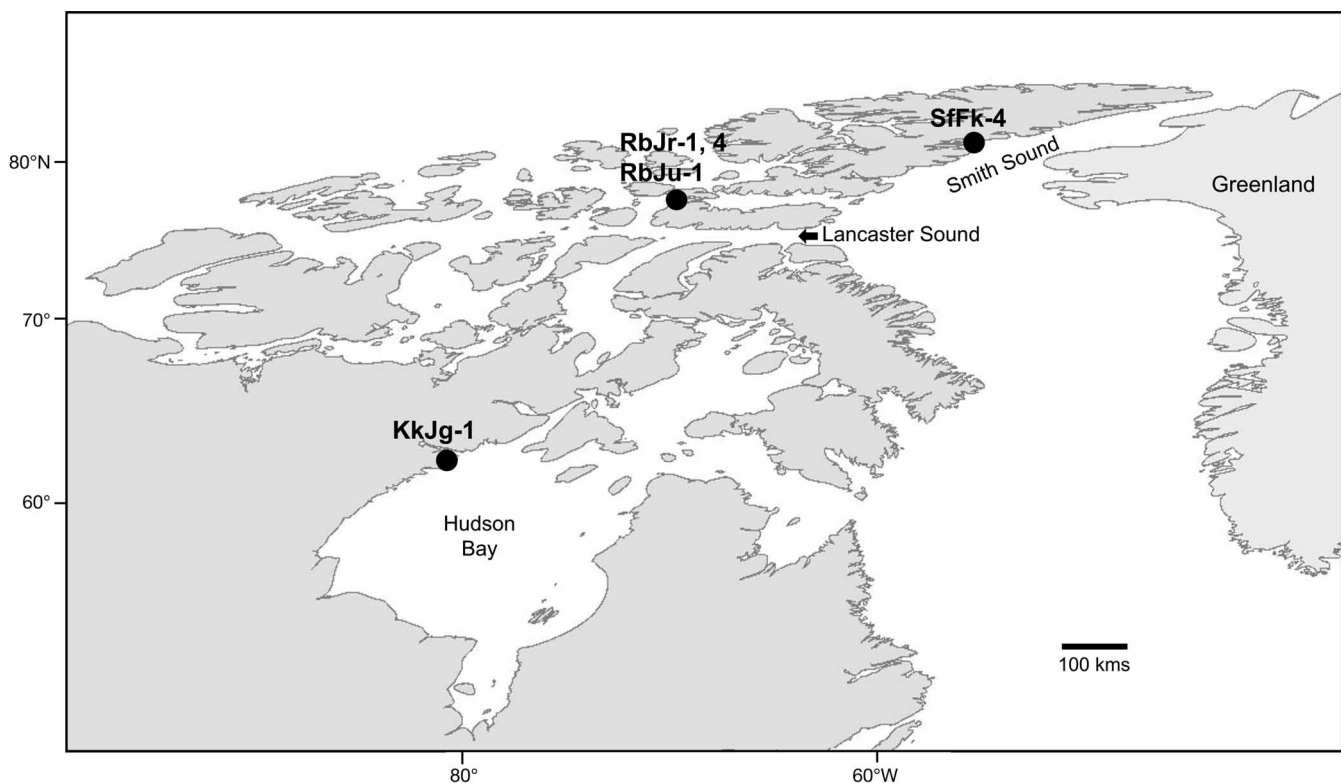


Fig. 1. Study region showing the locations of the sites from which samples were collected (adapted from mapchart.net)

with a diamond-tipped cutting wheel. Samples were demineralized under constant motion with an orbital shaker, in 0.5 M HCl at room temperature until they were soft (like hard cheese) indicating the mineral component was removed. After the samples were demineralized, they were rinsed 3 times with Type I water (resistivity >18.2 M Ω cm). Samples exhibiting dark coloration were treated with 0.1 M NaOH for 30 min to remove humic contaminants, consistent with methods tested by Wilson & Szpak (2022). Samples were rinsed twice with Type I water and then placed in 3.5 ml of 0.01 M HCl in a dry bath at 75°C for 36 h, to solubilize the collagen. Solubilized collagen was transferred to pre-weighed 4 ml glass vials and freeze-dried.

2.1. Elemental and isotopic analysis

Collagen samples (0.45–0.55 mg) were weighed into tin capsules and their carbon and nitrogen isotopic and elemental compositions ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %C, %N) were determined 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, Peterborough, Ontario, Canada. Samples were calibrated to Vienna PeeDee belemnite (VPDB) for carbon and air for nitrogen, using standards USGS40, USGS63 and USGS66 (values in Table S1 in Supplement 1 at www.int-res.com/articles/suppl/meps15102_suppl.pdf). Quality assurance was monitored through in-house reference materials SRM-1 (caribou bone collagen), SRM-14 (polar bear bone collagen), SRM-26 (commercial marine collagen), SRM-27 (commercial marine collagen) and SRM-28 (alanine) (values in Table S1). The majority of the samples were analysed at least twice to assess homogeneity. Analytical uncertainty was calculated based on Szpak et al. (2017) to be $\pm 0.18\%$ for $\delta^{13}\text{C}$ and $\pm 0.30\%$ for $\delta^{15}\text{N}$.

Collagen samples weighing approximately 8 mg were combined with approximately 10 mg of vanadium pentoxide in tin capsules and their $\delta^{34}\text{S}$ and %S values were determined with a Europa ANCA-SL/20-20 elemental analyser/isotope-ratio mass spectrometer at Iso Analytical in Cheshire, UK. Calibration relative to Vienna Canyon Diablo troilite (VCDT) was conducted with standards IA-R061 (Ba_2SO_4) and IA-R025 (Ba_2SO_4) (values in Table S1). Quality assurance was monitored by interspersing the reference materials IAEA-SO-5 (Ba_2SO_4), IA-R068 (soy protein) and IA-R069 (tuna protein) (values in Table S1). Approximately 10% of

samples were analysed in duplicate. Analytical uncertainty for $\delta^{34}\text{S}$ based on best practices suggested by Szpak et al. (2017) was determined to be $\pm 0.3\%$. Based on $\text{C:N}_{(\text{atomic})}$ (DeNiro 1985, Guiry & Szpak 2021), %C, %N, (Ambrose 1990), $\text{C:S}_{(\text{atomic})}$ and $\text{N:S}_{(\text{atomic})}$ (Nehlich & Richards 2009) quality control criteria, the collagen was determined to have isotopic compositions that were not modified in the burial environment.

2.2. Statistical analysis

Statistical analyses were conducted using PAST 4.07b (Hammer 2020). Normality of data in comparisons and correlations was assessed through a Shapiro-Wilk test. Assessment of equal variances in ANOVA comparisons was conducted through Levene's test for homogeneity of variance.

In order to assess the importance of the variables in question (trophic ecology and foraging environment) to $\delta^{34}\text{S}$ values of the entire data set, differences in isotopic compositions among species and among locations were assessed using 2-way, random effects ANOVA (2-way ANOVA) followed by Tukey's HSD test with significance set at 95% confidence. In order to assess differences between species in each region, normality was assessed through Shapiro-Wilk and Levene's tests for homogeneity of variance. Differences were assessed between species in each region using ANOVA followed by Tukey's pairwise comparison when variances were equal and Kruskal-Wallis followed by Dunn's post hoc test when variances were unequal or data were not normally distributed. Within each region, the interspecific isotopic offsets ($\Delta^{34}\text{S}$, $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$) were calculated using the mean $\delta^{34}\text{S}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of each species. Regionally specific correlations between $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ values as well as between $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$ values were assessed through Pearson's r when data were normally distributed or Spearman's r_s when data were not normally distributed.

3. RESULTS

Data used in ANOVA comparisons and correlations were assessed through a Shapiro-Wilk test to be normally distributed with the exceptions of the nitrogen data for polar bears in northwest Hudson Bay ($W = 0.73$, $p = 0.01$), Smith Sound nitrogen data ($W = 0.88$, $p = 0.004$), Lancaster Sound nitrogen data ($W = 0.86$, $p = 0.009$) and Lancaster Sound sulfur data ($W = 0.89$,

$p = 0.02$). Equal variances for ANOVA comparisons were conducted through Levene's test for homogeneity of variance. Unequal variances were found in carbon data in northwest Hudson Bay as well as sulfur and nitrogen data in Smith Sound. Instances where data were not normally distributed or variances were unequal led to assessment through non-parametric tests (Kruskal-Wallis followed by Dunn's post hoc as analogous to ANOVA followed by Tukey's pairwise comparison and Spearman's r_s as analogous to Pearson's r for correlations). Species and location data (summarized in Table 2 and fully reported in Supplement 2 at www.int-res.com/articles/suppl/meps15102_supp2.xlsx) were assessed for differences in $\delta^{34}\text{S}$ values through 2-way ANOVA (summarized in Table S2 and Fig. S1 in Supplement 1), which indicated that this data set was not characterized by statistically significant differences in $\delta^{34}\text{S}$ values driven by species identification (species $F_{2,53} = 2.21$, $p = 0.12$) or location (location $F_{2,53} = 2.22$, $p = 0.12$); however, there was a significant difference driven by the interaction between the 2 variables (interaction $F_{4,53} = 5.08$, $p = 0.002$) (significant interactions reported in Table 3).

In terms of interactions between species and location, a few notable comparisons emerge. In the Smith Sound population, walrus had significantly lower $\delta^{34}\text{S}$ values than polar bears ($p < 0.001$) and ringed seals ($p < 0.001$) (Fig. 2). Walrus in the Smith Sound population had significantly lower $\delta^{34}\text{S}$ values than walrus in the Lancaster Sound population ($p < 0.001$). The Lancaster Sound ringed seals had significantly higher $\delta^{34}\text{S}$ values relative to northwest Hudson Bay ringed seals ($p = 0.03$). Conversely, it is also interesting to note that several comparisons provided p -values rounding to 1, indicating that the comparators are statistically indistinguishable. It is therefore extremely likely that the $\delta^{34}\text{S}$ values in these comparisons are the product of a food web exploiting a single homogeneous sulfur pool with no TDF associated with species trophic position. Specifically, all species in northwest Hudson Bay had $\delta^{34}\text{S}$ values that were statistically indistinguishable, as were polar bears and walrus in

Table 2. Mean (\pm SD) isotopic compositions for each of the 3 species in each of the 3 study areas. VCDT: Vienna Canyon Diablo troilite; VPDB: Vienna PeeDee belemnite

Location	Species	N	$\delta^{34}\text{S}_{\text{VCDT}}$ (‰)	$\delta^{13}\text{C}_{\text{VPDB}}$ (‰)	$\delta^{15}\text{N}_{\text{Air}}$ (‰)
NW Hudson Bay	Polar bear	6	$+15.2 \pm 0.4$	-14.16 ± 0.35	$+19.06 \pm 1.50$
	Ringed seal	4	$+15.2 \pm 0.6$	-14.13 ± 0.98	$+17.92 \pm 1.54$
	Walrus	4	$+15.3 \pm 0.2$	-14.41 ± 0.57	$+13.14 \pm 0.61$
Lancaster Sound	Polar bear	11	$+15.8 \pm 0.3$	-13.32 ± 0.94	$+22.62 \pm 1.07$
	Ringed seal	4	$+16.1 \pm 0.2$	-13.86 ± 0.35	$+16.52 \pm 1.10$
	Walrus	5	$+15.7 \pm 0.6$	-14.59 ± 0.62	$+12.70 \pm 1.21$
Smith Sound	Polar bear	11	$+15.6 \pm 0.2$	-13.61 ± 0.43	$+21.41 \pm 0.93$
	Ringed seal	9	$+15.7 \pm 0.6$	-14.14 ± 0.20	$+16.00 \pm 1.27$
	Walrus	8	$+14.6 \pm 0.4$	-14.89 ± 0.34	$+10.07 \pm 0.44$

Table 3. Comparisons of interactions of $\delta^{34}\text{S}$ values between species and location produced by 2-way ANOVA followed by Tukey's post hoc comparison. Significant differences ($p < 0.05$) are in **bold**

Species:Location interaction	Comparator Species:Location interaction	p
Polar Bear–NW Hudson Bay	Polar Bear–Lancaster Sound	0.11
Polar Bear–NW Hudson Bay	Polar Bear–Smith Sound	0.40
Polar Bear–NW Hudson Bay	Ringed Seal–NW Hudson Bay	1.00
Polar Bear–NW Hudson Bay	Walrus–NW Hudson Bay	1.00
Polar Bear–Lancaster Sound	Polar Bear–Smith Sound	0.98
Polar Bear–Lancaster Sound	Ringed Seal–Lancaster Sound	0.81
Polar Bear–Lancaster Sound	Walrus–Lancaster Sound	1.00
Polar Bear–Smith Sound	Ringed Seal–Smith Sound	1.00
Polar Bear–Smith Sound	Walrus–Smith Sound	<0.001
Ringed Seal–NW Hudson Bay	Ringed Seal–Lancaster Sound	0.03
Ringed Seal–NW Hudson Bay	Ringed Seal–Smith Sound	0.30
Ringed Seal–NW Hudson Bay	Walrus–NW Hudson Bay	1.00
Ringed Seal–Lancaster Sound	Ringed Seal–Smith Sound	0.62
Ringed Seal–Lancaster Sound	Walrus–Lancaster Sound	0.80
Ringed Seal–Smith Sound	Walrus–Smith Sound	<0.001
Walrus–NW Hudson Bay	Walrus–Lancaster Sound	0.72
Walrus–NW Hudson Bay	Walrus–Smith Sound	0.07
Walrus–Lancaster Sound	Walrus–Smith Sound	<0.001

the Lancaster Sound population and polar bears and ringed seals in the Smith Sound population.

The analysis of the entire data set uncovered some regionally specific isotopic characterizations for $\delta^{34}\text{S}$. We therefore examined correlations between $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ by location, using $\delta^{13}\text{C}$ as a proxy indicator for environmental differences and $\delta^{15}\text{N}$ as an indicator of trophic position. In the northwest Hudson Bay region, there was a statistically significant correlation between $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ values (Pearson's $r = -0.64$, $p = 0.01$), which was driven by the very strong correlation observed between the $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ values of the ringed seals (Pearson's $r = -0.99$, $p = 0.009$); however, the sample size was too small to make a meaningful interpretation. There was

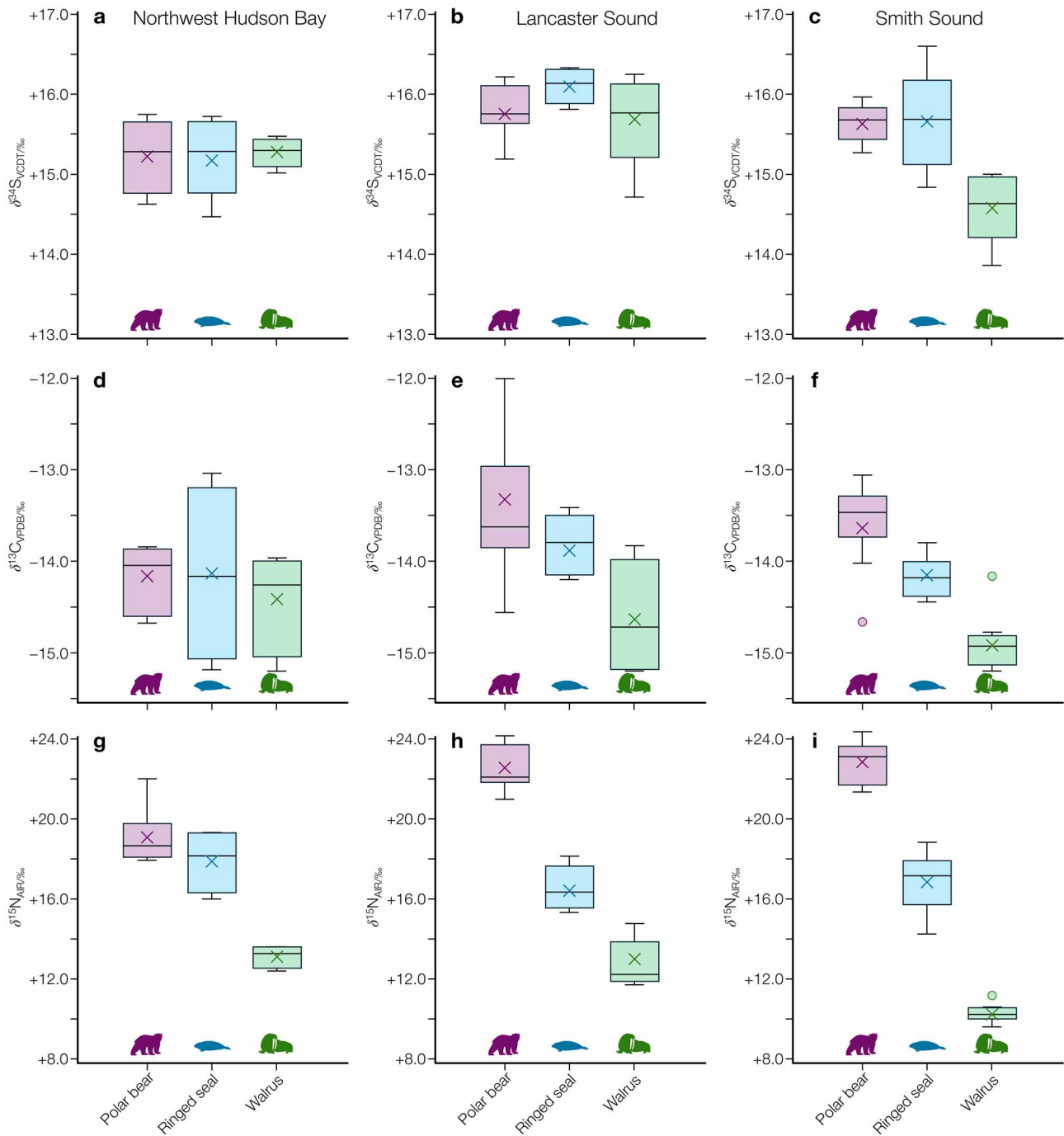


Fig. 2. Bone collagen (a–c) $\delta^{34}\text{S}$, (d–f) $\delta^{13}\text{C}$ and (g–i) $\delta^{15}\text{N}$ values of the 3 species in the northwest Hudson Bay, Lancaster Sound and Smith Sound regions, respectively. Boxes indicate the interquartile (Q1–Q3) range. Horizontal bars within the boxes indicate medians, 'x' indicates the mean. Error bars indicate the range. Circles are outliers

no significant correlation between $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$ in northwest Hudson Bay (Pearson's $r = -0.20$, $p = 0.49$) (Fig. 3). There was no correlation between $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ values (Spearman's $r_s = 0.05$, $p = 0.82$) or $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$ values (Spearman's $r_s = -0.03$, $p = 0.88$) across the species in the Lancaster Sound region.

In the Smith Sound region, there was a significant correlation between $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ values (Pearson's $r = 0.59$, $p < 0.001$), which was driven by the low $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ values of the walrus (Fig. 3). There was also a correlation between $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$ values across all 3 studied species from Smith Sound (Spearman's

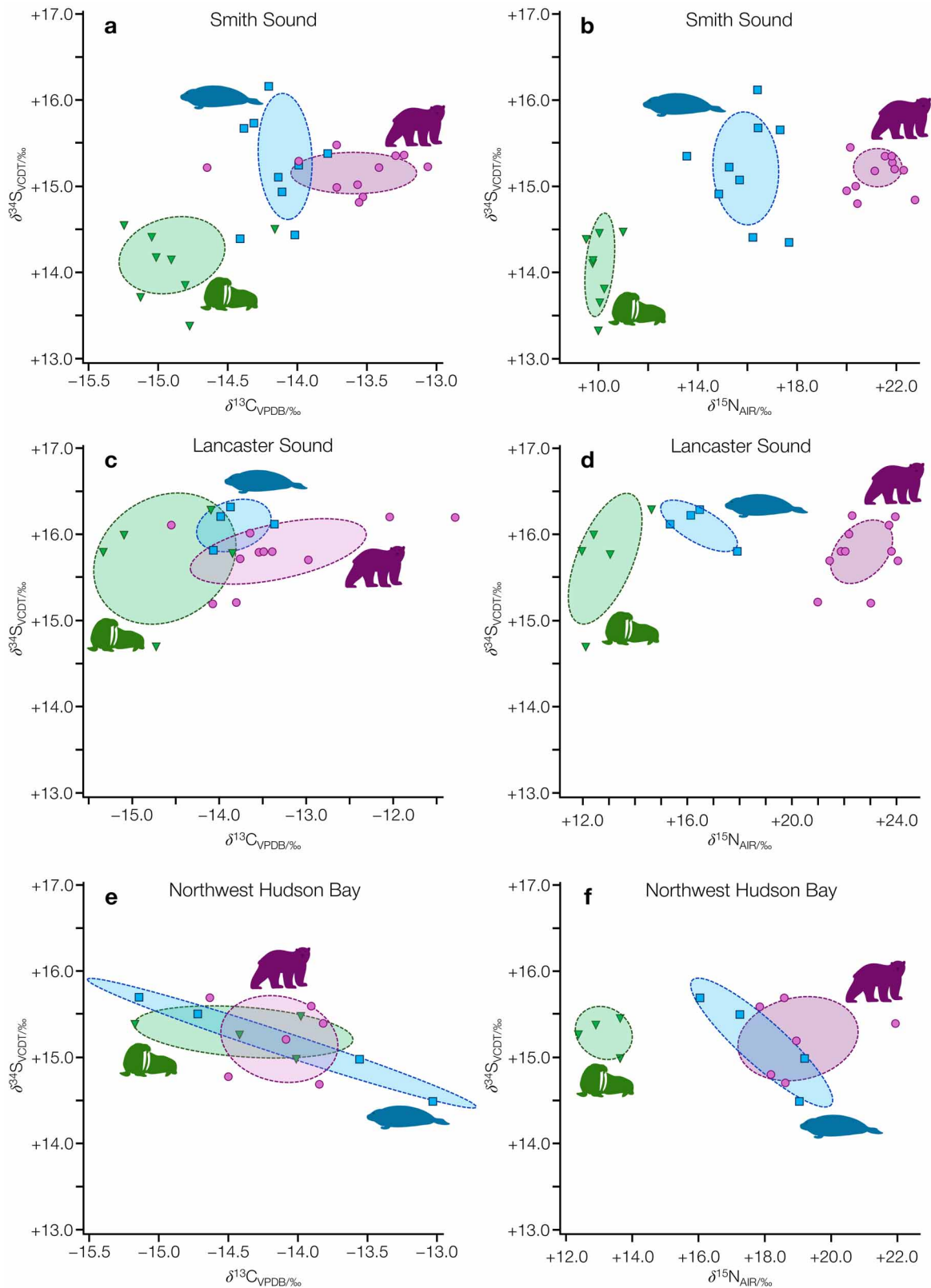


Fig. 3. Bivariate plots depicting the isotopic compositions of the 3 species analysed in this study from Smith Sound: (a) $\delta^{13}\text{C}$ vs. $\delta^{34}\text{S}$ and (b) $\delta^{15}\text{N}$ vs. $\delta^{34}\text{S}$; Lancaster Sound: (c) $\delta^{13}\text{C}$ vs. $\delta^{34}\text{S}$ and (d) $\delta^{15}\text{N}$ vs. $\delta^{34}\text{S}$; northwest Hudson Bay: (e) $\delta^{13}\text{C}$ vs. $\delta^{34}\text{S}$ and (f) $\delta^{15}\text{N}$ vs. $\delta^{34}\text{S}$. Shaded ellipses represent standard ellipse areas (Jackson et al. 2011)

Table 4. Comparisons of isotopic offsets between species, based on location and isotope system. Values are the difference between the mean for each species pair. Differences that provided significant p-values are in **bold**. VCDT: Vienna Canyon Diablo troilite; VPDB: Vienna PeeDee belemnite

Isotope system	Species compared	Lancaster Sound	Smith Sound	NW Hudson Bay
$\Delta^{34}\text{S}_{\text{VCDT}}$ (‰)	Polar bear–ringed seal	0.3 ($F_{2,17} = 1.36$, $p = 0.35$)	0.1 ($F_{2,25} = 19.43$, $p = 0.85$)	0.1 ($F_{2,11} = 0.08$, $p = 0.97$)
	Ringed seal–walrus	0.4 ($F_{2,17} = 1.36$, $p = 0.30$)	1.1 ($F_{2,25} = 19.43$, $p < 0.001$)	0.1 ($F_{2,11} = 0.08$, $p = 0.92$)
	Polar bear–walrus	0.1 ($F_{2,17} = 1.36$, $p = 0.93$)	1.1 ($F_{2,25} = 19.43$, $p < 0.001$)	0.1 ($F_{2,11} = 0.08$, $p = 0.97$)
$\Delta^{15}\text{N}_{\text{Air}}$ (‰)	Polar bear–ringed seal	6.10 ($F_{2,17} = 149.5$, $p < 0.001$)	5.41 ($F_{2,25} = 326.7$, $p = 0.007$)	1.14 ($F_{2,11} = 25.08$, $p = 0.76$)
	Ringed seal–walrus	3.82 ($F_{2,17} = 149.5$, $p < 0.001$)	5.93 ($F_{2,25} = 326.7$, $p = 0.03$)	4.77 ($F_{2,11} = 25.08$, $p < 0.001$)
	Polar bear–walrus	9.92 ($F_{2,17} = 149.5$, $p < 0.001$)	11.34 ($F_{2,25} = 326.7$, $p < 0.001$)	5.91 ($F_{2,11} = 25.08$, $p = 0.007$)
$\Delta^{13}\text{C}_{\text{VPDB}}$ (‰)	Polar bear–ringed seal	0.54 ($F_{2,17} = 4.425$, $p = 0.49$)	0.53 ($F_{2,25} = 32.5$, $p = 0.005$)	0.03 ($F_{2,11} = 0.25$, $p = 0.94$)
	Ringed seal–walrus	0.73 ($F_{2,17} = 4.425$, $p = 0.38$)	0.75 ($F_{2,25} = 32.5$, $p < 0.001$)	0.28 ($F_{2,11} = 0.25$, $p = 0.50$)
	Polar bear–walrus	1.27 ($F_{2,17} = 4.425$, $p = 0.02$)	1.28 ($F_{2,25} = 32.5$, $p < 0.001$)	0.25 ($F_{2,11} = 0.25$, $p = 0.42$)

rs = 0.55, $p = 0.002$). This correlation was also driven by the low $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values of walrus.

Analysis of significant differences in the isotopic offsets between species, within regions (Table 4), indicates a significant difference between walrus and ringed seals and between walrus and polar bears in the Smith Sound region ($\Delta^{34}\text{S}$ 1.1‰), as well as significant differences in $\Delta^{13}\text{C}$ and greater than expected differences in $\Delta^{15}\text{N}$ (Bocherens & Drucker 2003)

4. DISCUSSION

4.1. $\delta^{34}\text{S}$ and trophic position

In this study, 3 species with distinct habitat use and trophic positions, recovered from 3 discrete locations, were examined. A 2-way ANOVA of the data set indicated that a relationship could not be established between $\delta^{34}\text{S}$ values and species identity, nor was there a relationship between $\delta^{34}\text{S}$ values and location; however, there was a significant interaction between the 2 variables, affecting $\delta^{34}\text{S}$ values. This interaction was driven by unusually low $\delta^{34}\text{S}$ values in walrus in Smith Sound, likely indicating an environmental variable affecting the $\delta^{34}\text{S}$ of the benthos in this region. This clarifies some of the ambiguity that surrounds the issue of TDF in mammalian collagen-to-collagen comparisons for $\delta^{34}\text{S}$ and supports previous research that suggested the TDF for $\delta^{34}\text{S}$ is $\sim 0\%$ (Krajcarz et al. 2019). We emphasize that this study is not a diet-to-tissue comparison where there may be a mismatch between the amino acid composition of the consumed versus the analysed tissues, leading to observation of trophic level offsets (Tanz & Schmidt 2010, Webb et al. 2017). Here, we conducted a tissue-to-tissue comparison of bone collagen from subjects occupying different trophic positions, in keeping with the

study design of Bocherens & Drucker (2003) in their foundational study establishing TDF for stable isotopes of carbon and nitrogen. In our collagen–collagen assessments, we see the $\Delta^{34}\text{S}$ between species, within regions (Table 4), meaningfully exceeding analytical uncertainty in the Smith Sound walrus comparisons. Our findings point to the environmental availability of an alternate sulfur source for the Smith Sound walrus population, rather than a trophic level effect.

At the regional level, we found that $\delta^{34}\text{S}$ values among polar bears, ringed seals and walrus in the northwest Hudson Bay and the Lancaster Sound regions were statistically indistinguishable. This indicates regional homogeneity in the $\delta^{34}\text{S}$ values throughout the local food web, without observable fractionation associated with foraging habitat or trophic position. Consistent with this observation, there were no correlations between $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$ values across the species in either of these regions, again indicating that trophic position is not a driver of variation in collagen $\delta^{34}\text{S}$ values. For Smith Sound, the $\delta^{34}\text{S}$ values of the polar bears and ringed seals were statistically indistinguishable, while the walrus in this region had significantly lower $\delta^{34}\text{S}$ values relative to the other 2 species examined. With the lone exception of walrus in the Smith Sound region, the $\delta^{34}\text{S}$ values are consistent across species at different trophic levels within their respective environments. In conjunction with the lack of a correlation between $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$ values, our findings indicate that trophic position is not an important cause of variation in bone collagen $\delta^{34}\text{S}$ values for these marine mammals. The differentiation of walrus from polar bears and ringed seals, only in the Smith Sound group, is likely a function of the $\delta^{34}\text{S}$ value of the sulfur source in the benthos of this region relative to the $\delta^{34}\text{S}$ values of the open-water and sympagic foraging environments

exploited by ringed seals and polar bears. This is investigated in greater depth below.

In answer to our primary research question, we find that the offset for $\delta^{34}\text{S}$ in collagen-to-collagen comparisons is close to 0‰. In the northwest Hudson Bay and Lancaster Sound regions, small differences are in the range of analytical error. Smith Sound is the only location in this study to demonstrate a difference in $\delta^{34}\text{S}$ with significantly lower values in the walrus, which can be explained by exploitation of an alternative resource pool, as will be explained below. Given that methionine is an essential amino acid and is the only sulfur-bearing amino acid in isolated collagen (Eastoe 1955), it is reasonable to expect negligible discrimination against ^{34}S or ^{32}S between diet and consumer. Importantly, we do not extend this recommendation to tissues other than collagen, as additional investigation of those tissues is still necessary. Tissues containing both cysteine and methionine (e.g. hair, nail/claw), appear to present $\delta^{34}\text{S}$ values higher than collagen within the same animal (Tanz & Schmidt 2010, Webb et al. 2017). Fractionations resulting from *in vivo* synthesis of cysteine from methionine and any TDF that may occur between tissues have yet to be determined. Muscle, connective tissue and nervous system tissues also contain sulfur-bearing compounds such as taurine, chondroitin sulfate and sulfo-lipids, but the variation in isotopic compositions for these compounds within organisms is presently unknown. In addition to elucidating the $\delta^{34}\text{S}$ values of these tissues as potential analytical substrates, characterization of the $\delta^{34}\text{S}$ values of these tissues is important to assess the impact they may have as contaminants of purified analytes such as the collagen extracted from bone.

An added finding that is worthy of note while discussing trophic position is the observation that in the northwest Hudson Bay region, there is no statistically significant difference in $\delta^{15}\text{N}$ values between polar bears and ringed seals. While it is common across the Arctic for polar bears to predominantly consume ringed seals, this observation indicates that in northwest Hudson Bay, the 2 species feed at approximately the same trophic level. This does not affect our interpretation with regard to sulfur trophic level effects but is of regional interest. Other ecological studies have noted that polar bears in northwest Hudson Bay frequently prey on and may individually specialize on bearded seals and perhaps walrus (Thiemann et al. 2008, 2011, Sciullo et al. 2017), both of which occupy a lower trophic position than ringed seals (Jaouen et al. 2016, Trites 2019). Using the previously mentioned TDF of 3.4‰ per trophic level and a difference in

means of 5.92‰ between polar bears and walrus in our data for this region, it is unlikely that walrus was an important contributor to the local polar bear diet. Nevertheless, we find it likely that alternate prey, especially bearded seal, was a significant contributor to polar bear diet in northwest Hudson Bay in the past, implying that this has been a consistent foraging behaviour in this region across hundreds of years at least.

4.2. $\delta^{34}\text{S}$ and environment

To reiterate, a 2-way ANOVA did not reveal a correlation between $\delta^{34}\text{S}$ values and location; however, an association was uncovered in the interaction between species and location. The interaction was established through differences related to a slightly higher $\delta^{34}\text{S}$ baseline for the Lancaster Sound samples relative to the other 2 locations, as well as the striking difference in $\delta^{34}\text{S}$ values in the Smith Sound walrus population relative to sympatric polar bears and ringed seals. Apart from the Smith Sound walrus population, the 3 studied species reflect a relatively homogeneous, regional $\delta^{34}\text{S}$ signal. Walrus are benthic specialists and therefore have the potential to exploit a food web that is sourced differently from polar bears and ringed seals. We suggest that while the 3 species in northwest Hudson Bay and Lancaster Sound consume a purely photosynthetically derived diet with uniform $\delta^{34}\text{S}$ values, in the Smith Sound populations, the walrus stand apart and fit a pattern suggesting a contribution of chemosynthetically derived resources.

When marine mammal $\delta^{34}\text{S}$ values have been observed to deviate from expectations (i.e. unusually low), the animals are clearly associated with the exploitation of isotopically distinguishable environments (i.e. benthos, seagrass) (Szapak & Buckley 2020, Guiry et al. 2021a,b, 2025). To understand the $\delta^{34}\text{S}$ values of the Smith Sound walrus, we suggest the potential relevance of contributions of both photosynthetic and chemosynthetic primary producers. The chemosynthetic source could originate from the consumption of bivalves associated with hydrothermal seeps or vents. Invertebrate uptake of chemosynthetic primary production has been documented at cold seeps around Svalbard, the Laptev Sea north of Siberia, and in spiny lobsters at thermal vents in the Caribbean Sea (Higgs et al. 2016, Åström et al. 2022, Kokarev et al. 2023). Notably, cold seeps are prevalent in circumpolar shelf environments and given the stark seasonality of photosynthetic processes in the Arctic, it has been proposed that chemosynthetic pri-

primary production provides an underappreciated resource in the food web (Åström et al. 2022).

Walrus feed in the benthos, consuming on the order of 6000 clams per feeding session (Ray et al. 2006). In certain environments, particularly in the immediate vicinity of cold seeps and thermal vents, bivalves may develop a symbiotic relationship with sulfur-oxidising bacteria which use reduced sulfur compounds from the vents/seeps as electron donors to fix inorganic carbon to organic carbon taken up by the host (Yamanaka et al. 2000, Dubilier et al. 2008, Higgs et al. 2016). There is a preferential uptake of the lighter isotope of both sulfur and carbon in this process, meaning that a consistent and significant contribution of chemosynthetic primary production should produce relatively low $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ values (Higgs et al. 2016, Åström et al. 2022). The $\delta^{13}\text{C}$ values of the walrus in Smith Sound are significantly lower than those of ringed seals and polar bears (-0.75‰ and -1.28‰ , respectively). These differences are within the range of expected $0\text{--}1\text{‰}$ for $\delta^{13}\text{C}$ values with each trophic position (Bocherens & Drucker 2003); however, benthic specialist walrus should have increased $\delta^{13}\text{C}$ due to environmental factors like low aquatic turbulence causing thickening of cellular boundary layers, which should more than compensate for the TDF of $\delta^{13}\text{C}$ (Fry 1981, Hobson 1993, France 1995, Tamelander et al. 2006). The $\delta^{13}\text{C}$ values of the Smith Sound walrus are therefore lower than expected, relative to polar bears and ringed seals. Additionally, the presence of chemosynthetic symbionts has been observed to coincide with low $\delta^{15}\text{N}$ values derived from local nitrogen fixation (Levin & Michener 2002). Relatively low $\delta^{15}\text{N}$ values are also observed in the Smith Sound walrus, having bone collagen that is, on average 5.93‰ below ringed seals and 11.34‰ below polar bears.

In northern regions, the absence of daylight prevents photosynthetic primary producers from consistently assimilating sulfur. The interruption in photosynthesis likely has consequences for the food web. Chemosynthetic consumers are much more common at vent environments of >200 m depths because photosynthetically derived organic matter is not sufficiently delivered to, nor does sunlight reach, these depths to permit microphytobenthic growth (Tarasov et al. 2005, Gattuso et al. 2006). A study by Åström et al. (2022) found that photosynthetic resources dominate the food web of most benthic consumers. We found this to be the case in our Lancaster Sound and northwest Hudson Bay walrus populations. The clams that dominate the walrus' diets are filter feeders taking in available POM, which is likely exclusively photo-

synthetically derived. Even when chemosynthetic resources are available, photosynthetic resources tend to dominate, likely because the assimilation of photosynthetic carbon is less energetically expensive than the incorporation of chemosynthetically-derived resources and also avoids the toxic burden associated with sulfide ingestion (Åström et al. 2022). Nevertheless, the same study by Åström et al. (2022) found numerous occurrences of invertebrates around shallow cold-seeps with $\delta^{13}\text{C}$ values reflecting a chemosynthetic contribution, sometimes estimated to be as high as 50%. In the Arctic it has also been observed that chemosynthetic contributions are made to food webs at relatively shallow depths. Off the northern coast of Russia, in seep environments in the Laptev Sea, where the depth averages around 50 m, several species including bivalves were observed to include a contribution of chemosynthetic resources, as indicated by low $\delta^{13}\text{C}$ values (Kokarev et al. 2023). Because there is a seasonal interruption in the benthic/pelagic coupling of photosynthetic organic matter in circumpolar environments, there is a potential advantage to the adaptation of chemosynthetic symbiotic relationships for some macrofauna around shallow vents and seeps. The systematic presence and absence of photosynthetic assimilation of sulfur likely makes other sources of sulfur from the benthos more quantitatively important and isotopically detectable. These include sulfur derived from benthic redox sediments and sulfur taken up through chemosynthetic symbiotic relationships between bacteria and bivalves in specific environments. The region between Ellesmere Island and western Greenland is in proximity to the West Greenland Rift and hydrocarbon seeps have been documented in conjunction with potential sites for oil and gas exploration off western Greenland (Christiansen et al. 2020). This region is likely a productive chemosynthetic environment that walrus could frequent with some regularity, consistent with the pattern of relatively low $\delta^{34}\text{S}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values observed in the Smith Sound walrus.

Traditionally, there has been negligible emphasis on the importance of benthic primary production in the Arctic, with the understanding that the marine food web is supplied by phytoplankton and ice-algal blooms (Welch et al. 1992, Leu et al. 2015). In shallow coastal areas in the Arctic, a significant contribution of benthic microalgae has been identified on a local scale (Gattuso et al. 2006, Glud et al. 2009) but these contributions are of negligible importance on an oceanic scale (Leu et al. 2015), suggesting a more important contribution in the Arctic than is assumed globally. A robust assessment of benthic contributions

to the food web would result from a combined isotopic approach that includes analysis of $\delta^{34}\text{S}$, recognising the distinctly low values originating in reducing sediments (Fry & Sherr 1989). The contribution of chemosynthetic primary production to Arctic marine food webs is rarely considered and relatively understudied. The pattern observed in our results suggests that chemosynthetic primary production likely provides a more important contribution to some Arctic food webs than has been realized to date. Further studies, targeting primary consumers in relation with Arctic seeps and vents, should employ a combined stable isotope approach including $\delta^{34}\text{S}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values as a mechanism to quantify the admixture of chemosynthetic/photosynthetic resource uptake.

In the Lancaster Sound population, walrus had significantly lower $\delta^{13}\text{C}$ values than polar bears (-1.27‰ , Table 4), though, as discussed above, this difference does not exceed the expected TDF for $\delta^{13}\text{C}$ of an increase of $0\text{--}1\text{‰}$ with each trophic position (Bocherens & Drucker 2003), assuming that walrus and polar bears approximately occupy the third and fifth trophic positions, respectively. Nevertheless, because walrus are specialist benthic consumers, we would predict them to present higher $\delta^{13}\text{C}$ values than other marine mammal species, more than compensating for the TDF (Fry 1981, Hobson 1993, France 1995, Tamelander et al. 2006). The $\delta^{34}\text{S}$ values are homogeneous across the 3 species from Lancaster Sound. The $\delta^{13}\text{C}$ values of open-water resources are $\geq 4\text{‰}$ lower than organic matter from sympagic or benthic resources (France 1995, Sørense et al. 2006). A pattern of lower-than-anticipated $\delta^{13}\text{C}$ values in a benthic consumer, in conjunction with $\delta^{34}\text{S}$ values that match the expectations for marine consumers suggest that tight benthic/pelagic coupling is delivering photosynthetically derived POM to suspension feeders in sufficient amounts to negate the need to find alternatives to photosynthetic primary production (Tamelander et al. 2006). In this case, relying on $\delta^{13}\text{C}$ values alone could lead to the interpretation of the contribution from chemosynthetic primary production, while the inclusion of $\delta^{34}\text{S}$ values might change the interpretation. Studies that have relied on $\delta^{13}\text{C}$ values alone to interpret chemosynthetic food web contributions have been useful (e.g. Åström et al. 2022, Kokarev et al. 2023); however, the addition of $\delta^{34}\text{S}$ values disambiguates the sources at the base of the food web and increases confidence in interpretations that may be based on subtle but significant isotopic differences (Raoult et al. 2024).

The unique isotopic pattern exhibited by the walrus in Smith Sound is, to our knowledge, the first

time that a contribution of chemosynthetic primary production has been suggested as a cause of isotopic variation in a predatory marine mammal. The increase in open-water and ice-free days in the Arctic, coupled with changes in circulation patterns and increased nutrient flow has resulted in dramatic increases (as much as 57%) in net photosynthetic primary production across much of the Arctic between 1998 and 2018 (Arrigo & van Dijken 2015, Lewis et al. 2020). This is a dramatic change in the ecosystem that is likely to have unpredictable effects across the water column. Increased productivity should improve delivery of photosynthetic organic matter to suspension feeders around shallow Arctic seeps, potentially negating the need for symbiotic relationships that result in assimilation of chemosynthetic organic matter. We suggest future research examine the possibility that local food web admixture of chemosynthetic/photosynthetic resources could be altered by warming Arctic conditions as this could provide an additional means to monitor the impacts of climate change on food webs. Furthermore, museum collections and additional archaeological excavations can provide samples dating back centuries or even millennia (e.g. Clark et al. 2022) allowing potential reconstruction of the admixture of primary sources over thousands of years. In regions where benthic bivalves assimilate chemosynthetically derived carbon and sulfur, it may be possible to use the combination of $\delta^{34}\text{S}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, obtained from bivalve specialist consumers, to trace the importance of the contribution of chemosynthetic production to the local food web. This would, however, require the assessment of baseline changes related to the natural succession of hydrothermal vents. Moving forward, as the Arctic warms, we can expect a continued increase in the amount of photosynthetic productivity, facilitated by thinner ice and more ice-free days. We predict that this may be demonstrated in an increase in circumpolar marine $\delta^{34}\text{S}$ values over time, in environments where chemosynthetic production has been observable.

4.3. Conclusions

We analysed the bone collagen of polar bears, ringed seals and walrus from archaeological sites in northwest Hudson Bay, Lancaster Sound (Devon Island), and Smith Sound (Ellesmere Island). Variation in $\delta^{34}\text{S}$ values was not driven by trophic position, suggesting that when making collagen-to-collagen comparisons, an offset between predator and prey of $\sim 0\text{‰}$ is appropriate. Circumpolar regions may pre-

sent unique benthic $\delta^{34}\text{S}$ values relative to regions at lower latitudes due to the seasonal absence of photosynthesis. Contributions of chemosynthetic primary production, as observed in the walrus food web in Smith Sound, may be a more significant contributor to Arctic production than has been understood previously. The seasonal absence of photosynthetic assimilation of sulfur makes the incorporation of chemosynthetic resources adaptive.

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