

ILLUMINATING THE HISTORICAL ECOLOGY OF POLAR BEARS (*URSUS
MARITIMUS*) FROM THE LANCASTER SOUND SUBPOPULATION,
NUNAVUT, USING STABLE ISOTOPE ANALYSIS

by

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A thesis submitted to the Faculty of Graduate and Postdoctoral Affairs
in partial fulfillment of the requirements for the degree of

Master of Science

in

Biology

Carleton University
Ottawa, Ontario
July 7th, 2021

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ABSTRACT

Polar bears (*Ursus maritimus*) are among the Arctic species that are most threatened by climate change. However, little is known about the ecology of polar bears over extended temporal intervals (>50 years). The goal of my thesis is to determine whether historic polar bears from the Lancaster Sound subpopulation underwent ecological shifts in response to a changing Arctic climate throughout the 20th century (1950s–1970s) using stable isotope analysis. Historic polar bears did not undergo significant dietary shifts, remaining apex predators. The consistent reliance on seals and whales as their primary prey indicates continued access to optimal hunting conditions (i.e., sea ice). There is evidence that suggests environmental changes occurred from 1950–1970. This thesis offers novel insights into the historical ecology of polar bears, and provides a long-term isotopic baseline for polar bear ecology that will enable future studies to assess ongoing ecological changes of modern polar bears.

ACKNOWLEDGEMENTS

First and foremost, I would like to acknowledge that Carleton University is located on the traditional unceded territory of the Algonquin Anishnaabeg People, and that the specimens used in this project were collected from the traditional territory of the Inuit. As settlers, we must make the collective commitment to make the promise and the challenge of Truth and Reconciliation real in our communities, to honour the Treaty Rights of all Indigenous Peoples, and bring justice for murdered and missing Indigenous women and girls across the country.

I would like to thank my thesis supervisors, Dr. Danielle Fraser and Dr. Root Gorelick. I can say with absolute certainty that this thesis would not exist in its current form without their guidance and endless support. I would especially like to thank Dr. Fraser for reading every single draft of my thesis without fail, and always offering helpful comments and suggestions. I would not be the scientist I am today without Dr. Fraser's influence – she is one of the most talented and passionate scientists I have met, and I am extremely grateful to have her as my mentor. I thank the members of my defense committee, Dr. Clément Bataille, Dr. Joseph Bennett, and Dr. Rachel Buxton, for their support throughout my degree and helpful commentary on my thesis.

I would also like to thank the following people for their contributions to this study: Dr. Kamal Khidas for providing access to the Zoology Collections and polar bear specimens at the Canadian Museum of Nature; Roger D. Bull for granting access to the Laboratory of Molecular Biodiversity; Dr. Seth Newsome and Dr. Nicu-Viorel Atudorei for conducting stable isotope analyses at the University of New Mexico; Marisa Gilbert for her aid in coordinating sample shipment and ordering laboratory materials; and Dr.

Catherine Cullingham for chairing my defense. I thank my friends, family, and labmates for providing me with never-ending kindness, love, and support, throughout the completion of my degree and beyond. I especially thank my friends Jade Atkins and Brigid Christison, for encouraging me to pursue my dream of becoming a scientist, and inspiring me every day with their own passions for science. I also thank my pets, Luna and Kiki, for their moral support and comforting snuggles. Finally, I thank my partner, Tom Dudgeon, without whom I would not have been able to successfully complete this thesis. Thank you for always believing in me, even when I didn't believe in myself.

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CHAPTER 1: INTRODUCTION

Human-driven climate change on a global scale is one of the greatest threats to modern ecosystems (King, 2004; Thomas et al., 2004; Harley et al., 2006; Hoegh-Guldberg and Bruno, 2010; Wassmann et al., 2011; Pecl et al., 2017; Díaz et al., 2019; He and Silliman, 2019). The Canadian Arctic is among those ecosystems that are experiencing the most drastic changes as a result of climate change (Derocher et al., 2013). The global mean surface temperature has risen by 0.6-0.8°C throughout the 20th century, while surface temperatures in the Arctic have increased by at least twice as much over the same time period (Glig et al., 2012; McKinney et al., 2013; Hoberg et al., 2017). Such northern amplification of warming has resulted in significant negative effects, including an alarming loss of sea ice of nearly 50% over 50 years (Copland et al., 2007; Stirling and Derocher, 2012; Gormezano and Rockwell, 2013; Rode et al., 2015; White et al., 2015). The amount of sea ice cover is predicted to further decrease, along with increases in the duration of the ice-free period during the summer months (Tivy et al., 2011; Hamilton et al., 2014), with some projections suggesting a completely ice-free summer in the Arctic by the year 2040 (Overland and Wang, 2013). Sea ice is a critical component of the Arctic, providing habitat, breeding grounds, and prey access for a multitude of species (Laidre et al., 2008; Post et al., 2013; Laidre et al., 2015). Sea ice loss may therefore have devastating impacts on animals that rely heavily upon sea ice for survival.

Polar bears (*Ursus maritimus* Phipps, 1774) are among the animals that could experience dire consequences as a result of the cumulative effects of sea ice loss

(Derocher et al., 2004; Amstrup et al., 2010; Regehr et al., 2016; Laidre et al., 2018a; Laidre et al., 2020a). They are the apex predators of the Arctic, and require access to summer sea ice in order to hunt their primary prey of ringed seals (*Pusa hispida* Schreber, 1775) and bearded seals (*Erignathus barbatus* Gill, 1866; Stirling and McEwan, 1975; Stirling and Archibald, 1977; Stirling and Derocher, 2012; Rogers et al., 2015). Seals and other marine mammals are crucial components of the polar bear diet as they are rich in blubber (Stirling and McEwan, 1975; Stirling and Archibald, 1977). Blubber is important for providing energy, contributing to endogenous fat stores, and building muscle (Cherry et al., 2011). Polar bears rely on seal kills to build up their fat stores to survive the winter and the ice-free period during the summer (Derocher and Stirling, 1990; Derocher et al., 2004; Gormezano and Rockwell, 2013). Seal kills are especially important for pregnant females that need to maximize their fat stores before moving into their maternity dens, where they will give birth to cubs that they need to nurse and care for (Stirling and Derocher, 2012). As sea ice decreases, polar bears may have increasingly reduced access to seals and other marine mammals, which will likely result in increased mortality rates of both males and females (Molnár et al., 2010; Stirling and Derocher, 2012; Rode et al., 2015; Hamilton and Derocher, 2019).

Several studies have investigated how modern polar bears may be altering their diets in order to adapt to the loss of summer sea ice in the Arctic. Polar bears in western Hudson Bay have been documented consuming terrestrial prey such as caribou (*Rangifer tarandus* Linnaeus, 1758), as well as snow geese (*Chen caerulescens caerulescens* Linnaeus, 1758) and their eggs (Gormezano and Rockwell, 2013; Rode et al., 2015). In Alaska, bears are known to scavenge bowhead whale (*Balaena mysticetus* Linnaeus,

1758) carcasses left over from subsistence harvests (Rogers et al., 2015; Laidre et al., 2018c; Whiteman et al., 2018; Petherick et al., 2021). Although these studies have addressed how recent polar bears may be shifting their diets in response to the changing environmental conditions of the Arctic, none have directly and quantitatively addressed changes in polar bear ecology over extended time periods (>50 years).

1.1. Thesis objectives

The goal of my thesis is to determine whether polar bears may have undergone ecological shifts as a response to the changing Arctic climate from the 1950s–1970s by using stable isotope analysis. The objectives of my thesis are as follows: 1) to analyze the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ compositions from bulk bone collagen of polar bears as a proxy for potential ecological shifts from the 1950s–1970s; 2) to assess whether any observed isotopic shifts are driven primarily by either environmental changes (i.e., climate, baseline shifts) or by changes in dietary components, and; 3) to analyze any changes in the relative contributions of various sources of potential prey to the diet of polar bears by using Bayesian stable isotope mixing models, and determine whether the primary prey species consumed by polar bears has changed over time.

1.2. Background

1.2.1. Polar bear ecology

Polar bears are the apex predators throughout the circumpolar Arctic, including the Canadian Arctic (Stirling and Derocher, 2012; van Beest et al., 2016). They are non-territorial (van Beest et al., 2016), solitary animals with the largest home range size of

any bear species (Owen et al., 2015). Polar bears exhibit site fidelity, returning each summer to the same geographic region (Sahanatien et al., 2015; Auger-Méthé et al., 2016). As polar bears are coastal hunters, they spend a significant amount of time on drifting pack ice and on annual land-fast sea ice as a platform that provides them with access to prey (Iverson et al., 2014; Auger-Méthé et al., 2016). The polar bear diet consists of marine mammals, primarily ringed seals and bearded seals (Stirling and McEwan, 1975; Stirling and Archibald, 1977; Stirling and Derocher 2012; Rogers et al., 2015), which they hunt from small openings in the ice (Tartu et al., 2016; Whiteman et al., 2018). In certain geographic ranges, they will hunt other available prey such as harp seals (*Pagophilus groenlandicus* Erxleben, 1777; Galicia et al., 2016) and beluga whales (*Delphinapterus leucas* Pallas, 1776; Freeman, 1973; Heyland and Hay, 1976; Smith and Sjare, 1990; Rugh and Shelden, 1993; Thiemann et al., 2008; Galicia et al., 2016). Alaskan bears are also known to scavenge bowhead whale carcasses (Rogers et al., 2015; Whiteman et al., 2018; Petherick et al., 2021). All of these marine mammals have large reservoirs of fat (blubber), which is the primary component of the diets of polar bears, supplemented with muscle, skin, and visceral tissues (Cherry et al., 2011). Blubber is an important food resource for polar bears as it allows them to rapidly build the fat stores they need in order to survive their winter hibernation (Stirling and McEwan, 1975).

Sexual dimorphism is exhibited in polar bears, with males being about twice as large in mass and roughly one-sixth larger in body length compared to females (Derocher et al., 2010; Biddlecomb et al., 2019). Males reach sexual maturity around three years old, though they typically do not breed until several years later, while females are sexually mature and begin mating at approximately four to six years old (Biddlecomb et

al., 2019). As solitary animals, polar bears only seek out members of the opposite sex during breeding season (Owen et al., 2015), after which they return to their respective home ranges. Pregnant females den during the winter months (November to April; Ramsay and Stirling, 1988) and give birth to one to two cubs, which they will nurse without access to food, producing milk exclusively from their fat stores (Stirling and McEwan, 1975; Molnár et al., 2010; Whiteman et al., 2018). Cubs will stay with their mothers for approximately two and a half years, during which time they rely heavily on their mothers for food and protection as they grow and learn how to hunt and defend themselves (Derocher et al., 2010; Whiteman et al., 2018; Biddlecomb et al., 2019). This puts additional energetic stress on female bears compared to males, and has resulted in many females with cubs resorting to feeding on alternative prey sources (i.e. avian prey), while females without cubs are able to more consistently feed on seals and other marine animals of higher trophic levels (Tartu et al., 2016).

1.2.2. Threats to polar bear survival

There are many threats to polar bear survival that have increased over the past decades. The majority of these threats come from human-driven climate change, which is altering their natural habitat (Hunter et al., 2010; Molnár et al., 2010; Stirling and Derocher, 2012; Derocher et al., 2013; Whiteman et al., 2018). The primary threat to polar bear populations is the alarming loss of Arctic sea ice. From 1960 to 2008, Canadian Arctic ecosystems have experienced declines in summer sea ice cover ranging from 2.9% to 11.3%, driven primarily by significant increases in early summer surface air temperature (Tivy et al., 2011). This has in turn extended the ice-free period during the

summer months in several regions, with earlier spring ice breakup and later winter ice freeze-up, which has had negative consequences for many polar bear subpopulations resulting in some instances of starvation (Gormezano and Rockwell, 2013; Sahanatien et al., 2015). Early spring is a critical period for polar bears because they have the highest seal hunting success rate, as moulting adults and newborn pups are at their most vulnerable (Stirling and Archibald, 1977; Pilfold et al., 2015).

As a result of continually earlier spring sea ice breakup, polar bears are losing access to this valuable prey resource, which has led to decreased reproductive rates, increased cub mortality, and overall population declines in many subpopulations (Regehr et al., 2007; Molnár et al., 2010; Regehr et al., 2010; Stirling and Derocher, 2012; Rode et al., 2015; Whiteman et al., 2018; Hamilton et al., 2019). Polar bears move to the shores and fast throughout the duration of the summer ice-free period following the spring sea ice breakup (Amstrup et al., 2010; Regehr et al., 2016), where they rely on their fat reserves for survival (and lactation, in the cases of females with cubs; Rode et al., 2015). Lengthening of the ice-free period driven by warming temperatures has already negatively impacted polar bear survival in many subpopulations (Molnár et al., 2020). Future business-as-usual climate projections predict that Arctic sea ice cover will continue to decline in every region inhabited by polar bears, and may experience two to five months of ice-free conditions, which are unprecedented (Hamilton et al., 2014). Based on these climatic predictions, polar bears could be faced with near-certain extinction as early as the end of the 21st century (Hunter et al., 2010; Hamilton et al., 2014; Molnár et al., 2020).

There are many other factors that are contributing to the threats that polar bears face. As a result of habitat loss, many polar bears are moving further inland to seek terrestrial sources of food to supplement their diets (Derocher et al., 1993; Derocher et al., 2000; Dyck and Romberg 2007; Rockwell and Gormezano, 2009; Iles et al., 2013; Iverson et al., 2013; Rode et al., 2015). This has led to increased human-polar bears encounters and conflicts (Stirling and Derocher, 2012) as polar bears venture into populated areas in search of food, where they often must be killed (Dyck, 2006). Polar bears moving in-land also face competition for limited terrestrial food resources from Arctic brown bears (*Ursus arctos* Linnaeus, 1758), as brown bears are known to displace polar bears from feeding locations on land (Miller et al., 2015; Rode et al., 2015).

The culmination of harsh climatic effects and habitat loss has resulted in decreases of polar bear reproductive rates, which has already caused many subpopulations to decline in numbers (Regehr et al., 2007; Regehr et al., 2010; Lunn et al., 2016; Obbard et al., 2018). It is indeed possible that, with the high greenhouse gas emissions, rapidly declining rates of reproduction and cub survival, and seemingly inflexible diets of polar bears, that the species could be faced with extinction by the end of the 21st century (Hunter et al., 2010; Hamilton et al., 2014; Molnár et al., 2020). As a result of the factors discussed above, polar bears are listed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as “Special Concern” (COSEWIC, 2008) as of 2008, and by the International Union for Conservation of Nature (IUCN) as ‘Vulnerable’ as of 2020, with no Action-Recovery plan in place to aid in monitoring efforts (Wiig et al., 2015; IUCN, 2020). Polar bear numbers are still alarmingly low, and they will require careful and extensive monitoring programs to help ensure their survival.

As apex predators, polar bears exert an important top-down control on their ecosystems, and are indicators of the stability of their ecosystem (Hunter et al., 2010). If polar bear numbers fall too low and populations are unable to recover, the risk of extirpation and/or extinction will become alarmingly high (Molnár et al., 2010; Molnár et al., 2020), and it is unknown how the loss of polar bears will affect Arctic ecosystems.

Currently, knowledge of historically important food resources for polar bears is limited, although the Inuit possess a great deal of traditional ecological knowledge (TEK) on this subject (Voorhees et al., 2014; Laforest et al., 2018). TEK is extremely important for understanding the ecology of polar bears. It is a collective body of knowledge that is derived from both personal and collective observations of the natural world that is constantly evolving and being passed from generation to generation (Huntington et al., 2004; Dowsley, 2005; Freeman and Wenzel, 2005; Berkes, 2009), thus encapsulating an extended timescale. The majority of TEK that has been published in scientific papers concerns the status and sizes of polar bear subpopulations (e.g., Tyrrell, 2006; Dowsley, 2007; Henri et al., 2010; Peacock et al., 2010; Maraj, 2011; Voorhees et al., 2014; York et al., 2015; York et al., 2016; Laidre et al., 2018b). However, some have included TEK relating to the effects of climate change on polar bears (Dowsley, 2005; Dowsley, 2007; Laforest et al., 2018; Laidre et al., 2018), harvest management strategies (Freeman and Wenzel, 2005; Dowsley and Wenzel, 2008; Pearce et al., 2015; Laidre et al., 2018), changes in polar bear foraging behaviours (Voorhees et al., 2014; Laforest et al., 2018), and their distributions (Urquhart and Schweinsburg, 1984). Unfortunately, to my knowledge, there are currently no published resources that contain TEK that is specifically from Inuit communities situated in the Lancaster Sound. At present, this

study will be conducted without the addition of TEK, however, future committed efforts will be made to include TEK that would complement the findings of the present study.

It is possible that polar bears could be more adaptable than previous studies have suggested, and may be able to cope with climate change by shifting their diets to incorporate either terrestrial food sources, or by making greater use of carcasses left by Inuit hunters. If historical polar bears were able to successfully take advantage of these food sources, it is possible that modern and future bears will be able to expand this component of their dietary niche, which may allow them to survive even as climate change alters their habitat. New, additional insights could therefore allow conservation programs to prioritize protecting resources that are key for polar bear survival, in an effort to give them the best chance to persist as climate change continues to alter Arctic ecosystems.

1.2.3. Lancaster Sound

The Lancaster Sound region forms the eastern area of the Northwest Passage in Nunavut (Welch et al., 1992; Cosens and Dueck, 1993), encompassing several major islands (including Cornwallis Island, Devon Island, Bathurst Island, and the southwestern tip of Ellesmere Isle) and the surrounding waters (Figure 1A). Lancaster Sound is bordered by Devon Island to the north, and the northern shore of Baffin Island to the south (Duck et al., 1977; Figure 1B). The terrain of Lancaster Sound is generally higher and more rugged than nearby regions (Agnew et al., 2008), with well-defined drainage patterns, though some northern regions (i.e., Borden Peninsula) are characterized as a rolling coastal plain (Schweinsburg et al., 1982). Large ice caps cover the majority of the

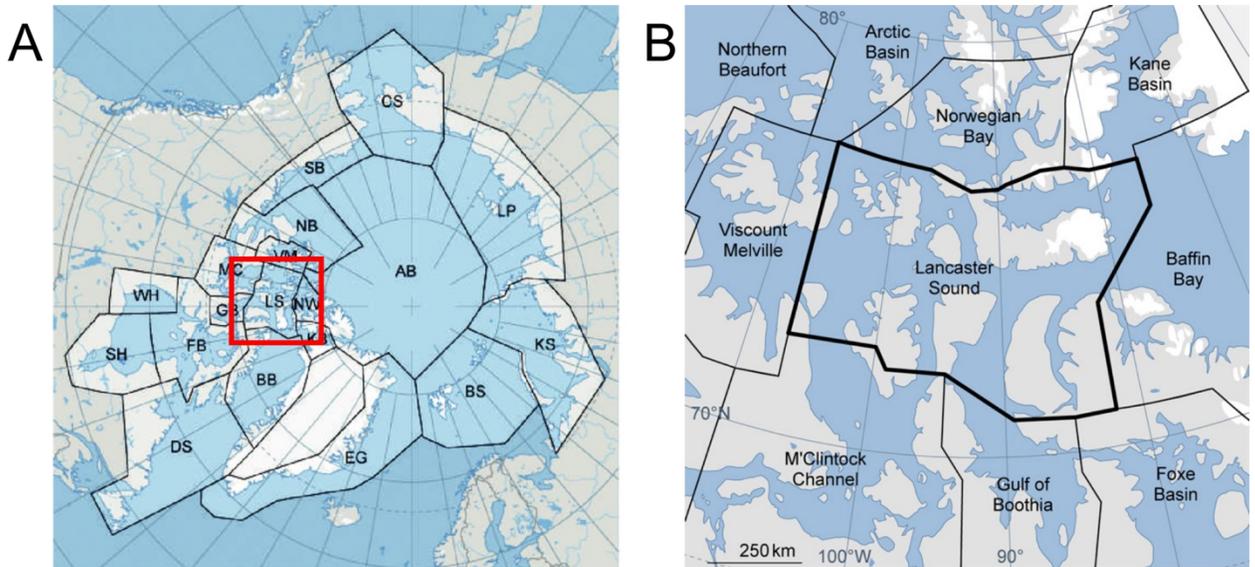


Figure 1. A) The region of Lancaster Sound polar bear subpopulation relative to other polar bear subpopulations (modified from Obbard et al., 2010), and B) a close up view of the Lancaster Sound enclosed in the red box (from IUCN/SSC Polar Bear Specialist Group, 2019).

eastern areas of Devon and Bylot islands, while small ice caps are present on the Borden and Brodeur peninsulas (Schweinsburg et al., 1982). The entire defined Lancaster Sound region consists of approximately 98 000 km² of sea surface area in total (Welch et al., 1992), with Arctic water entering through Barrow Strait in the west and from McDougall Sound and Wellington Channel in the north (Leblond, 1980; Welch et al., 1992). The water then moves eastwards along the south coast of Lancaster Sound, leaving the region and entering the Baffin Bay area (Marmen et al., 2017). Within Lancaster Sound, there are four predominantly Inuit communities: Pond Inlet, Arctic Bay, Nanisivik, and Resolute Bay (Welch et al., 1992). There is also an out-post camp at Creswell Bay on Somerset Island, which consists of a sole extended family (Welch et al., 1992). Lancaster Sound was proposed as a federal Marine Protected Area in the Arctic in December 2009 (Peacock et al., 2011), and could achieve this protected status soon (Archambault et al., 2016), though as of yet it has not been designated as such.

Freeze-up of water typically begins halfway through September, when temperatures rapidly fall, in the western bays and channels of the region and proceeds seaward (Duck, 1977; Welch et al., 1992), and ends between February and early March due to high currents that prevent rapid ice consolidation (Gorman, 1988; Hamilton et al., 2013). There is often an abundance of ice keels and ridges because of strong currents and frequent early winter storms (Welch et al., 1992). In north Baffin Bay, the North Water polynya extends into Lancaster Sound as a flaw lead (a waterway opening between the fast ice and the pack ice) with annually varying dimensions and amounts of ice-free water (Welch et al., 1992; Marmen et al., 2017). The degree of final ice consolidation changes depending on the year (Marmen et al., 2017), and may leave a flaw lead as far east as

Resolute Bay, or the ice could become fast as far west as Bylot Island (Welch et al., 1992); usually, the pack ice that covers Lancaster Sound remains fairly open throughout the winter (Schweinsburg et al., 1982), and is unconsolidated downstream from the Barrow Strait due to the formation of an ice bridge (Agnew et al., 2008).

In the spring, ice begins to break away sequentially starting in the east, and breakup begins to occur at Resolute Bay between the months of June and July (Duck, 1977; Schweinsburg et al., 1982; Welch et al., 1992; Hamilton et al., 2013; Marmen et al., 2017). As the ice loosens throughout Lancaster Sound, the flaw lead along the coast of Devon Island widens towards the open waters located southeast of Cornwallis Island (Schweinsburg et al., 1982). Around midway through August, Lancaster Sound and the majority of the bordering Baffin Island inlets are ice-free, although ice remains for longer periods of time in deep bays in the areas (Schweinsburg et al., 1982). Throughout the summer months, icebergs drift about in Lancaster Sound (Duck, 1977; Schweinsburg et al., 1982). Historically, there is no point in time where the region is completely ice-free (Welch et al., 1992), although the extent of sea ice has fluctuated over time (Prinsenbergh and Hamilton, 2005), most notably in the 1950s and 1970s (Sou and Flato, 2009). The state of constant ice presence could no longer be the case in future decades as climate change progressively alters the environment. Indeed, the extent sea ice cover has declined in Lancaster Sound (and throughout the entire Canadian Arctic Archipelago; Kinnard et al., 2008; Polyak et al., 2010), and while the loss of sea ice is so far less pronounced in this region compared to those of lower latitudes, it is an ongoing issue that is likely to escalate as climate trends continue as predicted (Sou and Flato, 2009).

The Lancaster Sound region has a high rate of primary productivity relative to other areas of the Canadian Arctic (Welch et al., 1992), supporting a large population of zooplankton during the summer months (Longhurst et al., 1984; Sameoto et al., 1986). The zooplankton are a vital food source that support several populations of seabirds (Marmen et al., 2017) and marine mammals in the region (Mallory and Fontaine, 2004). The central and western areas of Lancaster Sound are home to high densities of ringed seals and polar bears (Schweinsburg et al., 1982; Kingsley et al., 1985; Welch et al., 1992). The polar bears that reside in Lancaster Sound are part of the designated Lancaster Sound subpopulation, one of 19 recognized subpopulations by the IUCN (Obbard et al., 2010). These subpopulations are not distinct evolutionary entities (Jensen et al., 2020), and all present-day polar bears belong to a single evolutionary significant unit (Paetkau et al., 1999). Although genetic diversity is similar across all polar bear subpopulations (Paetkau et al., 1999), there does appear to be some underlying genetic structures that allow bears in adjacent subpopulations to be distinguished from one another (Jensen et al., 2020). As such, the population of polar bears that reside in Lancaster Sound is recognized as distinct and separate from the adjoining subpopulations of Viscount Melville Sound, M'Clintock Channel, Gulf of Boothia, Baffin Bay, and Norwegian Bay (Figure 1; Taylor et al., 2001; Obbard et al., 2010; Jensen et al., 2020). The assignment of polar bears to the subpopulation from which they were collected is relatively accurate based on both genetic signatures (Jensen et al., 2020) and high site fidelity exhibited by Lancaster Sound polar bears (Schweinsburg et al., 1982).

Despite Lancaster Sound being documented as never being completely ice-free, climate change may alter this northern region sufficiently to render this status to be only

historically true. Although the polar bears that inhabit Lancaster Sound may be at an advantage compared to bears that live in regions of lower latitudes (Laidre et al., 2020b), this is unlikely to last as climate change progresses. Additionally, as climate change does continue to affect Lancaster Sound, these polar bears may be more vulnerable than other subpopulations due to never having experienced ice-free seasons in the past. Lancaster Sound is considered by the IUCN to be a data-deficient region (IUCN, 2020), likely due to how remote the area is, which makes consistent and thorough monitoring of its polar bear population a challenging endeavor that has not yet been undertaken. It is currently uncertain whether Lancaster Sound polar bears will be able to adapt to an ice-free season – specifically, will Lancaster Sound polar bears be able to successfully meet their nutritional needs by using novel terrestrial food sources? Have Lancaster Sound polar bears in the past engaged in similar foraging behaviours? Obtaining a comprehensive understanding of the historic dietary ecology and trophic interactions of Lancaster Sound polar bears will be instrumental in answering both of these questions.

1.2.4. Stable isotope analysis

Without a consistent monitoring program in place alongside the TEK of the Inuit (York et al., 2016), it can be difficult to determine the diets and trophic relationships of wide-ranging, highly mobile animals such as polar bears. Further, it becomes a near-impossible task to accurately track changes in the diets of these animals through time. Commonly used methods of studying animal diets include analyzing scat (Gormezano and Rockwell 2013; Iverson et al., 2013), stomach contents, directly observing feeding activities (Tomberg and Reif, 2007; Rockwell and Gormezano 2009; Bakaloudis et al.,

2012; Iles et al., 2013; Iverson et al., 2014), and TEK (Voorhees et al., 2014; Laforest et al., 2018). However, these methods can be financially costly, biased towards hard materials and/or difficult to digest foods (Davies-Mostert et al., 2010; Klare et al., 2011), invasive for the animal, or otherwise unrealistic to implement. Commonly used methods are therefore unlikely to be of use in studying the dietary ecology of Lancaster Sound polar bears, especially over extended periods of time (>50 years).

Stable isotope analysis (SIA) can be used in place of the previously mentioned methods of determining dietary ecology (Newsome et al., 2010). The majority of elements on Earth occur in more than one stable form, which are referred to as isotopes, which differ from each other based on the number of neutrons within the nucleus (Ben-David and Flaherty 2012). The different stable isotopes of an element therefore differ in their atomic masses. There are natural variations in the ratios of stable isotopes with lighter isotopes typically being more abundant than the heavier isotopes (Ben-David and Flaherty, 2012). Ratios of heavy to light isotopes are expressed in δ notation (i.e., for carbon, $^{13}\text{C}/^{12}\text{C}$, $\delta^{13}\text{C}$) in per mil (parts per thousand, ‰). Stable isotopes can be used to determine the trophic positions of animals and to reconstruct their diets. This is based on the principle that “you are what you eat and drink,” plus the added effects of physiology. The isotopic compositions of an animal’s tissues are primarily controlled by the food and water it ingests, as well as the gas it inhales, because these are used to synthesize soft tissues and biological minerals (Cerling and Harris, 1999; Koch, 2007; Howland et al., 2003; Newsome et al., 2010). By analyzing the isotopic compositions of various tissues, the diets of animals can be inferred and accurately reconstructed. Although SIA is an indirect method of obtaining information about an animal’s diet, it is often implemented

when this information would otherwise be unobtainable (Newsome et al., 2012). SIA is not only useful in studying animal diets; habitat use (Dunton et al., 2006; Domingo et al., 2016; Jürgensen et al., 2017; Boucher et al., 2019), foraging locations (Schoeninger and DeNiro, 1984; Ramsay and Hobson, 1991; Hobson et al., 2002; Drucker et al., 2012; Whitney et al., 2018), and internal physiological processes (Kennedy and Krouse, 1989; Hobson et al., 1993) can all be studied using SIA. For the purpose of this thesis, the focus shall be primarily SIA as means of reconstructing dietary ecology, including both dietary components (i.e., consumed prey species) and foraging behaviours (i.e., nearshore vs offshore environments).

It is important to note that the different stable isotopes of elements are not uniformly distributed among an animal's tissues, as certain dietary macromolecules are preferentially used to synthesize a specific tissue type (i.e., proteins used to synthesize muscle; Hedges 2003). Trophic transfer of stable isotopes is also not direct nor instantaneous (Martínez del Rio and Carleton, 2012). Through metabolic processes, isotopes undergo fractionation (i.e., separation of isotopes of different atomic masses) as they are incorporated into the tissues of the consumer (DeNiro and Epstein, 1977; Steele and Daniel, 1978; Hobson et al., 1996; Becker et al., 2007; Wessels and Hahn, 2010; Remien, 2015). Fractionation results in predictable offsets (enrichment) between the stable isotope values of the dietary components and the consumer's various tissues. This offset is specific to each tissue type, and is referred to as the trophic enrichment factor (TEF; McClelland and Montoya 2002; Chikaraishi et al., 2009), and is expressed as such:

$$\Delta X = \delta X_{\text{consumer}} - \delta X_{\text{prey}} \quad (1)$$

where X is the element.

The tissues of animals incorporate isotopes at varying rates, and combined with differences in tissue turnover time, this causes differences in the stable isotope compositions among tissues (Martínez del Rio and Carleton, 2012). For example, bone collagen has a slower turnover rate compared to more metabolically active tissues such as blood (Bocherens and Drucker, 2003; Cerling et al., 2007; Koch, 2007; Newsome et al., 2010), and undergoes little diagenesis post-mortem (DeNiro, 1985; Keenan and DeBruyn 2019). Bone collagen is thought to reflect the average diet of the animal over the last several years of its life (Chisholm et al., 1982; Ambrose and Norr, 1993; Koch, 2007; Newsome et al., 2010), which makes it the ideal tissue for this study. Turnover time of bone collagen does change with an animal's age (Geyh, 2001), sex (Hedges et al., 2007), and the surface-to-volume ratio of the bone (Matsubayashi and Tayasu, 2019). Thus, to ensure that isotopic compositions can be compared among individuals, it is important to have an approximation of the age (i.e., juvenile, subadult, adult), knowledge of the sex, and use bones that have been demonstrated to be directly comparable (Clark et al., 2017). Although SIA can be performed on any element that has more than one stable form, the majority of studies that investigate dietary ecology in animals use stable isotopes of two elements: carbon and nitrogen.

1.2.4.1. Carbon stable isotopes

Carbon isotopes (expressed as $^{13}\text{C}/^{12}\text{C}$, hereafter $\delta^{13}\text{C}$) are extremely useful in studying the dietary ecology and trophic interactions of animals (DeNiro and Epstein, 1978; Bocherens and Drucker, 2003). Many studies have successfully used $\delta^{13}\text{C}$ values from bone collagen to reconstruct the diets of animals that are no longer alive, including

animals belonging to now-extinct species (e.g., Chisholm et al., 1982; Ramsay and Hobson, 1991; Fox-Dobbs et al., 2007; Fox-Dobbs et al., 2008; O'Regan et al., 2008; Domingo et al., 2016; Jürgensen et al., 2017; Landry et al., 2021). There are multiple sources of dietary carbon that can be incorporated into animal tissues from consumed proteins, carbohydrates, and lipids, although carnivores obtain the majority of their dietary carbon through proteins and lipids (Hedges, 2003). $\delta^{13}\text{C}$ is accumulated throughout the trophic levels of an ecosystem, originating in the primary producers of the given food web (i.e., plants, phytoplankton), with the tissues of consumers being enriched in the order of $\sim 1\text{‰}$ per trophic level increase (DeNiro and Epstein, 1978); $\delta^{13}\text{C}$ values are generally highest in the apex predator(s) of an ecosystem (Kelly, 2000). Previous work done by Ramsay and Hobson (1991) determined that the TEF of $\delta^{13}\text{C}$ in polar bear bone collagen was $+0.5\text{‰}$, however, this study was based solely on the comparison of polar bear $\delta^{13}\text{C}$ values to those of ringed seals, and further research into the bone collagen $\delta^{13}\text{C}$ TEF of polar bears is required. $\delta^{13}\text{C}$ values are expressed in terms of Vienne PeeDee Belemnite (VPDB; the carbonate shell of a Cretaceous-aged mollusc). Since VPDB has a higher $^{13}\text{C}/^{12}\text{C}$ abundance ratio compared to organic materials, $\delta^{13}\text{C}$ values of plants and animals are negative (Kennedy and Krouse, 1989).

$\delta^{13}\text{C}$ values are generally higher in animals that inhabit marine ecosystems compared to those of terrestrial ecosystems (DeNiro and Epstein, 1978; Schoeninger and DeNiro, 1984; Kennedy and Krouse, 1989; Ramsay and Hobson, 1991; Schulting, 1998; Kelly, 2000; Newsome et al., 2010). The reasons are two-fold. Firstly, marine ecosystems are more complex than their terrestrial counterparts, due to their more intricate food webs and greater number of trophic levels, which results in higher $\delta^{13}\text{C}$ values due to multiple

trophic transfers (Schoeninger and DeNiro, 1984; Schulting, 1998). Second, the main primary producers of marine environments are phytoplankton and aquatic macrophytes (Welch et al., 1992; France, 1995), whereas land plants are the primary producers of terrestrial ecosystems (Blake, 1991; Kelly, 2000; Hobbie et al., 2009; Newsome et al., 2010). The photosynthetic pathways of phytoplankton are somewhat poorly understood, but are believed to be the most similar to the Calvin Cycle of C₃ plants, with carbon fixation being largely controlled by the ribulose-1,5-biphosphate carboxylase-oxygenase (RuBisCo) enzyme (Mortain-Bertrand et al., 1987; Mortain-Bertrand et al., 1988a; Mortain-Bertrand et al., 1988b; Descolas-Gros and Oriol, 1992). The different methods of photosynthesis in terrestrial and marine primary producers discriminate differently between the heavier ¹³C and lighter ¹²C isotopes, which results in differing δ¹³C values (Sackett et al., 1965; DeNiro and Epstein, 1978; O'Leary, 1981; Kennedy and Krouse, 1989; France, 1995). This is in part driven by the difference in diffusional resistance to carbon dioxide (CO₂) between terrestrial and marine environments, being four orders of magnitude higher in water than in air (Keeley and Sandquist, 1992) due to the greater viscosity of water that restricts CO₂ diffusion, posing a major limitation on the rate of photosynthesis (Smith and Walker, 1980).

Terrestrial C₃ plants are characterized by having low δ¹³C values, ranging between -35‰ to -25‰ (Kluge and Ting, 1978; Marshall et al., 2007), while C₄ plants exhibit higher δ¹³C values that range between -15‰ to -11‰ (Kluge and Ting, 1978; Dawson et al., 2002, Marshall et al., 2007). However, because there are no C₄ plants in the Arctic (Harris and Elliott, 2019), they do not need to be considered hereinafter. Arctic C₃ plants have a range of δ¹³C values just under 10‰, with values ranging between -30‰

to -20‰ (Blake, 1991; Hobbie et al., 2009; Kristensen et al., 2011). In Lancaster Sound, the average $\delta^{13}\text{C}$ value of the primary producers, including phytoplankton, ice algae, and kelp, is about -24.7‰, with an approximate range of -27.3‰ to -22.5‰ (based on estimates derived from macroinfaunal data; Mäkelä et al., 2017). Thus, although the $\delta^{13}\text{C}$ values of terrestrial Arctic plants and marine primary producers do overlap, the average $\delta^{13}\text{C}$ baseline of the marine ecosystem of Lancaster Sound is more constrained than the terrestrial ecosystem of the region, which will aid in distinguishing between marine- and terrestrially-sourced foods in polar bear diets.

1.2.4.2. Nitrogen stable isotopes

Nitrogen isotopes (expressed as $^{15}\text{N}/^{14}\text{N}$, hereafter $\delta^{15}\text{N}$) are similarly useful in studies involving the dietary ecology of animals, and are largely reflective of trophic level (DeNiro and Epstein, 1981; Schulting, 1998; Bocherens and Drucker, 2003; Cherry et al., 2011). As is the case with $\delta^{13}\text{C}$ values, $\delta^{15}\text{N}$ values tend to be higher in marine animals than terrestrial animals (Schoeninger and DeNiro, 1984), which is also believed to reflect the increased number of marine trophic levels (Schoeninger and DeNiro, 1984; Schulting, 1998). Most frequently used alongside $\delta^{13}\text{C}$ values, $\delta^{15}\text{N}$ values have similarly been successfully used in various studies to reconstruct the feeding ecology and trophic position of animals (e.g., Hobson et al., 1996; Fox-Dobbs et al., 2007; Fox-Dobbs et al., 2008; Cherry et al., 2011; Kristensen et al., 2011; Jørgensen et al., 2017; Landry et al., 2021). Unlike carbon stable isotopes, which have multiple dietary sources, nitrogen stable isotopes are derived primarily from consumed protein (Koch et al., 2007; Newsome et al., 2010). Nitrogen stable isotopes are more strongly fractionated within consumers than

carbon stable isotopes (Koch, 2007), which yields greater differences in $\delta^{15}\text{N}$ values between the primary producers that initially fix nitrogen and the subsequent consumer(s) (Schoeninger and DeNiro, 1984). The tissues of consumers are typically enriched in ^{15}N and have higher $\delta^{15}\text{N}$ values on the order of approximately 3‰ to 5‰ per trophic level, which yields the highest $\delta^{15}\text{N}$ values in apex predators (DeNiro and Epstein, 1981; Koch, 2007; Cherry et al., 2011). Enrichment in $\delta^{15}\text{N}$ values from diet to consumer is due to the preferential removal of amine groups that contain ^{14}N during the processes of peptide bond hydrolysis and deamination (Macko et al., 1986; Macko et al., 1987; Gannes et al., 1997; Balter et al., 2006). Furthermore, mammals, including polar bears, preferentially excrete ^{14}N in the form of urea, which contributes further to the diet-to-consumer offset (Steele and Daniel, 1978; Sutoh et al., 1993). The investigation of $\delta^{15}\text{N}$ is more complex than that of $\delta^{13}\text{C}$, and there are several well-known challenges associated with interpreting $\delta^{15}\text{N}$ data. These challenges are largely connected to the uncertainty associated with two key parameters: spatiotemporal variation in the $\delta^{15}\text{N}$ baseline (i.e., of primary producers), and variation in isotopic fractionation during trophic transfer (i.e., among species and tissues; McMahon and McCarthy, 2016).

Firstly, there is significant spatiotemporal variability in $\delta^{15}\text{N}$ baseline values across ecosystems, which is largely caused by differences in the community of primary producers, the type of inorganic nitrogen that producers utilize (i.e., N_2 , NO_3^- , or NH_3 , which are all isotopically distinct), and how efficiently they use the nitrogen they uptake (McMahon et al., 2013a; McMahon et al., 2013b; McMahon and McCarthy, 2016).

Terrestrial Arctic plants tend to have very low $\delta^{15}\text{N}$ values, ranging between -8‰ to +1‰ (Hobbie et al., 2009; Kristensen et al., 2011). Marine phytoplankton typically have $\delta^{15}\text{N}$

values that range between +1 to +16‰, with an average of about +7‰ (Shoeninger and DeNiro, 1984; Kelly, 2000). Unfortunately, there is little data available for $\delta^{15}\text{N}$ values of marine primary producers in the Arctic. As an alternative, Mäkelä et al. (2017) have published macroinfaunal $\delta^{15}\text{N}$ data from Lancaster Sound, which can be used as a proxy for baseline $\delta^{15}\text{N}$ values. Macroinfaunal species that occupied trophic levels from 0.7 to 3.2 exhibited $\delta^{15}\text{N}$ values ranging from +7.0‰ to +16.7‰ (Mäkelä et al., 2017). Since marine-based food webs yield higher $\delta^{15}\text{N}$ values in carnivores compared to terrestrial food webs (Chisholm et al., 1982; Schoeninger and DeNiro, 1984; Cherry et al., 2011; Harris et al., 2019), the isotopic difference can help determine the food web that the historic polar bears primarily relied on. Additionally, there is some spatiotemporal variation in $\delta^{15}\text{N}$ values associated with differences in climate; more arid environments tend to have higher $\delta^{15}\text{N}$ values, whereas environments with more precipitation/humidity have comparatively lower $\delta^{15}\text{N}$ values (Heaton et al., 1986; Amundson et al., 2003). Because Lancaster Sound is an arid habitat, we expect to observe consistently high $\delta^{15}\text{N}$ values among polar bears. Therefore, documented changes in temperatures, and subsequently precipitation, could explain observed changes in $\delta^{15}\text{N}$ values through time.

Secondly, the average $\delta^{15}\text{N}$ TEF for animals is assumed to be between 3‰ to 5‰, but TEFs can vary widely (DeNiro and Epstein, 1981; Caut et al., 2009), even up to 1‰ to 6‰ (McMahon et al., 2015). TEF variation can be attributed to quality of the diet, tissue type, and physiological/nutritional stress. The quality of an animal's diet, specifically of dietary protein, has been demonstrated to account for a significant proportion of the variation of $\delta^{15}\text{N}$ TEFs (Robbins et al., 2005). As the quality of dietary protein increases, the TEF decreases (Robbins et al., 2005). Since polar bears diets

consist primarily of blubber, muscle, and other proteinaceous tissues (i.e., skin, viscera) from seals (Stirling and McEwan, 1975; Stirling and Archibald, 1977), it is likely that a shift in the type of consumed protein (i.e., from marine to terrestrial protein), and thus protein quality, could be a significant contributor to variation in polar bear $\delta^{15}\text{N}$ values and/or TEFs. Different tissues also have different and specific associated TEFs (DeNiro and Epstein, 1981; Hobson et al., 1996; Bearhop et al., 2002). Although all consumer tissues have higher $\delta^{15}\text{N}$ values than those of the diet, formation of the tissues fractionates stable isotopes differently during the processes of diet-to-tissue assimilation (DeNiro and Epstein, 1981). It is therefore imperative to use TEFs that are specific to the type of tissue being analyzed. In the context of this study, the only TEFs used will be those that are associated with bone collagen, which are relatively well-established for carnivorous mammals (Schoeninger and DeNiro, 1984; Ramsay and Hobson, 1991; Szepanski et al., 1999; Bocherens and Drucker, 2003; Fox-Dobbs et al., 2007; Krajcarz et al., 2018). Nutritional stress has also been shown to have an effect on $\delta^{15}\text{N}$ values, where tissues become enriched in ^{15}N likely due to the catabolization of protein from lean (i.e. muscle) tissues and reusing the protein elsewhere within the body (Hobson and Clark, 1992; Hobson et al., 1993). TEFs can be up to +6‰ higher in animals that are experiencing nutritional stress compared to those that have sufficient food and protein intake (Hobson and Clark, 1992). Because pregnant female polar bears den for ~8 months during the winter (Nelson et al., 1983; Ramsay and Stirling, 1988; Derocher et al., 2004), and all polar bears can undergo periodic fasting during the summer months when significant ice breakup occurs (Derocher and Stirling, 1990; Derocher et al., 2004; Gormezano and Rockwell, 2013), it is possible that long-term nutritional stress will affect

$\delta^{15}\text{N}$ values, especially in female polar bears. These factors are all important considerations that could account for the potential intrapopulation variability in $\delta^{15}\text{N}$ values of the polar bears from Lancaster Sound.

1.2.5. Bayesian stable isotope mixing models

Bayesian stable isotope mixing models (BSIMMs) are useful tools in isotopic studies because they are able to estimate the contributions of various food sources to the overall diet of a consumer (Moore and Semmens, 2008; Franco-Trecu et al., 2013; Arostegui et al., 2019). This is done by fitting probability models to isotopic data (Hopkins and Ferguson, 2012), comparing the isotopic composition of prey (i.e., source) tissue to that of the consumer (Arostegui et al., 2019), which determines the probability distributions of all the potential source contributions to the consumer (Moore and Semmens, 2008).

There are several assumptions that are made when using BSIMMs, including: 1) the samples of prey and consumers that are analyzed are representative of the entire isotopic variability of those members (Phillips et al., 2014), 2) the TEFs used and their associated uncertainties are appropriate for the organism/tissue that is analyzed (Arostegui et al., 2019), 3) consumers are at isotopic equilibrium relative to the isotopic composition of the source (i.e., the ratios of the stable isotopes between consumer and source remain constant at a particular temperature; Arostegui et al., 2019), 4) isotope mixing is constrained through mass balance (Harvey et al., 2002), and 5) isotopes are completely mixed within the consumer, so that any dietary macromolecule can be broken

down into atoms and then randomly used to synthesize consumer compounds *de novo* (Martínez del Rio et al., 2009).

Prior knowledge of the consumer diet is required in order to correctly select prey sources for BSIMMs (Lerner et al., 2018). The inclusion of too many or unlikely prey sources leads to increased uncertainty in the contribution of any single source to the consumer's diet (Moore and Semmens, 2008). Although BSIMMs do incorporate sources of uncertainty within the data, they cannot be expected to precisely estimate the diet when the priors (i.e., 0.5, 1, 2) contain information of only moderate importance (Franco-Trecu et al., 2013). The ability of BSIMMs to discriminate among isotopic sources also decreases with the number of prey sources because it is strongly influenced by the isotopic separation (distinctiveness) of the sources, and can produce biased results if too many, overlapping sources are included (Lerner et al., 2018). Thus, only including a few sources that are known to be eaten at least semi-frequently by the consumer is the optimal means of source selection; fortunately, the prey species consumed by polar bears are relatively well documented (Stirling and McEwan, 1975; Stirling and Archibald, 1977; Smith, 1980; Smith, 1985; Ramsay and Stirling, 1988; Calvert and Stirling, 1990; Smith and Sjare, 1990; Derocher et al., 1993; Rugh and Shelden, 1993; Derocher et al., 2000; Gormezano and Rockwell, 2013; Galicia et al., 2015; Rode et al., 2015), facilitating their selection.

BSIMMs also require an accurate TEF that is specific to both the tissue type and species of the consumer in question. Unfortunately, there is no well-supported TEF available that is specific to polar bear bone collagen. TEFs for polar bears have been determined for other tissues such as hair (L'Hérault et al., 2018), and muscle and blood

(Cherry et al., 2011). Bocherens and Drucker (2003) published mean fractionation estimates ($\Delta\delta^{13}\text{C} = 1.0\text{‰}$, $\Delta\delta^{15}\text{N} = 3.6\text{‰}$) calculated from wolf (*Canis lupus* Linnaeus 1758) bone collagen. Previous studies that have used BSIMMs to reconstruct the diets of carnivores have either used these TEFs (Bocherens and Drucker, 2003; Savory et al., 2014), or very similar TEFs (Fox-Dobbs et al., 2007; Krajcarz et al., 2018; Landry et al., 2021). For the purposes of BSIMMs, we will use the TEFs determined by Bocherens and Drucker (2003; $\Delta\delta^{13}\text{C} = 1.0\text{‰}$, $\Delta\delta^{15}\text{N} = 3.6\text{‰}$) for the polar bears, but will use the wide error margins suggested by Savory et al. (2014) to account for uncertainty in the polar bear bone collagen fractionation, as Bocherens and Drucker (2003) did not estimate error in their study.

1.3. Hypotheses and predictions

The polar bears included in this study are from the Lancaster Sound subpopulation in Nunavut, and were collected between 1923 and 1975. I hypothesize that 1) during the 1970s polar bears began to experience nutritional stress due to reduced access to summer sea ice (Stirling and Derocher, 2012; Rogers et al., 2015). Nutritional stress is apparent as enrichment in $\delta^{15}\text{N}$ that is unmatched by an enrichment in $\delta^{13}\text{C}$, resulting from catabolizing stored nitrogen (i.e., in fat reserves; Whiteman et al., 2018). Due to the extra physiological stress that females undergo as a result of pregnancy and caring for cubs, I predict that females will have more variation in $\delta^{15}\text{N}$ values. I also predict females will show earlier evidence of nutritional stress in the form of higher $\delta^{15}\text{N}$ values, likely resulting from climate change, compared to males due to this sex-based difference, 2) at the same time, polar bears began to rely on more terrestrial sources of

nutrition (i.e. Arctic birds, eggs; Iverson et al., 2014; Rode et al., 2015). As polar bears began to rely on more terrestrial food sources, they remained in more in-land habitats, venturing out onto the sea ice increasingly rarely. Baseline isotopic values are different for marine and terrestrial ecosystems (Wada et al., 1987; Montoya, 2007; Ben-David and Flaherty, 2012), as well as nearshore and offshore environments (Schell et al., 1998; Dunton et al., 2006; Newsome et al., 2010; Harris et al., 2018). Thus, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values will illuminate shifts from marine to terrestrial foods. The Bayesian stable isotope mixing model will determine what prey species the polar bears were primarily feeding on throughout the last years of their lives, and in what proportions. I predict that isotopic values will begin to shift to be more similar to terrestrial signatures in the 1970s, as the effects of climate change and sea ice loss began to accumulate and polar bears began to consume terrestrial foods to meet their nutritional needs.

1.4. Structure of thesis

In this thesis, I produce the first dataset of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of polar bears from the Lancaster Sound subpopulation during the 20th century (1950s–1970s). I offer novel insights into the historical ecology of these polar bears, both regarding their behaviours and diets through the use of SIA and BSIMMs. In the second chapter of my thesis, I describe the polar bears specimens used in this study, and outline the methods that I used for SIA and statistical analyses. In the third chapter of my thesis, I present the results of this study. In the fourth chapter of my thesis, I discuss the ecological implications of my isotopic data ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and characterize the diets of polar bears as determined by BSIMMs. In the fifth and final chapter, I summarize the key findings of

my thesis, and offer suggestions about what future research endeavors should entail to provide a more thorough understanding of Lancaster Sound polar bear ecology from the 1950s to the 1970s. The insights of my thesis will aid in the understanding of how polar bears have adapted to past environmental changes, and can be used by the IUCN, COSEWIC, and other biodiversity conservation programs in efforts to implement protections for prey and habitat resources that are key to the persistence of polar bears throughout the 21st century and beyond.

CHAPTER 2: MATERIALS AND METHODS

2.1. Stable isotope analysis

Polar bear specimens were obtained from the Canadian Museum of Nature (CMN) Zoology Collection (Appendix I, Appendix II). Specimens were selected based on geographic location (within the Lancaster Sound subpopulation boundary) and based on the maturity of the individual (if age was not recorded, the degree of suture fusion and size of skull was used to estimate maturity). Only adults and a few subadults were sampled in an effort to reduce isotopic signals related to nursing and weaning in juveniles. In total, 80 individual polar bears were selected for isotopic analysis. These bears were divided into four discrete groups based on decade of collection: 1920 ($n = 1$), 1950 ($n = 21$), 1960 ($n = 29$), and 1970 ($n = 29$). It is important to note that the specimens are not distributed evenly within each decade, as the dates of collection are clustered around the early and late years (Figure 2). The groups were further subdivided by sex, to account for sex-specific differences in reproductive physiology (namely, pregnancy and lactation). In total, there were 39 males, 40 females, and one individual of unknown sex.

Selected polar bear specimens were sampled using a Dremel tool with a diamond tapered point bit (part #7144) and the powdered bone was collected in safe lock micro test tubes. In most cases, bone samples were taken from the mandible or maxilla, although several samples were taken from long bones. Due to similarity in rates of isotopic turnover among bones and the homogenization of isotopic signals within individual bones (Newsome et al., 2010), isotopic values from bones sampled at different physical locations can be directly compared (Clark et al., 2017).

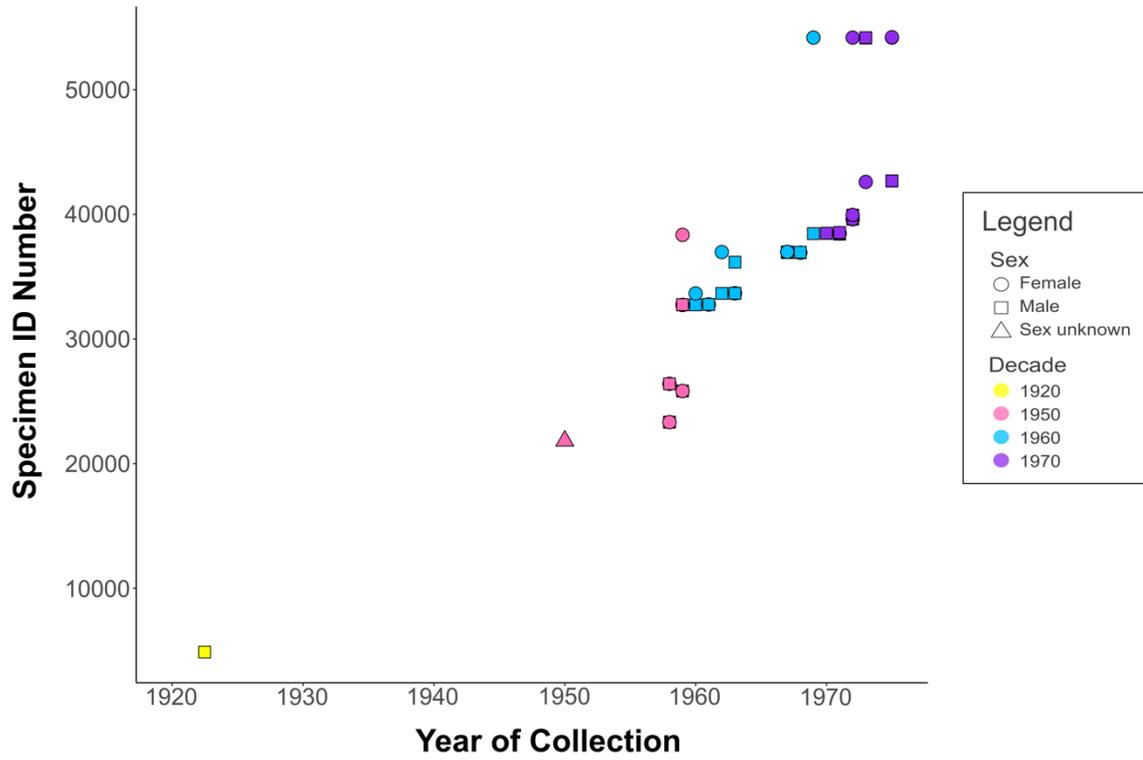


Figure 2. Distribution of the years of collection for the polar bear specimens ($n = 80$) used in this study.

For collagen analysis, ~30 to 40 mg of bone powder was transferred into a 15 mL PYREX™ Disposable Conical-Bottom Glass Centrifuge Tube (ID #C9950215) and demineralized with ~1.5 mL 0.1M HCl for 30 to 60 minutes at 4°C, and rinsed five times using deionized water; a shorter than typical period of demineralization was used because the samples were powdered. Lipids affect the $\delta^{13}\text{C}$ values substantially, being between 6‰ to 8‰ lower in samples that contain lipids compared to those without (DeNiro and Epstein 1977; DeNiro and Epstein 1978; McConnaughey and McRoy, 1979), and are removed to ensure the comparability of samples with differing lipid contents. Samples were therefore defatted in two ~10 mL petroleum ether washes and rinsed twice with deionized water. Collagen samples were frozen overnight, and subsequently dried in an oven at 40 °C for 48 hours.

Carbon and nitrogen isotope ratios of the samples were measured by Elemental Analyzer Continuous Flow Isotope Ratio Mass Spectrometry in the Center for Stable Isotopes, University of New Mexico using a Costech ECS 4010 Elemental Analyzer coupled to a ThermoFisher Scientific Delta V Advantage mass spectrometer via a CONFLO IV interface. Isotope ratios are expressed using the standard δ notation:

$$\delta^h X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \quad (2)$$

where $\delta^{13}\text{C}$ values are reported relative to the standard Vienna Pee Dee Belemnite (VPDB) and $\delta^{15}\text{N}$ values are reported relative to air (AIR). Three internal laboratory standards were run at the beginning, at intervals between samples, and at the end of analytical sessions. Analytical precision calculated from the standards is $\pm 0.1\%$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Analyses were normalized to the laboratory standards, which were calibrated against NBS 21, NBS 22, and USGS 24 for $\delta^{13}\text{C}$, and IAEA N1, IAEA N2, and

USGS 43. The three internal laboratory standards are: UNM-CSI Protein Std#1, casein purchased from Sigma Aldrich, where $\delta^{13}\text{C} = -26.52\text{‰}$ and $\delta^{15}\text{N} = 6.43\text{‰}$; UNM-CSI Protein Std#2, soy protein purchased from Sigma Aldrich, where $\delta^{13}\text{C} = -25.78\text{‰}$ and $\delta^{15}\text{N} = 0.98\text{‰}$; and UNM-CSI Protein Std#4, house-made tuna protein, where $\delta^{13}\text{C} = -16.17\text{‰}$ and $\delta^{15}\text{N} = 13.32\text{‰}$.

Out of the 80 analyzed samples, only 49 had C:N ratios within the acceptable range for pure collagen (between 2.9 and 3.5; DeNiro, 1985; DeNiro and Weiner, 1988; Ambrose, 1990). In contrast, 31 of the samples had C:N ratios higher than 3.5, indicating that they had not been successfully lipid-extracted and that the $\delta^{13}\text{C}$ values were likely not reflective of the $\delta^{13}\text{C}$ values of pure collagen (DeNiro and Epstein, 1978; McConnaughey and McRoy 1979; Post et al., 2007). Fortunately, $\delta^{13}\text{C}$ values contaminated by lipids can be normalized to account for the degree of lipid contamination using a correction factor determined by the following equation by Post et al. (2007):

$$\delta^{13}\text{C}_{\text{lipid-normalized}} = \delta^{13}\text{C}_{\text{uncorrected}} - 3.32 + 0.99 \times \text{C:N} \quad (3)$$

where 3.32 and 0.99 are constants, and C:N refers to the ratio of carbon to nitrogen of the sample that is being normalized. The $\delta^{13}\text{C}$ values for all samples with $\text{C:N} > 3.5$ were corrected using Equation 3, which eliminated the linear relationship and appears to have successfully normalized the samples (Figure 3A & B). Lipid content does not influence $\delta^{15}\text{N}$ values in bone collagen (Guiry et al., 2016), so no additional corrections were necessary.

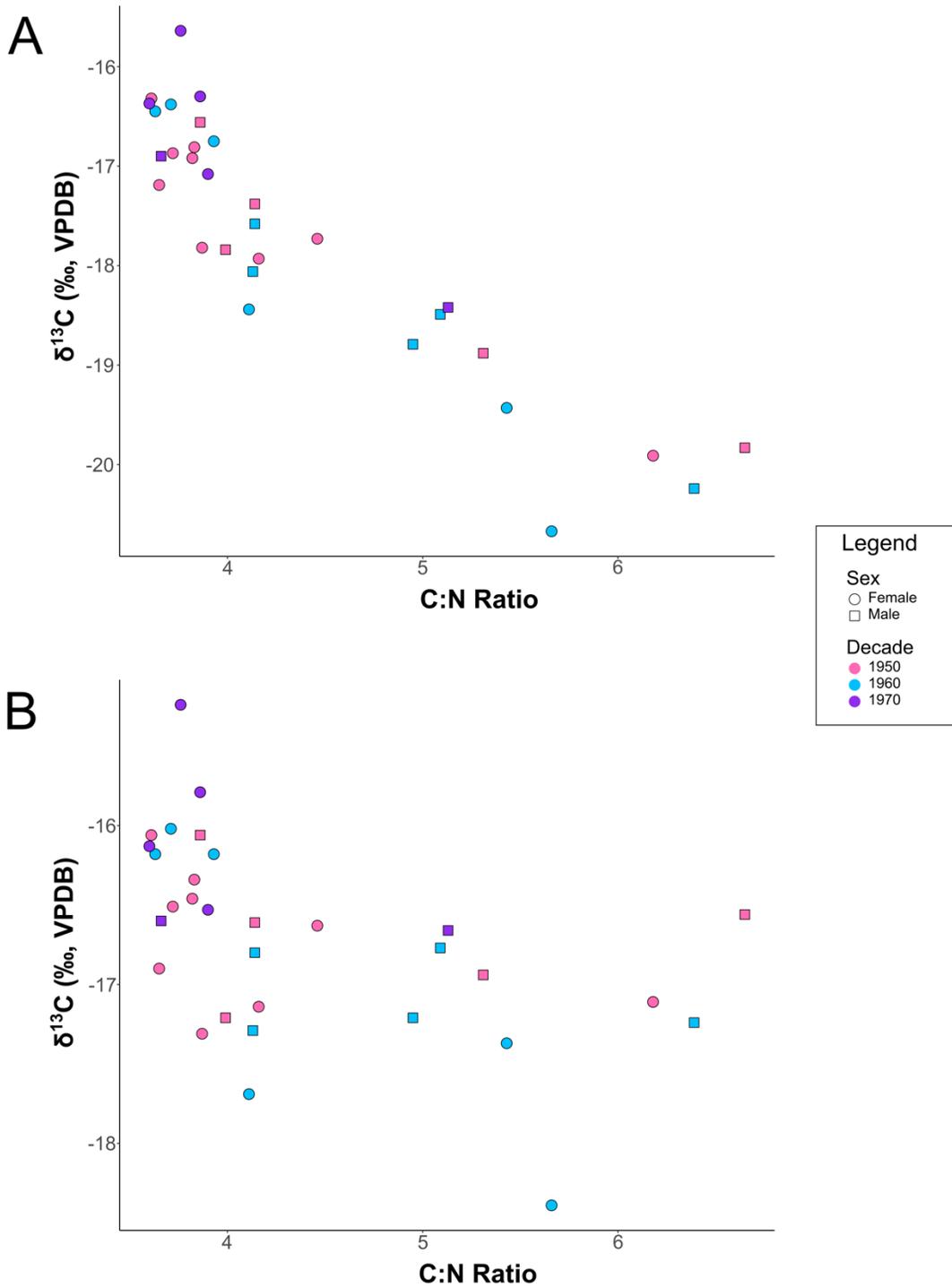


Figure 3. A) $\delta^{13}\text{C}$ and C:N ratios of the polar bears ($n = 31$) that were unsuccessfully chemically lipid-extracted prior to mathematical normalization; B) $\delta^{13}\text{C}$ and C:N ratios of the polar bears ($n = 31$) that were unsuccessfully chemically lipid-extracted after mathematical normalization.

2.2. Suess effect correction

The Suess effect refers to a change in the ratio of the atmospheric and oceanic concentrations of the heavy carbon isotopes (^{13}C and ^{14}C) caused by the admixture of large amounts of anthropogenically-produced CO_2 , which is depleted in ^{13}C and contains no ^{14}C (Tans et al., 1979; Sonnerup et al., 1999). In order to compare temporal isotopic variation and changes, it is necessary to adjust $\delta^{13}\text{C}$ values of specimens from the late 19th century and onward due to the changes in atmospheric and oceanic dissolved inorganic carbon (DIC) that have occurred after the Industrial Revolution (Quay et al., 1992; Eide et al., 2017). The baseline $\delta^{13}\text{C}$ value of the ocean has decreased due to the influx of isotopically light DIC (Quay et al., 1992), so any differences observed in the comparisons of polar bear $\delta^{13}\text{C}$ values without correcting for the Suess effect would have largely reflected the overall change in DIC isotopic composition, rather than a true ecological signal. Similarly, prey species included in the BSIMMs that had not been corrected for the Suess effect for their respective publications were corrected for use in the BSIMMs to avoid misinterpretations of dietary compositions.

The $\delta^{13}\text{C}$ values for all samples (pure collagen and lipid normalized) were corrected for the Suess effect using the following equation from Seymour et al. (2014), which was modified from Misarti et al. (2009) and originally created by Hilton et al. (2006):

$$\delta^{13}\text{C}_{\text{Suess correction factor}} = a^{(b \times 0.027)} \quad (4)$$

where a is the maximum annual rate of $\delta^{13}\text{C}$ decrease in the North Pacific, determined to be -0.014 (Quay et al., 1992). This estimate may slightly overestimate the magnitude of the local Suess effect, as polar regions are characterized by relatively small changes in

oceanic surface water dissolved inorganic $\delta^{13}\text{C}$ (Quay et al., 2003), but there are no calculations for Arctic regions currently available. However, this correction has been used in previous studies involving Arctic ecosystems (Seymour et al., 2014; Szpak et al., 2018), and is thus considered acceptable to use in this study. b is the subtraction of 1850 (the start of the Industrial Revolution) from the year of the animal's death (Seymour et al., 2014). The constant 0.027 represents the curve of change in $\delta^{13}\text{C}$ values of the world's oceans between 1945 and 1997 as determined by Gruber et al. (1999).

2.3. Statistical analyses

The pure collagen (C:N \leq 3.5, $n = 49$; Appendix I) $\delta^{13}\text{C}$ values (hereafter, $\delta^{13}\text{C}_{\text{collagen}}$) were analyzed alone and again when combined with the lipid normalized $\delta^{13}\text{C}$ values (hereafter, $\delta^{13}\text{C}_{\text{lipid-normalized}}$, C:N $>$ 3.5, $n = 31$; Appendix II). It is important to note that the statistical results involving $\delta^{13}\text{C}_{\text{lipid-normalized}}$ values must be interpreted with some caution, given the limits of lipid normalization (e.g., error associated with the regression equation).

The datasets of the pure collagen samples and combined pure collagen and lipid normalized samples, including $\delta^{13}\text{C}$ values, $\delta^{15}\text{N}$ values, sex, and decade of collection (i.e., time), were translated into the R software environment (R Core Team, 2019). The polar bear of unknown sex was included in the following analyses despite not having a binary sex assignment, as it was the only bear from the year 1950, and was thus required to represent the early years of the decade. A Shapiro-Wilk normality test was performed in R (R Core Team, 2019) on the residuals of the linear regressions from both the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (dependent variables) in relation to sex and decade (independent

variables) to confirm a normal distribution. Both multivariate and univariate two-way MANOVA tests were performed to test for statistically significant differences in mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (response variables) between the sexes and among decades (independent variables). If a significant difference was observed, a subsequent one-way ANOVA was performed to enable Tukey's honestly significant difference (HSD) tests, given they cannot be performed with MANOVA. Tukey's HSD was then used to determine which groups were significantly different (i.e., isotopic differences between sexes and/or between decades).

Climate data from Resolute, Nunavut, was obtained from the Historical Data archives of the Government of Canada (Canada, Environment and Climate Change, 2021; Appendix III). To investigate whether changes in climatic conditions (i.e., mean annual temperature, total annual precipitation) are correlated with changes in $\delta^{13}\text{C}$ values, I used Pearson's correlations. Only bears from the year 1950 and onward were included in the correlations, as no climate data were available for the prior years.

2.4. Trophic level calculations

The trophic level for each bear was calculated from its $\delta^{15}\text{N}$ value using the following equation modified from Hobson et al. (2002):

$$\text{TL} = 2 + (\delta^{15}\text{N}_{U. maritimus} - \delta^{15}\text{N}_{C. hyperboreus})/3.6 \quad (5)$$

The calculated trophic level was determined relative to the calanoid copepod, *Calanus hyperboreus*, which is common in Arctic waters, including Lancaster Sound (Buchanan and Sekerak, 1982; Gilfillan et al., 1986; Welch et al., 1992). Hobson et al. (2002) used a fractionation value of 3.8‰, however, this value was based on muscle tissue. As trophic

level is being estimated using $\delta^{15}\text{N}$ values from bone, the isotopic enrichment per trophic level was assumed to be constant at 3.6‰ based on mean fractionation estimates on wolf bone collagen (Bocherens and Drucker, 2003).

2.5. Bayesian stable isotope mixing models

For the Bayesian stable isotope mixing models (BSIMMs), only $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{15}\text{N}$ values were used ($n = 49$). BSIMMs were performed in the MixSIAR package (v.3.1.10; Stock et al., 2018) using the JAGS software package (v.4.3.0) in R (R Core Team, 2019). One BSIMM was performed per polar bear to achieve individualized feeding profiles, and to allow for comparisons in overall dietary composition between the sexes and through time. Since all polar bear samples were initially lipid-extracted due to the obvious lipid content of the bones, and all of the prey data borrowed from the literature had been lipid-extracted as well, the pure-collagen dataset was acceptable to use in the BSIMMs. Six potential prey species were included in the model: bowhead whale (*Balaena mysticetus*), beluga whale (*Delphinapterus leucas*), bearded seal (*Erignathus barbatus*), ringed seal (*Pusa hispida*), walrus (*Odobenus rosmarus* Linnaeus 1758), and caribou (*Rangifer tarandus*). The $\delta^{13}\text{C}$ values and $\delta^{15}\text{N}$ values of the prey species were borrowed from published literature (see Appendix IV; Schoeninger and DeNiro, 1984; Drucker et al., 2012; Clark et al., 2017; Szpak et al., 2018). To avoid preconceived biases on the preferred prey of polar bears, the models were run with uninformative priors, which automatically weigh all prey species as being equally likely to contribute to the diet of polar bears. The trophic enrichment factors (TEFs) used in the BSIMMs are as follows : $\Delta\delta^{13}\text{C} = 1.0\text{‰} \pm 1.0\text{‰}$ and $\Delta\delta^{15}\text{N} = 3.6 \pm 1.0\text{‰}$. Models were run through

100,000 iterations. Stacked barplots were created to show the various contributions of the six prey species to the overall diet of individual bears.

CHAPTER 3: RESULTS

3.1. Stable isotope analysis results

In the pure-collagen dataset, the mean $\delta^{13}\text{C}_{\text{collagen}}$ value is -15.59‰ (SD = $\pm 0.55\text{‰}$) and the mean $\delta^{15}\text{N}$ value is 22.27‰ (SD = $\pm 0.72\text{‰}$). In the lipid-normalized dataset, the mean $\delta^{13}\text{C}_{\text{lipid-normalized}}$ value is -15.70‰ (SD = $\pm 0.82\text{‰}$) and the mean $\delta^{15}\text{N}$ value is 22.37‰ (SD = $\pm 0.72\text{‰}$). The majority of the $\delta^{13}\text{C}$ values from both datasets are between -14.50‰ to -16.00‰ (Figure 4, Figure 5), and the majority of the $\delta^{15}\text{N}$ values from both datasets range between 21.50‰ to 23.00‰ (Figure 4, Figure 5), although there are a number of polar bears with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values that do not fall within these ranges. It is possible that the polar bears with $\delta^{13}\text{C}_{\text{lipid-normalized}}$ values that fall below -16.50‰ are still lower than what would be expected if the initial lipid-extraction performed in the laboratory had been successful, but at present this cannot be determined. Despite this, the overall $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the polar bears do appear to be reasonably consistent, and should provide an accurate means of investigating historical ecological characteristics of polar bears.

3.2. Statistical results

In the pure collagen dataset, the residuals of the $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{15}\text{N}$ values when regressed against both sex and decade were normally distributed based on the results of the Shapiro-Wilks normality tests (Table 1). The multivariate two-way MANOVA yielded significant results for decade, but not for sex or the interaction term (Table 2).

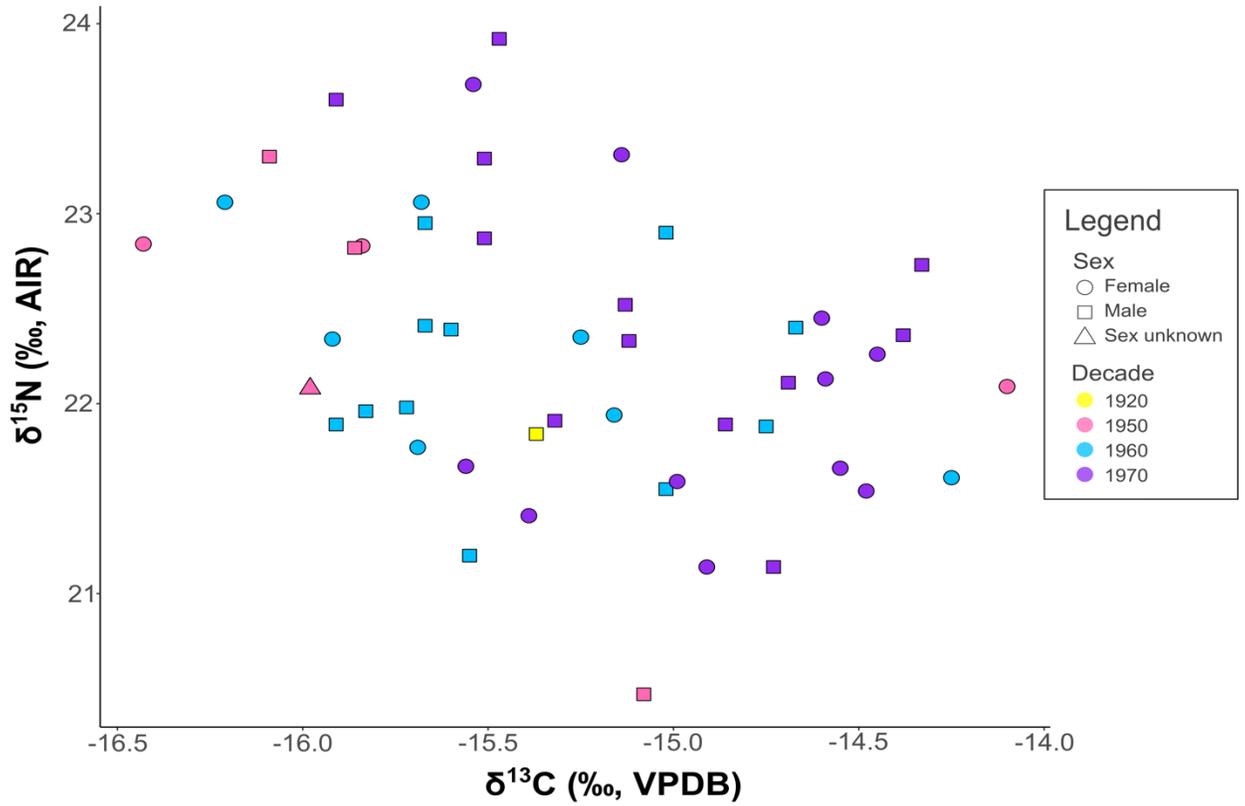


Figure 4. $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{15}\text{N}$ values of Lancaster Sound polar bears ($n = 49$) from the pure-collagen dataset.

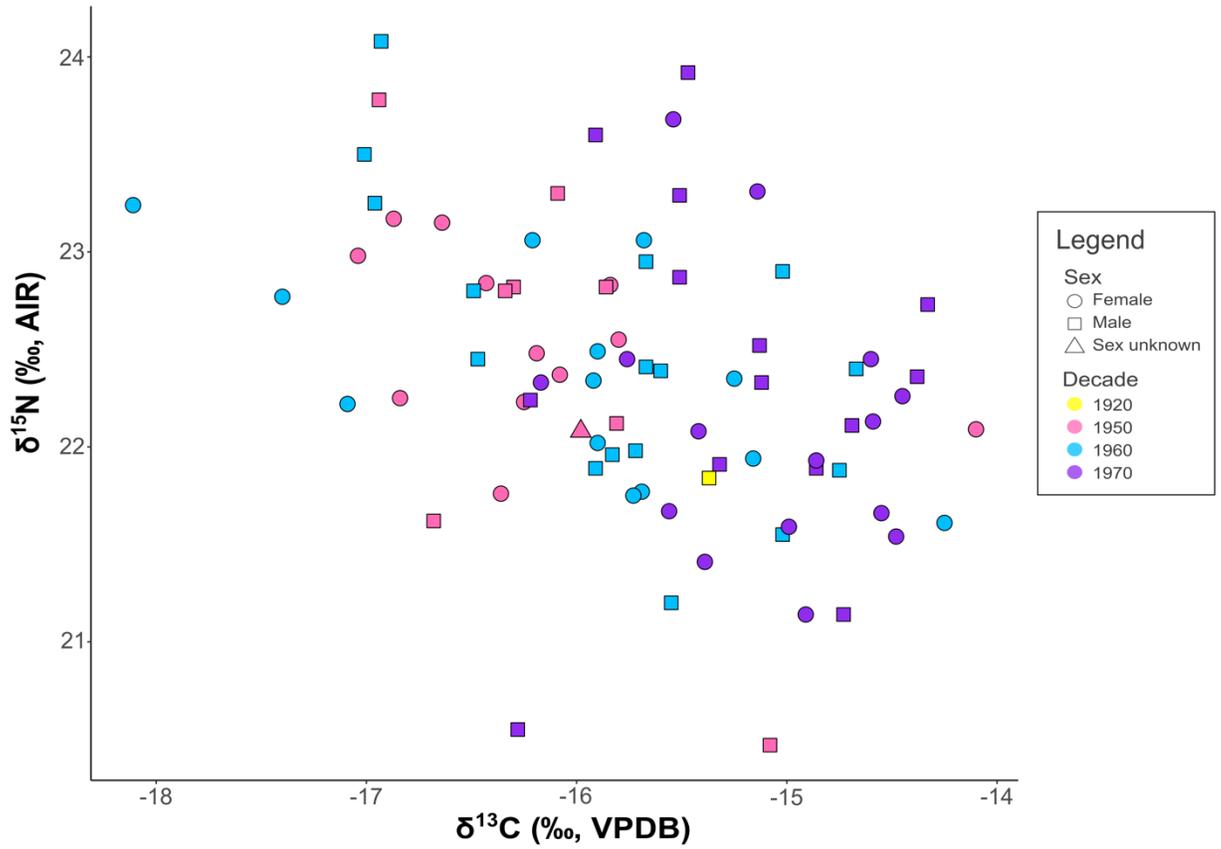


Figure 5. $\delta^{13}\text{C}_{\text{lipid-normalized}}$ and $\delta^{15}\text{N}$ values of Lancaster Sound polar bears ($n = 80$) from the lipid-normalized dataset.

Table 1. Results of the Shapiro-Wilk normality tests performed on the polar bear $\delta^{13}\text{C}_{\text{collagen}}/\delta^{13}\text{C}_{\text{lipid-normalized}}$ and $\delta^{15}\text{N}$ values and sex or decade.

Dataset	Interaction	<i>W</i> value	<i>p</i> value
Pure collagen	$\delta^{13}\text{C}_{\text{collagen}}$ and sex	0.979	0.518
Pure collagen	$\delta^{13}\text{C}_{\text{collagen}}$ and decade	0.956	0.063
Pure collagen	$\delta^{15}\text{N}$ and sex	0.987	0.864
Pure collagen	$\delta^{15}\text{N}$ and decade	0.989	0.927
Lipid-normalized	$\delta^{13}\text{C}_{\text{lipid-normalized}}$ and sex	0.986	0.5448
Lipid-normalized	$\delta^{13}\text{C}_{\text{lipid-normalized}}$ and decade	0.984	0.396
Lipid-normalized	$\delta^{15}\text{N}$ and sex	0.988	0.679
Lipid-normalized	$\delta^{15}\text{N}$ and decade	0.990	0.772

Table 2. Results of the multivariate two-way MANOVA tests performed on both isotopic systems ($\delta^{13}\text{C}_{\text{collagen}}/\delta^{13}\text{C}_{\text{lipid-normalized}}$ and $\delta^{15}\text{N}$) and sex, decade, and sex/decade.

Dataset	Factor	Pillai's Trace	<i>F</i> statistic	<i>df</i>	<i>p</i> value
Pure collagen	Sex	0.065	0.742	2	0.566
Pure collagen	Decade	0.135	3.349	1	0.044*
Pure collagen	Sex and Decade	0.060	1.363	1	0.267
Lipid-normalized	Sex	0.017	0.327	2	0.859
Lipid-normalized	Decade	0.176	7.883	1	< 0.001*
Lipid-normalized	Sex and Decade	0.049	1.914	1	0.154

The univariate two-way MANOVA revealed that there were significant differences in mean $\delta^{13}\text{C}_{\text{collagen}}$ values among decades (Table 3; Figure 6), but that the interaction term was not statistically significant and there were no statistically significant differences in mean $\delta^{13}\text{C}_{\text{collagen}}$ values between sexes (Table 3). There were no statistically significant differences in mean $\delta^{15}\text{N}$ values between sexes, among decades, or when considering the interaction term (Table 3; Figure 7).

A univariate one-way ANOVA also revealed a statistically significant difference for $\delta^{13}\text{C}_{\text{collagen}}$ values (Table 4). The Tukey's honestly significant difference test revealed a statistically significant difference in mean $\delta^{13}\text{C}_{\text{collagen}}$ values between the 1950s and the 1970s ($p = 0.048$; Figure 6).

There was a negative, albeit insignificant, correlation between $\delta^{13}\text{C}_{\text{collagen}}$ values and mean annual temperature (Table 5; Figure 8). No correlation was observed between $\delta^{13}\text{C}_{\text{collagen}}$ values and total annual precipitation (Table 5; Figure 9).

In the lipid-normalized dataset, the Shapiro-Wilks normality tests also confirmed that the residuals for regressions of $\delta^{13}\text{C}_{\text{lipid-normalized}}$ values and the $\delta^{15}\text{N}$ values with both sex and decade followed normal distributions (Table 1). The multivariate two-way MANOVA did not yield a statistically significant result for sex or the interaction term for either isotopic system (Table 2). However, the MANOVA did yield a statistically significant result for decade (Table 2).

The univariate two-way MANOVAs yielded no statistically significant difference in mean $\delta^{13}\text{C}_{\text{lipid-normalized}}$ values between sexes or when considering the interaction term (Table 3). There was, however, a statistically significant difference in mean $\delta^{13}\text{C}_{\text{lipid-normalized}}$ values among decades (Table 3; Figure 10). There was no statistically significant

Table 3. Results of the univariate two-way MANOVA tests performed on both isotopic systems ($\delta^{13}\text{C}_{\text{collagen}}/\delta^{13}\text{C}_{\text{lipid-normalized}}$ and $\delta^{15}\text{N}$) and sex, decade, and sex/decade.

Dataset	Isotopic System	Factor	<i>F</i> statistic	<i>df</i>	<i>p</i> value
Pure collagen	$\delta^{13}\text{C}_{\text{collagen}}$	Sex	1.125	2	0.334
Pure collagen	$\delta^{13}\text{C}_{\text{collagen}}$	Decade	4.630	1	0.037*
Pure collagen	$\delta^{13}\text{C}_{\text{collagen}}$	Sex and Decade	1.012	1	0.320
Pure collagen	$\delta^{15}\text{N}$	Sex	0.133	2	0.876
Pure collagen	$\delta^{15}\text{N}$	Decade	0.263	1	0.610
Pure collagen	$\delta^{15}\text{N}$	Sex and Decade	2.636	1	0.112
Lipid-normalized	$\delta^{13}\text{C}_{\text{lipid-normalized}}$	Sex	0.123	2	0.884
Lipid-normalized	$\delta^{13}\text{C}_{\text{lipid-normalized}}$	Decade	15.174	1	< 0.001*
Lipid-normalized	$\delta^{13}\text{C}_{\text{lipid-normalized}}$	Sex and Decade	3.267	1	0.075
Lipid-normalized	$\delta^{15}\text{N}$	Sex	0.279	2	0.757
Lipid-normalized	$\delta^{15}\text{N}$	Decade	0.604	1	0.439
Lipid-normalized	$\delta^{15}\text{N}$	Sex and Decade	2.115	1	0.150

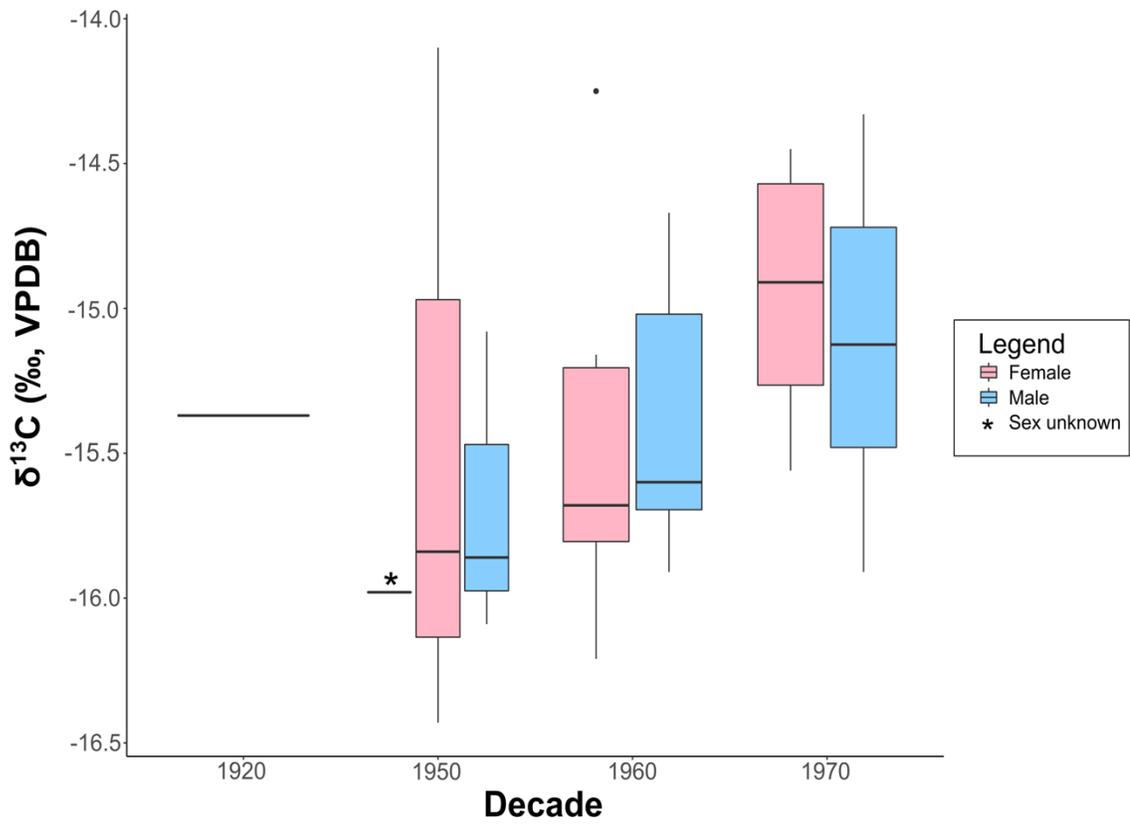


Figure 6. Boxplot of $\delta^{13}\text{C}_{\text{collagen}}$ values of Lancaster Sound polar bears ($n = 49$) from the pure-collagen dataset over time. The single bear from the 1920s is male.

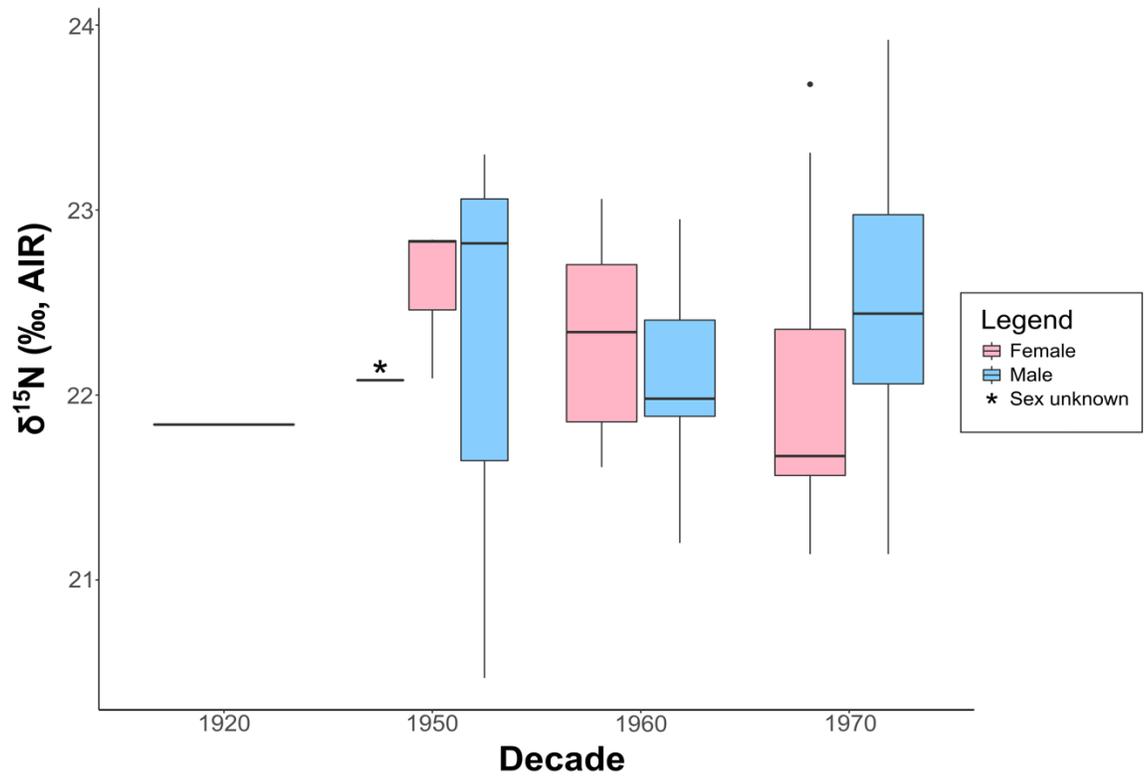


Figure 7. Boxplot of $\delta^{15}\text{N}$ values of Lancaster Sound polar bears ($n = 49$) from the pure-collagen dataset over time. The single bear from the 1920s is male.

Table 4. Results of the univariate one-way ANOVA tests performed on the $\delta^{13}\text{C}_{\text{collagen}}/\delta^{13}\text{C}_{\text{lipid-normalized}}$ values and decade.

Dataset	Isotope system	Factor	<i>F</i> statistic	<i>df</i>	<i>p</i> value
Pure collagen	$\delta^{13}\text{C}_{\text{collagen}}$	Decade	3.377	3	0.026*
Lipid-normalized	$\delta^{13}\text{C}_{\text{lipid-normalized}}$	Decade	9.200	3	< 0.001*

Table 5. Results of the Pearson's Correlation tests performed on $\delta^{13}\text{C}_{\text{collagen}}/\delta^{13}\text{C}_{\text{lipid-normalized}}$ values and mean annual temperature or total annual precipitation.

Dataset	Isotope system	Climate variable	<i>r</i> statistic	<i>df</i>	<i>p</i> value
Pure collagen	$\delta^{13}\text{C}_{\text{collagen}}$	Mean annual temperature (°C)	-0.199	46	0.175
Pure collagen	$\delta^{13}\text{C}_{\text{collagen}}$	Total annual precipitation (mm)	-0.061	46	0.682
Lipid-normalized	$\delta^{13}\text{C}_{\text{lipid-normalized}}$	Mean annual temperature (°C)	-0.126	77	0.267
Lipid-normalized	$\delta^{13}\text{C}_{\text{lipid-normalized}}$	Total annual precipitation (mm)	-0.149	77	0.190

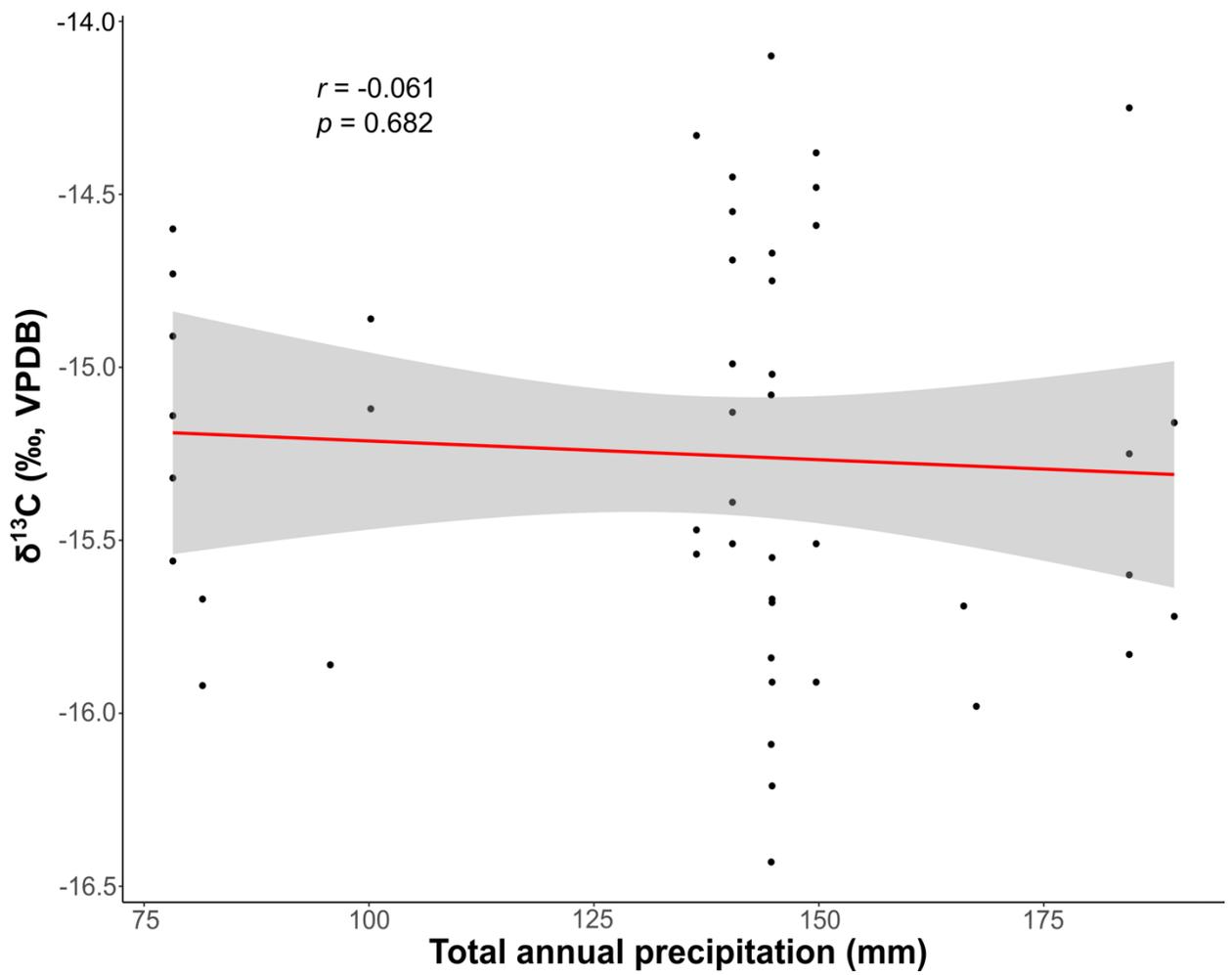


Figure 9. Correlation between total annual precipitation from Resolute and $\delta^{13}\text{C}_{\text{collagen}}$ values of Lancaster Sound polar bears ($n = 49$) from the pure-collagen dataset.

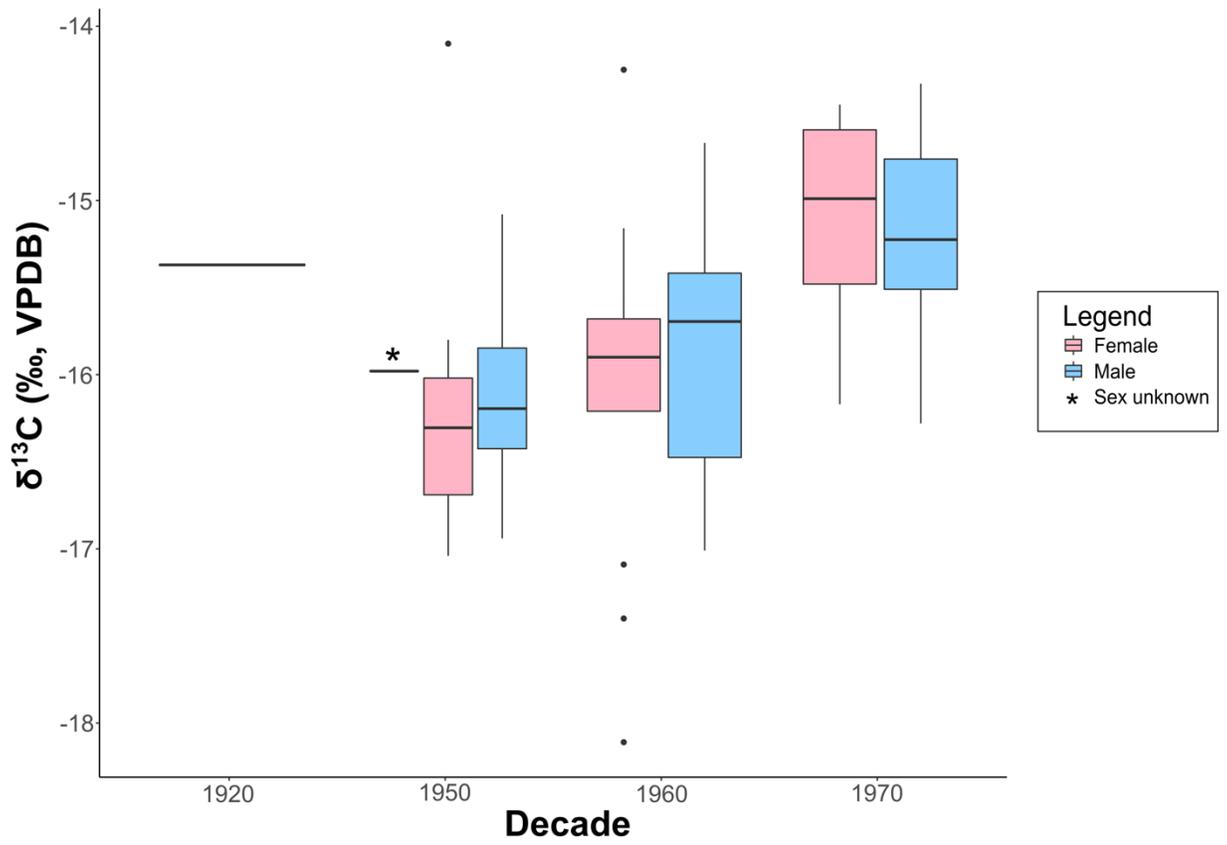


Figure 10. Boxplot of $\delta^{13}\text{C}_{\text{lipid-normalized}}$ values of Lancaster Sound polar bears ($n = 80$) from the lipid-normalized dataset over time. The single bear from the 1920s is male.

difference in mean $\delta^{15}\text{N}$ values between sexes, among decades, or when considering the interaction term (Table 3; Figure 11).

A univariate one-way ANOVA indicated that there was a statistically significant difference in mean $\delta^{13}\text{C}_{\text{lipid-normalized}}$ values among decades (Table 4). The Tukey's honestly significant difference test revealed that 1970 and 1950 ($p < 0.001$), and 1970 to 1960 ($p < 0.001$; Figure 10) differed significantly in $\delta^{13}\text{C}_{\text{lipid-normalized}}$ values.

As was the case with the pure-collagen dataset, neither of the Pearson's correlations, between $\delta^{13}\text{C}_{\text{lipid-normalized}}$ values and mean annual temperature (Figure 12), and between $\delta^{13}\text{C}_{\text{lipid-normalized}}$ values and total annual precipitation (Figure 13), were significant (Table 5).

3.3. Calculated trophic levels

The mean trophic level for all bears was $\text{TL} = 5.33$ ($\text{SD} = \pm 0.20$). Interestingly, both the highest calculated trophic level ($\text{TL} = 5.80$) and the lowest calculated trophic level ($\text{TL} = 4.80$) belonged to male bears from the 1960 and 1950 decades, respectively (Table 6; Appendix V). The mean trophic level calculated for male bears was $\text{TL} = 5.34$ ($\text{SD} = \pm 0.23$), and for female bears was $\text{TL} = 5.31$ ($\text{SD} = \pm 0.16$; Table 6; Appendix V).

3.4. Bayesian stable isotope mixing model results

Polar bears had the highest isotopic values of all the species, supporting their position as the apex predators of the ecosystem (Figure 14). Ringed seals remained the primary prey species consumed by polar bears throughout time, followed by beluga

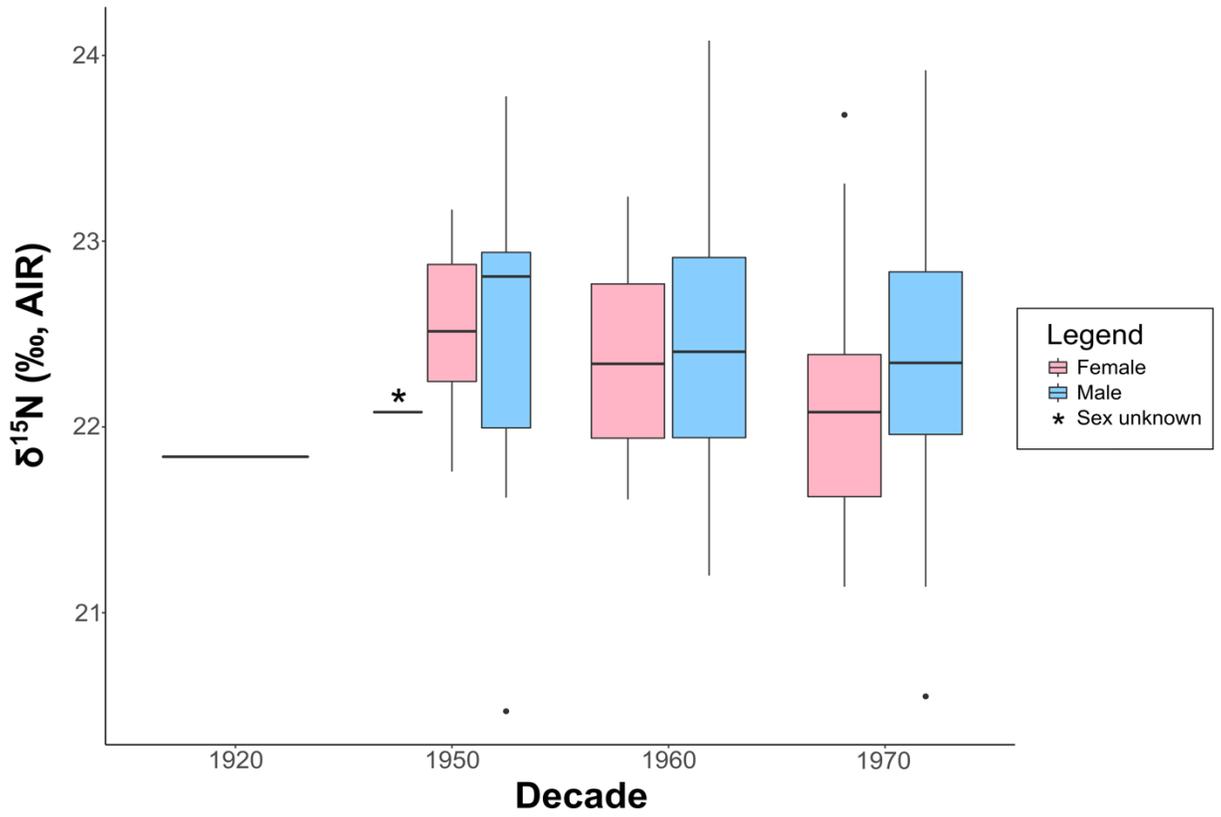


Figure 11. Boxplot of $\delta^{15}\text{N}$ values of Lancaster Sound polar bears ($n = 80$) from the lipid-normalized dataset over time. The single bear from the 1920s is male.

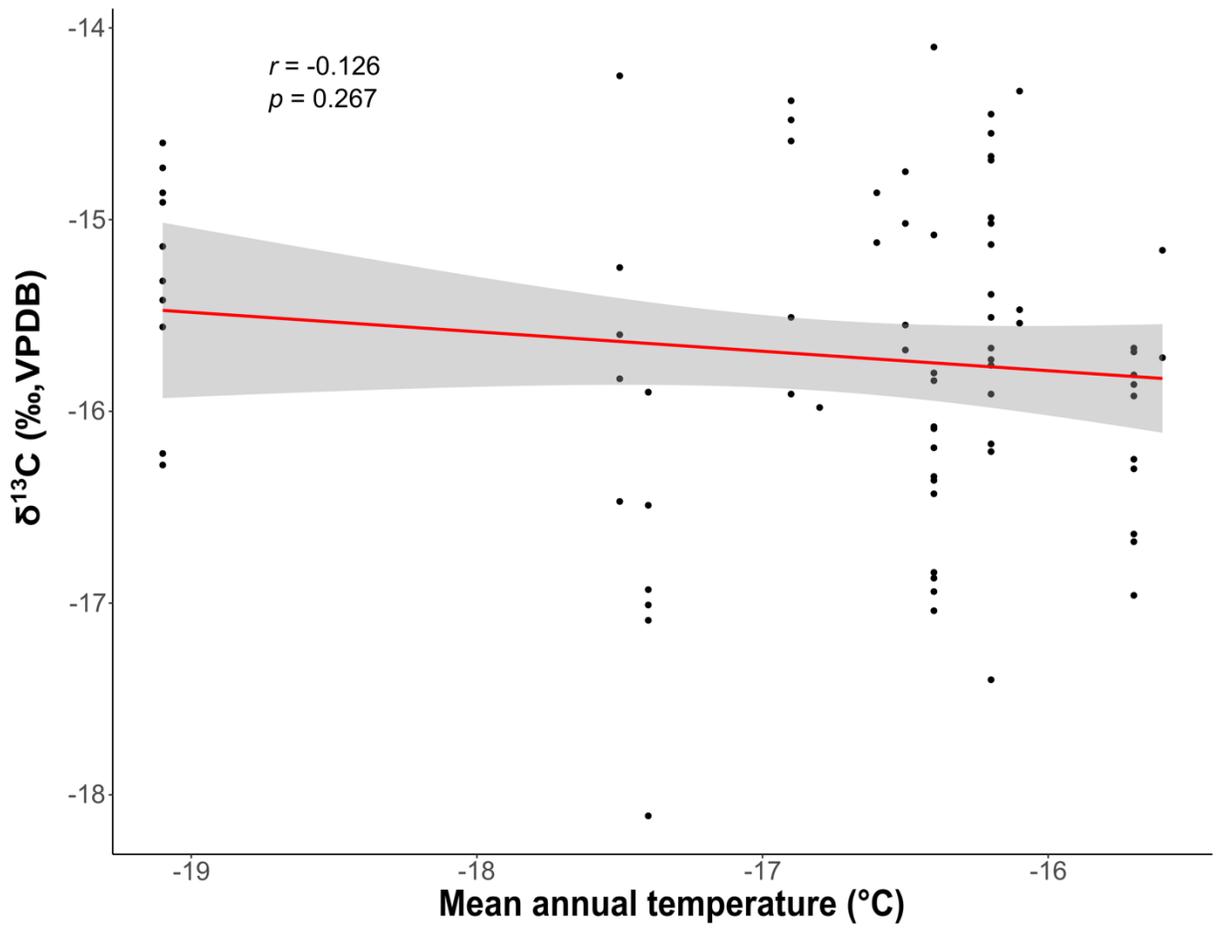


Figure 12. Correlation between mean annual temperature from Resolute and $\delta^{13}\text{C}_{\text{lipid-normalized}}$ values of Lancaster Sound polar bears ($n = 80$) from the lipid-normalized dataset.

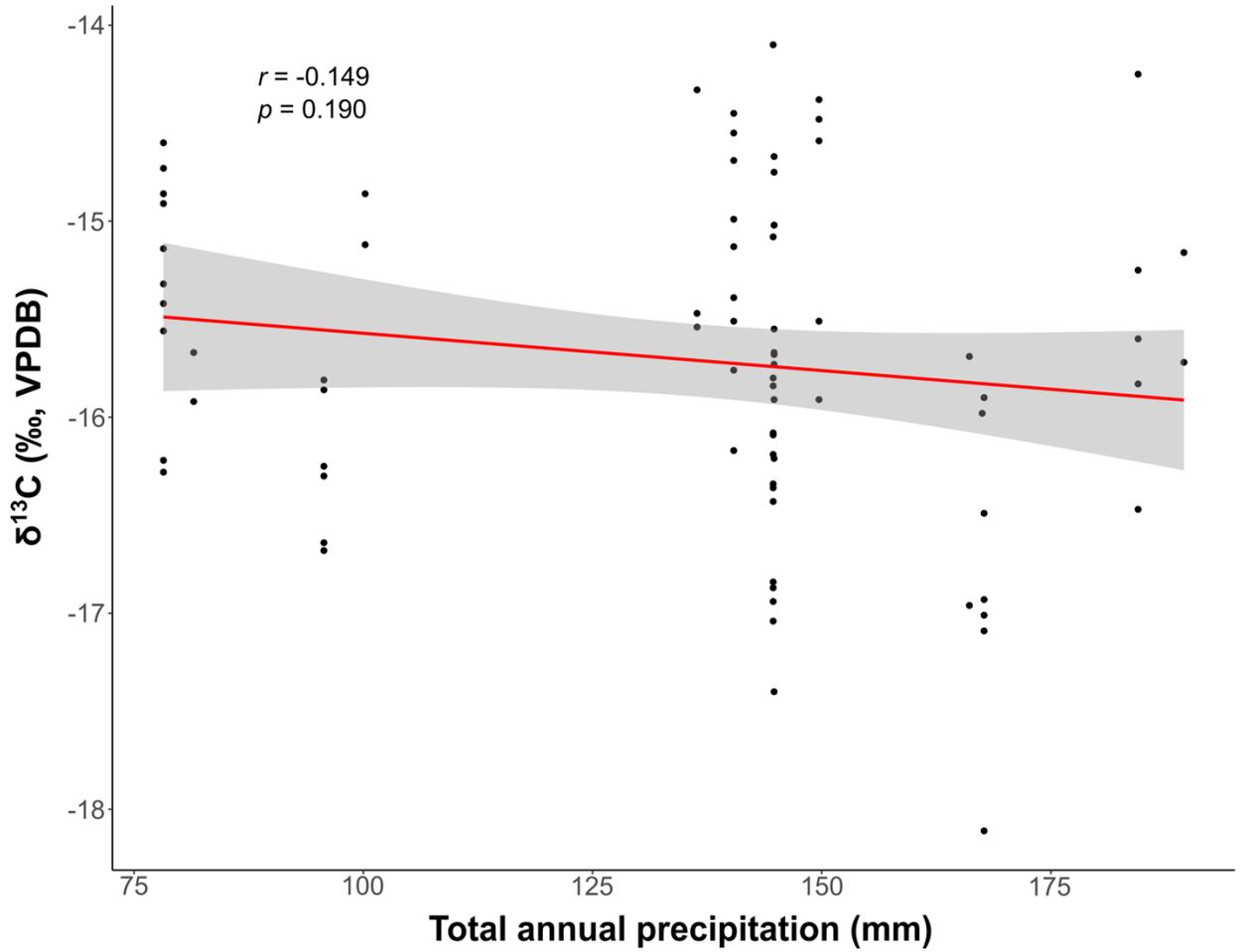


Figure 13. Correlation between total annual precipitation from Resolute and $\delta^{13}\text{C}_{\text{lipid-normalized}}$ values of Lancaster Sound polar bears ($n = 80$) from the lipid-normalized dataset.

Table 6. Means and ranges of calculated trophic level (TL) for male and female polar bears from the Lancaster Sound from each sampled decade.

	1920s	1950s	1960s	1970s
Overall mean TL	5.18	5.36	5.34	5.29
Male mean TL	5.18	5.35	5.35	5.33
Highest male TL	5.18	5.72	5.80	5.76
Lowest male TL	5.18	4.80	5.00	4.82
Mean female TL	–	5.37	5.32	5.25
Highest female TL	–	5.55	5.57	5.69
Lowest female TL	–	5.15	5.11	4.98

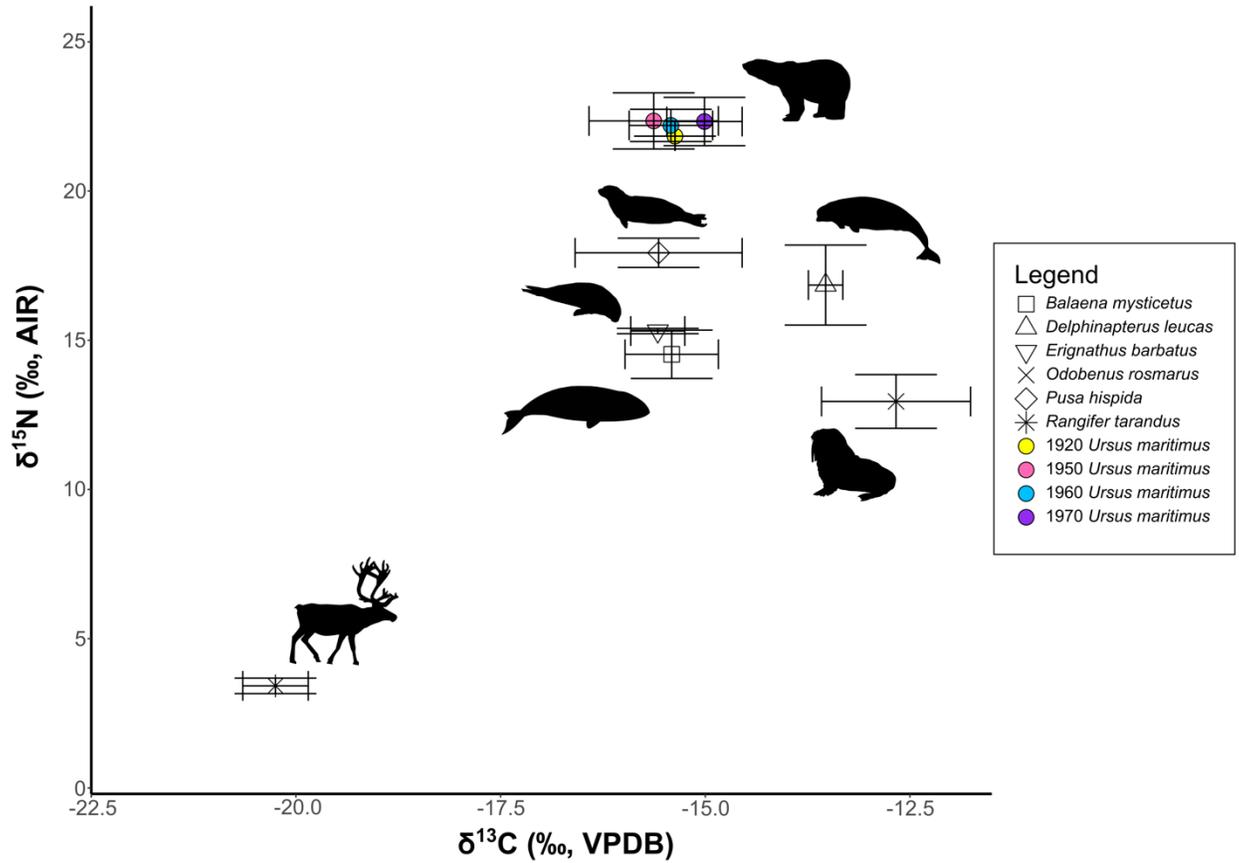


Figure 14. Isospace plot of mean $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{15}\text{N}$ values (\pm standard deviations) of Lancaster Sound polar bears from the pure-collagen dataset ($n = 49$) grouped by decade, and of the six potential prey species included in this study. *B. mysticetus*, *D. leucas*, and *O. rosmarus* values from Schoeninger and DeNiro (1984); *E. barbatus*, *O. rosmarus*, and *P. hispida* values from Szpak et al. (2018); *O. rosmarus* values from Clark et al. (2017); *R. tarandus* values from Drucker et al. (2012).

whales, bowhead whales, bearded seals, with caribou and walrus contributing little to the overall diets of bears (Table 7; Figure 15; Appendix VI).

Table 7. Mean diets (%) of male and female polar bears from the Lancaster Sound during each sampled decade based on the results of the Bayesian stable isotope mixing models.

Mean diet	<i>Balaena mysticetus</i>	<i>Delphinapterus leucas</i>	<i>Erignathus barbatus</i>	<i>Odobenus rosmarus</i>	<i>Pusa hispida</i>	<i>Rangifer tarandus</i>
1920s – overall	17.20	20.40	15.60	8.60	29.90	8.20
1920s – males	17.20	20.40	15.60	8.60	29.90	8.20
1920s – females	–	–	–	–	–	–
1950s – overall	17.03	21.73	15.39	8.44	27.06	10.34
1950s – males	17.30	21.07	15.97	8.47	26.40	10.83
1950s – females	16.63	23.37	14.83	8.70	26.43	10.00
1960s – overall	17.18	21.94	15.37	8.42	27.89	9.19
1960s – males	17.16	21.71	15.41	8.39	28.40	8.93
1960s – females	17.21	22.31	15.31	8.47	27.10	9.61
1970s – overall	16.96	23.95	15.51	9.27	25.70	8.60
1970s – males	16.98	24.26	15.45	9.10	25.03	9.15
1970s – females	16.95	23.62	15.57	9.45	26.42	7.99

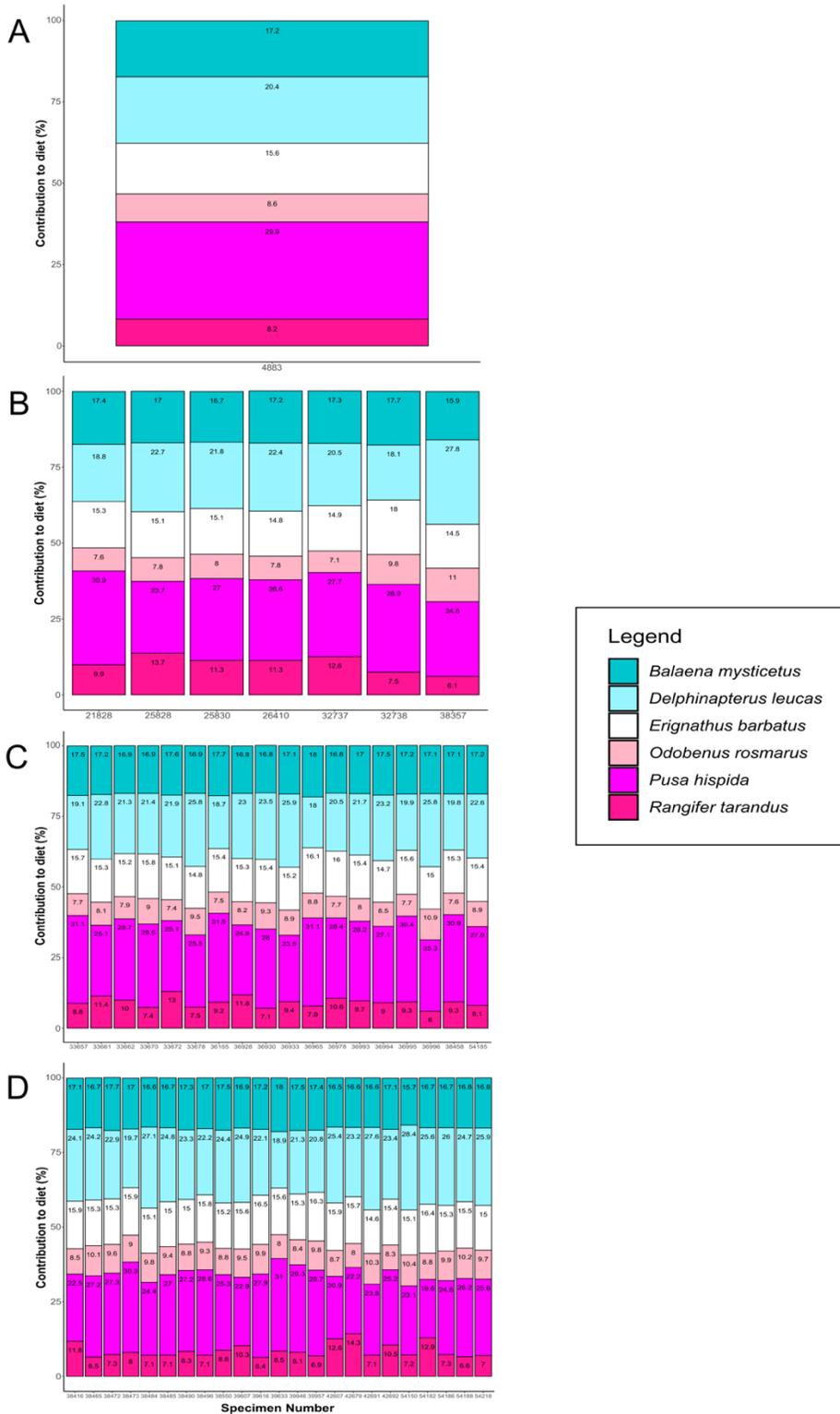


Figure 15. Barplots representing the contribution to diet of the six prey species based on the Bayesian stable isotope mixing models to: A) the polar bear from the 1920s ($n = 1$); B) polar bears from the 1950s ($n = 7$); C) polar bears from the 1960s ($n = 18$); and D) polar bears from the 1970s ($n = 23$). All bears are from the pure-collagen dataset.

CHAPTER 4: DISCUSSION

The present study aimed to determine whether polar bears from the Lancaster Sound subpopulation may have altered their ecology in response to a changing Arctic climate from the 1950s–1970s using stable isotope analysis (SIA). Throughout the early to mid-20th century, however, the polar bears of Lancaster Sound underwent limited changes in their dietary ecology. $\delta^{15}\text{N}$ values remained similar from the 1920s through the 1970s (Figure 7, Figure 11), although there was considerable (non-significant) variation among individuals. Despite the effects of anthropogenically-driven climate change (King, 2004; Hoegh-Guldberg and Bruno, 2010; Wassman et al., 2011; Hunter et al., 2010; Stirling and Derocher, 2012; Derocher et al., 2013), which have included a reduction in sea ice, polar bears maintained their position as the apex predators (Table 6; Figure 14; Appendix V) and did not experience significant nutritional stress, as evidenced using stable isotope analysis. There was, however, a significant increase in the $\delta^{13}\text{C}$ values of the polar bears through time, most notably from the 1950s to the 1970s (Figure 6, Figure 10). Given that Bayesian stable isotope mixing models (BSIMMs) were highly similar among bears and decades, showing a consistent preference for ringed seals (Table 7) changes in $\delta^{13}\text{C}$ values do not appear to be driven by changes in diet (Figure 15). Taken together, these results suggest that other (i.e., environmental) factors may have driven the changes in the $\delta^{13}\text{C}$ values of polar bear bone collagen, including space use change (Pomerleau et al., 2011; Pomerleau et al., 2016; Boucher et al., 2019) or baseline changes resulting from increasing marine primary productivity (Descolas-Gros and Fontugne, 1990; Pabi et al., 2008).

4.1. Historic polar bears did not undergo dietary shifts

Throughout the 20th century (1950s–1970s), polar bears from the Lancaster Sound subpopulation were the apex predators of the marine ecosystem; both male and female bears occupied trophic positions of ~5 (Table 6; Appendix V). This is supported by little change in polar bear $\delta^{15}\text{N}$ values over time (Figure 7, Figure 11), which remained consistent with expected values for a top marine predator (DeNiro and Epstein, 1978; Chisholm et al., 1982; Schoeninger and DeNiro, 1984; Ramsay and Hobson, 1991; Schulting, 1998). The similarity of $\delta^{15}\text{N}$ values among the decades does not support Hypothesis One, meaning that polar bears did not experience an increase in nutritional stress over time. Historically the Lancaster Sound region has never been completely ice-free during the summer (Welch et al., 1992), presenting little hindrance to the hunting activities of polar bears during the early and mid-20th century. Although some environmental changes did occur (primarily an accelerating loss of sea ice during the 1970s; Walsh and Johnson, 1979; Walsh and Chapman, 2001; Kinnard et al., 2008), the present study suggests they were not severe enough to necessitate a change in the foraging behaviours of polar bears. In all decades (1950s–1970s), seals made up the largest proportion of the diets of polar bears, while whales were the second largest dietary contributors (Table 7; Figure 15). Walrus and caribou contributed the least to polar bear diets and were likely not significant food resources for polar bears in the recent past (Table 7; Figure 15). Thus, Hypothesis Two, which stated that in the 1970s polar bears began to utilize more terrestrial resources of food, is not supported. Terrestrial food resources were not important resources to historic polar bears, which is consistent with

previous studies (Ramsay and Hobson, 1991; Derocher et al., 1993; Gormezano and Rockwell, 2013; Iles et al., 2013; Rode et al., 2015).

From the 1950s to the 1970s, ringed seals remained the largest contributing prey species to polar bear diets, consistent with previous studies (Stirling and McEwan, 1975; Stirling and Archibald, 1977; Stirling and Derocher 2012; Rogers et al., 2015; Table 7; Figure 15; Appendix VI). This result is unsurprising, given that, during the early spring months, polar bears feed almost exclusively on the abundant ringed seals to replenish the fat stores lost over the winter (Stirling and Archibald, 1977; Smith, 1980; Hammill and Smith, 1991; Pilfold et al., 2015; Whiteman et al., 2018). Ringed seals, like polar bears, are among the many Arctic species that rely heavily on sea ice for survival. They typically inhabit nearshore or coastal habitats where they have consistent access to land-fast ice (McLaren, 1958; Burns, 1970; Kingsley et al., 1985; Hammill and Smith, 1988; Matley et al., 2015). Ringed seals also occasionally occupy offshore areas with abundant pack ice (Finley et al., 1983; Freitas et al., 2008; Kelly et al., 2010).

Since ringed seals are most abundant in nearshore habitats, the female bears (often accompanied by cubs) that occupy these areas most frequently have best access to ringed seals, compared to the male bears that can venture into more pelagic environments to hunt (Stirling et al., 1977; Schweinsburg et al., 1982; Matley et al., 2015). Given the rarity of ringed seals in more pelagic environments and their high variability in reproductive success (Harwood et al., 2000), male polar bears could have resorted to feeding on other pelagic prey species (e.g. bearded seals, beluga whales) to fulfill their nutritional requirements, particularly as sea ice declined during the 1970s (Walsh and Johnson, 1979; Walsh and Chapman, 2001; Kinnard et al., 2008). There is some evidence

that ringed seal reproductive success was low and seal abundance declined slightly during the early 1960s and mid 1970s in Alaska (Quakenbush et al., 2011), which may be linked to concurrent decreases in sea ice (Walsh and Johnson, 1979; Walsh and Chapman, 2001; Kinnard et al., 2008). However, these data are not available for Lancaster Sound. It is possible, however, that a difference in access to ringed seals between female and male polar bears due differences in habitat use behaviours could explain the slight discrepancy in ringed seal consumption.

Bearded seals were only the fourth highest contributing species to polar bear diets (~15.44% overall diet; Table 7; Figure 15; Appendix VI). There is very little change in the contribution of bearded seals to the diets of both male and female polar bears over time from Lancaster Sound; indeed, consumption of bearded seals remained low from the 1950s to the 1970s (Table 7; Figure 15), which is somewhat surprising, considering that they are typically observed to be a significant prey source (Stirling and Derocher, 2012; Rogers et al., 2015; Bourque et al., 2020). However, bearded seal consumption by polar bears varies geographically. For example, bearded seals are less important prey resources to polar bears in the eastern Arctic (near Lancaster Sound) compared to polar bears that inhabit the western Arctic (Stirling and Archibald, 1977). The percentage of bearded seal in polar bear diets calculated here is similar to those determined by other studies on eastern Arctic populations (Galicía et al., 2015; Galicía et al., 2016), suggesting that the results presented here may accurately reflect the proportion of bearded seals consumed by Lancaster Sound polar bears.

Interestingly, whales were significant food resources for the polar bears of Lancaster Sound during the 1950s through the 1970s. Beluga whales were the second

highest contributing species to the overall diets of polar bears, followed by bowhead whales (Table 7; Figure 15; Appendix VI), in contrast to some previous studies (Stirling and Derocher, 2012; Rogers et al., 2015; Bourque et al., 2020). However, whales are known to comprise a significant portion of polar bear diets (Freeman, 1973; Heyland and Hay, 1976; Smith and Sjare, 1990; Rugh and Shelden, 1993; Thiemann et al., 2008), and to have been an historically important prey source to polar bears (Laidre et al., 2018c).

Although belugas contribute to the diets of all bears, only male polar bears demonstrated an overall (albeit very small) increase in beluga whale consumption over time (Table 7; Figure 15). An increase in beluga whale consumption could have contributed to the slight increase of male polar bear $\delta^{13}\text{C}$ values over time (Figure 6, Figure 10) and resulted from declines in ringed seal populations (Quakenbush et al., 2011), although admittedly the observed increase is very small and may not be indicative of any pronounced change. Male polar bears are large and are able to hunt beluga whales, which has been documented (Freeman, 1973; Smith and Sjare, 1990). Because the movements of male polar bears are not limited by cubs, as they are for females (Stirling et al., 1977; Schweinsburg et al., 1982; Pilfold et al., 2017), they are able to venture further offshore into the open water habitats that belugas occupy (Matley et al., 2015), giving them direct hunting access. It is fairly uncommon for female polar bears to hunt beluga whales due to the difference in size, though it has been documented when beluga whales were caught in ice entrapments (Freeman, 1973; Lowry et al., 1987). However, this is situational, and it is more likely that the contribution of beluga whale to female bear diets is due to scavenging carcasses left from subsistence harvests (Thiemann et al., 2008).

Bowhead whales were the third-highest contributor to polar bear diets. The dietary contributions of bowhead whales remained relatively stable throughout time for both sexes (Table 7; Figure 15; Appendix VI). Bowhead whales are the only species that is exclusively scavenged, not hunted, by polar bears. It is important to note that the contribution of bowhead whales to polar bear diets does not necessarily reflect the consumption of multiple whales – due to the extremely high consumable mass of bowhead whales (approximately 22,000 kg, roughly equivalent to 1,300 ringed seals; Laidre et al., 2018c), it is possible that concurrent bears in the study population fed upon on a single, or very few, bowhead whale(s). Since the remains left over from Inuit subsistence hunting still contain a large amount of unused tissues, they can feed large numbers of polar bears for months (Atwood et al., 2016). Exclusively feeding on a bowhead whale carcass for weeks to months would account for the high overall dietary contribution, especially if the rate of isotopic turnover is relatively high in polar bear bones (Huja et al., 2006). Regardless of the rate of isotopic turnover, it is evident that bowhead whales were a significant food source for polar bears during the 20th century (1950s–1970s), supporting previous studies that have recorded bowhead whales as important food sources for bears (Rogers et al., 2015; Laidre et al., 2018c; Whiteman et al., 2018; Petherick et al., 2021). It is possible, however, that as climate change continues to decrease the extent of sea ice and the hunting area of Lancaster Sound polar bears, their reliance on bowhead whale carcasses could increase as a means to cope with changing environmental conditions and reduced hunting access to other prey species.

Walrus are one of the lowest contributing species to polar bear diets (Table 7; Figure 15; Appendix VI). The low contribution of walrus to the diets of polar bears is

consistent with previous studies (Thiemann et al., 2008; Galicia et al., 2015; Galicia et al., 2016; Boucher et al., 2019), although the estimate generated in this study is slightly higher. Though rare, there are documented cases of polar bears successfully hunting walrus (Calvert and Stirling, 1990). But during the 19th century, walrus populations declined significantly, due intense hunting by colonizers working in the whaling industry (Bockstoce and Botkin, 1982); it is thought that approximately 140,000 walrus were killed by whalers from 1848 to 1914 (Bockstoce and Botkin, 1982). Walrus populations remained low throughout the period of study and to today (Stewart et al., 2013). Their low reproductive rates have greatly limited their ability to re-establish their former population size quickly (Garlich-Miller and Stewart, 1999). The combination of low hunting success and small population size of walrus likely explains why they contributed so little to the diets of Lancaster Sound polar bears.

Caribou also contributed very little to the diets of the polar bears (Table 7; Figure 15; Appendix VI). The dietary contribution of caribou decreased in both sexes over time (see Table 11), though it is unlikely that this shift is biologically meaningful. The low proportion of caribou included in polar bear diets is expected and is consistent with the estimate from a dietary study conducted by Gormezano and Rockwell (2013). Polar bears are known to occasionally scavenge caribou remains (Derocher et al., 2000; Rode et al., 2015), though they are not believed to be capable of actively hunting caribou (Brook and Richardson, 2002). However, polar bears may be forced to make greater use of terrestrial food sources such as caribou as climate change continues to alter the Arctic.

4.1.1. Limitations of dietary reconstructions

Though the dietary reconstructions for Lancaster Sound bears are largely consistent with previous studies, the input parameters for the BSIMMs can strongly influence model results and even mask dietary shifts. Firstly, the standard deviations associated with the dietary estimates generated by the BSIMMs are high (Appendix VI). Large standard deviations result from the use of uninformative priors, meaning that all prey species were weighted as being equally likely contributors to polar bear diets. This was done so as not to unintentionally bias the results with preconceived notions of what species make up the major components of polar bear diets. For example, although polar bears rarely hunt beluga whales and walruses, it is possible (Freeman, 1973; Lowry et al., 1987; Calvert and Stirling, 1990). Thus, informative priors based on, for example, the body mass of prey (as in Landry et al., 2021), would be inappropriate and could produce misleading results. Large standard deviations also result from uncertainty in trophic enrichment factors (TEFs). No TEFs exist that are specific to $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of polar bear bone collagen, thus the TEFs used here may not accurately reflect the degree of trophic enrichment from food to polar bear tissues. Because the TEFs used were not species-specific, the standard deviations used for the TEFs were also quite high at $\pm 1.0\%$, which likely also contributed to the high standard deviations for the dietary inputs estimates from the BSIMMs. Finally, none of the prey species that were used in the models were sampled from the Lancaster Sound region. Unfortunately, no isotopic data are available for the chosen prey species from the Lancaster Sound, which is unsurprising, considering that the area is remote and understudied compared to other Arctic regions. There is an effect of geography on isotopic composition (e.g., Burton and Koch, 1999; Hobson,

1999; Newsome et al., 2010; Boucher et al., 2019; Boucher et al., 2020) that cannot be corrected for, unlike the Suess effect. Inaccuracies may therefore have been introduced by the use of non-localized prey isotope values, thus resulting in the high associated standard deviations. Additionally, the error that is associated with the application of the Suess effect correction itself on isotopic data is believed to be very low, typically < 0.01‰, less than the analytical error commonly produced by mass spectrometers (Gruber et al., 1999; McNeil et al., 2001; Verburg, 2007), so it is unlikely that the Suess effect corrected contributed a significant amount of error to the dietary estimates.

Additionally, only six species of potential prey were included in the BSIMMs – the reasoning behind this is twofold. The first reason is that including too many prey species that are not thought to be possible important dietary contributors introduces significant and unnecessary additional uncertainty into the models (Moore and Semmens, 2008; Newsome et al., 2010). By including a large number of prey species, there is an increased effect of similarity in isotopic values and ranges of the prey species. Since some of the prey species that were important to include in the models already had similar isotopic values (i.e., bearded seal and bowhead whale; Figure 14), additional possible prey species were omitted from the models in an effort to maximize the ability of the model to produce precise and accurate dietary estimates. Isotopic data from bone collagen was also not available for other prey species that are thought to be a component of polar bear diets (e.g., sea birds). It is important to only include isotopic data from the specific tissue being analyzed because different tissues from the same animal can have very different isotopic compositions (Stenroth et al., 2006; Newsome et al., 2010; Cherry et al., 2011; Borrell et al., 2012; Codron et al., 2012; Clark et al., 2019; Vanderklift et al.,

2020). For example, seabirds and their eggs are often opportunistically consumed by polar bears (Stempniewicz, 1993; Rockwell and Gormezano, 2009; Smith et al., 2010; Iles et al., 2013; Iverson et al., 2014; Dey et al., 2017), but there is very little isotopic data of seabird collagen, as the majority of the isotopic studies conducted on seabirds sampled muscles, blood, and/or feathers from the birds (eg., Becker, et al., 2007; Choy et al., 2010; Wold et al., 2011; Moody et al., 2012; Horwath Burnham et al., 2018).

Although there is significant uncertainty associated with the diet estimates produced by the BSIMMs, the overall percentages of prey species in the diet are consistent with previous studies, with seals and whales being the two major groups that contribute to polar bear diets (Thiemann et al., 2008; Cherry et al., 2011; Galicia et al., 2015; Galicia et al., 2016; Boucher et al., 2019; Bourque et al., 2020). Thus, the dietary estimates produced in this study likely do reflect the diets of 20th century (1950s–1970s) Lancaster Sound polar bears, which remained generally static over time. Taken together, the present study shows that Lancaster Sound polar bears did not undergo significant changes in diet from the 1950s–1970s, definitively remaining at the top of the marine food web. Since polar bears did not shift their diets, what then drove the observed changes in $\delta^{13}\text{C}$ from the 1950s through 1970s?

4.2. Stable isotopes of polar bears may reflect their environment

The mean $\delta^{13}\text{C}$ values of both male and female polar bears from the Lancaster Sound has increased from the 1950s to the 1970s (Figure 6, Figure 10). There is little evidence to suggest a shift in the diets of polar bears based on the findings of this study (Table 7; Figure 15). Thus, it is most likely that this change is linked to an environmental

factor. Because the polar bear $\delta^{13}\text{C}$ values in both datasets have all been corrected to account for the Suess effect, the influence of isotopically light anthropogenically-produced dissolved inorganic carbon (i.e., dissolved CO_2) can be ruled out. I propose two possible explanations for the change in polar bear $\delta^{13}\text{C}$ values: 1) that polar bears altered their space use patterns over time, or 2) there was a change in the marine primary productivity of Lancaster Sound during the mid-20th century that shifted the carbon isotopic baseline.

4.2.1. A change in polar bear space use patterns

$\delta^{13}\text{C}$ values in phytoplankton are typically higher in coastal environments compared to pelagic environments (Cifuentes et al., 1988; Wainright and Fry, 1994). The coastal areas in the Canadian Arctic Archipelago, in which the Lancaster Sound is located, exhibit the same pattern (Pomerleau et al., 2011; Pomerleau et al., 2016). Increasing $\delta^{13}\text{C}$ values may therefore have resulted from polar bears increasing their use of coastal environments from the 1950s to the 1970s. Although $\delta^{13}\text{C}$ values in polar bears are thought to be poor predictors of their space use patterns (Boucher et al., 2019), a shift to increasing use of coastal environments is supported by the change in female bear $\delta^{15}\text{N}$ values.

Previous research has indicated that $\delta^{15}\text{N}$ values are closely linked to space use patterns in mammals (e.g., Burton and Koch, 1999; Hobson, 1999; Kurle and Worthy, 2002; Fontaine et al., 2007; Newsome et al., 2010; Boucher et al., 2019). Though it is not significant, there is a trend of decreasing $\delta^{15}\text{N}$ values of female polar bears over time in both the pure collagen and lipid normalized datasets (Figure 7, Figure 11). This trend

could be explained by female bears spending more time in coastal areas or even inland through time. This could offer partial support Hypothesis Two, that bears began spending more time in nearshore or inland areas, but it is still insufficient to truly support the hypothesis. Due to the limitations in mobility that cubs exert on their mother, females with cubs do not travel as far as males, single females, or females with older offspring in search of prey (Schweinsburg et al., 1982; Ramsay and Andriashek, 1986; Durner and Amstrup, 1995; Johnson et al., 2017; Pilfold et al., 2017), and tend to avoid large, open bodies of water due to the risk of hypothermia in young cubs (Blix and Lentfer, 1979). Females with cubs typically remain on land-fast ice to feed on ringed seal pups and to avoid male bears, which will occasionally prey on cubs (Derocher and Stirling, 1990; Stirling et al., 1993; Freitas et al., 2012). As climate change altered the Arctic and decreased the extend of land-fast ice (Walsh and Johnson, 1979; Walsh and Chapman, 2001; Copland et al., 2007; Kinnard et al., 2008; Meier et al., 2014; White et al., 2015), it is possible that female bears with cubs were forced to restrict their feeding grounds to nearer shore regions (Freitas et al., 2012). Males would not have needed to make this adjustment, given fewer restrictions on their movements.

Polar bears living in nearshore environments have also been reported to have lower $\delta^{15}\text{N}$ values compared to those in pelagic environments (Boucher et al., 2019), lending support to the space use hypothesis. Terrestrial ecosystems have lower $\delta^{15}\text{N}$ values compared to marine ecosystems (Wada et al., 1987; Montoya, 2007; Whitney et al., 2018), and animals that consume terrestrially-derived foods subsequently exhibit lower $\delta^{15}\text{N}$ values (Schoeninger and DeNiro, 1984). Additionally, nearshore marine environments have significant inputs of terrestrial organic material (Gearing, 1988;

Hedges et al., 1997; Raymond and Bauer, 2001), including nitrogen, resulting in nearshore environments having a higher nutrient content and comparatively lower $\delta^{15}\text{N}$ values than offshore pelagic environments (Schell et al., 1998; Dunton et al., 2006; Harris et al., 2018) because isotope fractionation is maximized (i.e., the lighter isotope, ^{14}N , is preferentially incorporated over the heavier isotope, ^{15}N ; Michener and Schell, 1994). Thus, even if female bears with cubs were not directly consuming terrestrial foods, the input of terrestrial nitrogen to marine waters could have altered the $\delta^{15}\text{N}$ values of the marine prey they consumed (i.e., ringed seal pups, bowhead whale carcasses), which could have contributed to the observed decrease in female $\delta^{15}\text{N}$ values.

However, it is arguably unlikely that a change in space use patterns is the primary driver of the increase in $\delta^{13}\text{C}$ values among the bears samples for this study. As previously mentioned, $\delta^{13}\text{C}$ is a poor predictor of spatial use in polar bears (Boucher et al., 2019). This, combined with the finding that only the $\delta^{15}\text{N}$ values of female polar bears exhibit only non-significant change and that the $\delta^{13}\text{C}$ values increase in both sexes, indicates that the possibility that a change in polar bear space use patterns is responsible for the shift in $\delta^{13}\text{C}$ values is quite small.

4.2.2. A shift in the carbon baseline

It is considerably more likely that the observed increase in polar bear $\delta^{13}\text{C}$ values over time is a reflection of a change in the carbon baseline of Lancaster Sound – that is, a change in the $\delta^{13}\text{C}$ values of the primary producers. Phytoplankton are the dominant primary producers in Arctic marine ecosystems and are responsible for ~90% of primary productivity in Lancaster Sound (Welch et al., 1992). Unlike terrestrial plants, the

dominant controls on phytoplankton photosynthesis, and by extension $\delta^{13}\text{C}$ values, are not temperature and precipitation (Tieszen, 1991; Stewart et al., 1995; Schulze et al., 1996; Heaton, 1999; Liu et al., 2005; Diefendorf et al., 2010; Linares et al., 2011), but rather light availability (Rysgaard et al., 1999) and the openness of the water (i.e., the extent of summer sea ice; Burkhardt et al., 1999; Leu et al., 2015). The photosynthetic process of phytoplankton is still relatively poorly understood, and their photosynthetic efficiency is highly variable (Sackett et al., 1965; Welch et al., 1992; Goericke and Fry, 1994; Burkhardt et al., 1999). What is known is that high primary productivity in the form of more efficient photosynthesis is linked to an enrichment of ^{13}C in phytoplankton due to reduced isotopic fractionation, resulting in an overall increase in phytoplankton $\delta^{13}\text{C}$ values (Descolas-Gros and Fontugne, 1990).

Unfortunately, there are no available data regarding phytoplankton (or any other primary producer) $\delta^{13}\text{C}$ values or primary productivity throughout the period of this study (1950s to 1970s) from Lancaster Sound. However, based on $\delta^{13}\text{C}$ values from the polar bears, I postulate that primary productivity gradually increased since the 1950s. Sea ice extent was relatively uniform prior to the early 1900s, but started to become more variable during the 1920s, although these observations are of varying degrees of accuracy and availability (Walsh and Chapman, 2001; Kinnard et al., 2008). During the 1950s, sea ice extent started to decline steadily, and an abrupt loss of sea ice occurred in the Arctic throughout the 1970s (Walsh and Johnson, 1979; Walsh and Chapman, 2001; Kinnard et al., 2008). In Lancaster Sound, the loss of sea ice was much less apparent than in other Arctic regions, only declining slightly from 1950 to 1970 (Sou and Flato, 2009), though there was pronounced increases in the fluctuations in the abundance of sea ice throughout

the same period of time (Prinsenberg and Hamilton, 2005), which could have similarly affected the $\delta^{13}\text{C}$ values of the phytoplankton, and subsequently, the polar bears. Since the 1970's, climate change has driven marked decreases in the extent of summer sea ice, increasing the duration of the open water period throughout the Arctic and increasing marine primary productivity from at least 1998 to 2006 (Arrigo et al., 2008; Pabi et al., 2008; Slagstad et al., 2015). Though observations do not exist, it is possible that the loss of sea ice from the 1950s to the 1970s caused an increase in phytoplankton photosynthesis throughout the Arctic Ocean, resulting in an overall increase in the baseline $\delta^{13}\text{C}$ value that is reflected throughout the marine food web and ultimately in the $\delta^{13}\text{C}$ values of polar bears.

Alternatively, it is also possible that there may have been a change in the community composition of the phytoplankton species from the 1950s to the 1970s. This shift may have been induced by changes in sea ice or other effects of climate change (Wassman et al., 2011; Coupel et al., 2012; Riebesell et al., 2013; Terrado et al., 2013; Thoisen et al., 2015), but could also be unrelated. Previous studies have determined that the relative abundances of various phytoplankton taxa are highly annually variable (Stockwell et al., 2001; Degerlund and Eilertsen, 2010; Ardyna et al., 2011; Hamilton et al., 2013; Blais et al., 2017), and even undergo significant changes in species assemblages from spring to fall within the same year (Michel et al., 1993; von Quillfeldt, 2000; Sukhanova et al., 2009; Lammers et al., 2017). Further, as climate change progresses and the ocean waters become warmer, novel species that were formerly restricted to lower latitudes have been observed to be moving further north and are now present in the high Arctic (Hegseth and Sundfjord, 2008). It is therefore possible that the

baseline shift of $\delta^{13}\text{C}$ values may have been the result of a change in the phytoplankton community structure in Lancaster Sound, as different types of phytoplankton are known to exhibit different $\delta^{13}\text{C}$ values (Wong and Sackett, 1978; Fontugne and Duplessy, 1981; Descolas-Gros and Fontugne, 1990; Hinga et al., 1994; Vuorio et al., 2006; Brutemark et al., 2009). However, there are unfortunately no historical records that exist of phytoplankton species abundances and community structure from the 1950s to the 1970s of Lancaster Sound that could help support or reject the above-mentioned hypotheses for $\delta^{13}\text{C}$ change among the sampled polar bears.

To investigate whether a baseline shift did occur, I will conduct future research on the same polar bear specimens using compound-specific SIA to test for shifts in bear essential amino acid (i.e., phenylalanine, lysine) $\delta^{13}\text{C}$ values, which closely reflect baseline $\delta^{13}\text{C}$ values (Wu, 2009; O'Connell, 2017; Whiteman et al., 2019). If there are changes in essential amino acid $\delta^{13}\text{C}$ values that are similar in magnitude to that which is observed in bulk $\delta^{13}\text{C}$ values, I will conclude that there was a shift in baseline $\delta^{13}\text{C}$ values (i.e., in phytoplankton) that drove increasing polar bear $\delta^{13}\text{C}$ values.

Although I consider it likely that a baseline shift was responsible for the observed increase in the observed $\delta^{13}\text{C}$ values from the 1950s to 1970s, it is highly unlikely that a similar $\delta^{15}\text{N}$ baseline shift occurred. Primary producers (namely, phytoplankton) uptake carbon and nitrogen through different mechanisms. Photosynthesis is the mechanism by which primary producers incorporate carbon isotopes, and the process is affected by a variety of factors, as previously discussed. The manner in which primary producers uptake nitrogen, however, is through nitrogen fixation. $\delta^{15}\text{N}$ values of primary producers therefore reflect the $\delta^{15}\text{N}$ value of the source of (inorganic) nitrogen, the isotope

fractionation during uptake, and the fraction of the total nutrient supply consumed (Altabet and Francois, 1994). In Arctic waters, the nitrogen source of primary producers is nitrate (NO_3^- ; Miyake and Wada, 1967). Nitrogen fixation is limited by the abundance of NO_3^- in the environment, and, because the Arctic Ocean is relatively limited in NO_3^- , (Sakshaug, 2003; Pabi et al., 2008), primary producers (phytoplankton) tend to have fairly high $\delta^{15}\text{N}$ values due to decreased fractionation (Michener and Schell, 1994). Since the concentration of NO_3^- in the Arctic Ocean has remained generally consistent in the past (1988–2008), regardless of changes in sea ice extent (Zhang et al., 2010), it is reasonable to assume that it had not changed significantly from the 1950s to the 1970s. Additionally, because the $\delta^{15}\text{N}$ values of polar bears remained similar over time (Figure 7, Figure 11), I find no evidence for a change in the nitrogen baseline.

4.3. A multi-decadal isotopic baseline for polar bears

In this thesis, I have developed an isotopic baseline for polar bears spanning over 50 years. To my knowledge, this work encompasses the longest span of time of any isotopic study conducted on polar bears, and is the first to obtain isotopic data on historic polar bears from the Lancaster Sound subpopulation. Although there were some environmental changes manifested in the polar bears over time, these were largely related to a change in the marine isotopic baseline, and are not indicative of changes in the ecology of polar bears themselves. Historic polar bears were the apex predators of their ecosystems, and fed almost exclusively on seals and whales. This study provides a novel dataset that future studies can use as a historic baseline to assess whether present-day

polar bears may be undergoing ecological changes (i.e., related to diet, habitat use) as a result of climate change.

CHAPTER 5: CONCLUSIONS

5.1. Conclusions

In this thesis, I provide insights into the historical ecology of polar bears from the Lancaster Sound subpopulation in Nunavut using stable isotope analysis (SIA). To my knowledge, this study is the first to use SIA to investigate historical ecology of polar bears from this subpopulation and to encompass such a long time interval (1923 to 1975). There was a change in polar bear $\delta^{13}\text{C}$ values over time, which I hypothesize reflects a shift in baseline $\delta^{13}\text{C}$ values (i.e., in phytoplankton) primarily driven by a change in sea ice dynamics. In contrast, the polar bear $\delta^{15}\text{N}$ values do not change over time, which indicates that the trophic, and thereby the dietary, ecology of polar bears likely remained similar throughout the 20th century (1950s–1970s); polar bears did not alter their diets over time, remaining the apex predators of the Arctic, feeding primarily on seals and whales. Slight, albeit insignificant changes in $\delta^{15}\text{N}$ values may reflect a shift in space use patterns of female polar bears, although there is currently insufficient evidence to support this hypothesis.

Taken together, these findings suggest that 20th century (1950s–1970s) Lancaster Sound polar bears were generally conservative in their ecology. Climate change and changes in sea ice extent and duration during the early to mid-20th century may not have been severe enough to necessitate ecological shifts among polar bears, enabling them to retain their ecological characteristics (i.e., hunting and space use behaviours). However, the lack of ecological change may also suggest that polar bears are ecologically inflexible, and are not able to change their ecology even during major events of climatic

change. This could pose a significant conservation challenge if polar bears are not able to adapt their feeding habits and space use to changing environmental conditions. Although this study cannot draw conclusions regarding the ecology of recent polar bears (i.e., late 20th century and early 21st century), it offers a means by which future studies that will use SIA to investigate modern polar bear ecology can be compared to the ecology of historic polar bears and determine whether any significant changes have occurred from the mid-1970s and onwards.

Further, this study provides additional evidence for seals and whales being key prey resources for polar bears over extended periods of time (>30 years), although this is a much shorter interval than what the traditional ecological knowledge (TEK) of the Inuit encompasses. Conservation programs aimed at protecting polar bears should thus take a multi-species protection approach, as the findings of this thesis may suggest that the reliance of polar bears on seals and whales possess limited ecological flexibility and will continue to specialize on seals and whales even as climate changes continue to impact the Arctic. Failure to preserve sufficient populations of seals and whales for polar bears to hunt could contribute to ongoing population declines, and ultimately the demise of polar bears as a species.

5.2. Future research directions

I plan to conduct further research that will build upon the findings of my thesis by re-analyzing the specimens that were unsuccessfully lipid-extracted, increasing the sample size, and implementing compound-specific stable isotope analysis (CS-SIA). Covid-19 limited my access to collections and lab space during 2020 and 2021, but I have

already re-sampled the 37 bears that were not successfully lipid-extracted during sample preparation, along with two additional specimens that previously did not contain enough collagen for isotopic analysis. Instead of collecting powdered bone, which posed significant problems for the preparation of samples prior to stable isotope analysis, I removed loose pieces of the nasal turbinates to be used in future analyses. This was done to increase the amount of bone samples and to minimize lipid content, as the nasal turbinates appeared to be less fatty (i.e., more dry, less greasy to the touch) than many of the other bones. I also plan to sample additional polar bear specimens in this same manner to increase sample size. Now that I am once again able to access lab space, I will prepare my samples following the protocol outlined in Chapter 3, with a modification to the solvent used. Instead of using petroleum ether, I will use a 2:1 chloroform-methanol mixture to achieve successful lipid extraction so that I will not have to mathematically lipid-normalize the samples.

Covid-19 prevented me from extending the methodology in my thesis to include CS-SIA. In the very near future, I plan to perform CS-SIA on a subsample of both male and female polar bears from each decade. CS-SIA involves analyzing individual organic compounds, specifically amino acids (e.g., Howland et al. 2003; McCarthy et al., 2004; McCarthy et al., 2007; Popp et al., 2007). It is a relatively new methodology that can be used to study food webs of ecosystems and to address some of the limitations of bulk SIA (McClelland and Montoya, 2002; Larsen et al., 2009; McMahan et al., 2010; Whiteman et al., 2019). CS-SIA of amino acids in dietary studies provides a means to distinguish between trophic and baseline contributions to bulk SIA values (McClelland and Montoya, 2002; Popp et al., 2007; Chikaraishi et al., 2009; McMahan et al., 2010; Larsen et al.,

2012; Larsen et al., 2013; Schiff et al., 2014). This is based on the predictable differences in the isotopic enrichment of various amino acids through trophic transfer (DeNiro and Epstein, 1978; Minagawa and Wada, 1984). Source amino acids (e.g., phenylalanine, serine) undergo little to no isotopic enrichment and thus exhibit $\delta^{15}\text{N}$ values that closely reflect the baseline isotopic signature, while trophic amino acids (e.g., glutamic acid, proline) undergo significant enrichment, and the $\delta^{15}\text{N}$ values provide insight into the animal's trophic level (McClelland and Montoya, 2002; Chikaraishi et al., 2009; McMahon et al., 2015). Essential amino acids (e.g., phenylalanine, leucine) have $\delta^{13}\text{C}$ values that are proxies for primary producers because animals exclusively obtain essential amino acids from their diets, and cannot synthesize them *de novo* (McMahon et al., 2011), meaning the $\delta^{13}\text{C}$ values remain largely unchanged throughout the food web (Larsen et al., 2012). In contrast, non-essential amino acids (e.g., glutamic acid, aspartic acid) do undergo isotopic enrichment, where the $\delta^{13}\text{C}$ values are thought to reflect the routing of the isotope in the food web and the dietary protein quality/quantity (McMahon et al., 2010; Schiff et al., 2014).

I will use CS-SIA of bone collagen from a subsample of polar bears to investigate whether the observed shift in $\delta^{13}\text{C}$ values is linked to a change in essential amino acid $\delta^{13}\text{C}$ values. If the change is reflected in essential amino acid $\delta^{13}\text{C}$ values, I will interpret this as support for a shift in baseline $\delta^{13}\text{C}$ values during the 20th century (primarily 1950s to 1970s). If no change is apparent in essential amino acid $\delta^{13}\text{C}$ values, but is observed in non-essential amino acid $\delta^{13}\text{C}$ values, then it is most likely a shift in polar bear diets – namely, in either dietary protein quantity or quality. I will also use CS-SIA to further explore polar bear $\delta^{15}\text{N}$ values beyond the limitations of bulk SIA. Analysis of source

amino acid $\delta^{15}\text{N}$ values will illuminate whether there has been a change in space use patterns of female bears over time, while analysis of trophic amino acid $\delta^{15}\text{N}$ values will provide insights into potential small changes in the diets of polar bears.

I will also use the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of phenylalanine and glutamic acid obtained through CS-SIA to calculate accurate TEFs for polar bear bone collagen using the following equation from Germain et al. (2013):

$$\text{TEF}_{\text{Glu-Phe}} = \Delta_{\text{Glu}} - \Delta_{\text{Phe}} = (\delta^{15}\text{N}_{\text{Glu,Consumer}} - \delta^{15}\text{N}_{\text{Glu,Food}}) - (\delta^{15}\text{N}_{\text{Phe,Consumer}} - \delta^{15}\text{N}_{\text{Phe,Food}}) \quad (6)$$

where $\delta^{15}\text{N}_{\text{Glu,Consumer}}$ and $\delta^{15}\text{N}_{\text{Phe,Consumer}}$ represent the values obtained for the polar bear, and $\delta^{15}\text{N}_{\text{Glu,Food}}$ and $\delta^{15}\text{N}_{\text{Phe,Food}}$ will be values obtained from ringed seals that will be sampled and used as the representative species for polar bear diets. By obtaining an accurate TEF for polar bear bone collagen, future studies that investigate the diets of polar bears can implement these TEFs in Bayesian stable isotope mixing (BSIMMs) to generate more accurate dietary estimates. Future BSIMMS should also attempt to use localized prey sources to more accurately reflect the isotopic composition of the trophic system in Lancaster Sound. I aim to reach out to Inuit communities in Lancaster Sound to inquire about their knowledge of local polar bear diets, and (if granted express permission) use the given information to generate accurate informative priors of prey consumption by polar bears in my BSIMMs. I will also be developing TEFs for additional tissues (blood serum, blood clot, and hair) of polar bears living in captivity at the Toronto Zoo, which may be used in future studies on the diets of wild bears.

Additional future studies should incorporate 21st century (early 2000s to present) polar bear specimens to assess more recent changes in their ecology (i.e., space use patterns, diets). Any observed changes could be indicative of increasing pressure of

climate change and sea ice loss on polar bears. I am in contact with the Wildlife Research Section of the Department of Environment from the Government of Nunavut to obtain such modern specimens. Similar studies should also be conducted on bears from other subpopulations, particularly those from understudied/data deficient subpopulations, such as East Greenland, Chukchi Sea, Gulf of Boothia, and Norwegian Bay (IUCN/SSC Polar Bear Specialist Group, 2019). By developing historical isotopic baselines for polar bears, present-day monitoring programs can more effectively determine when and if changes in polar bear ecology occurred, and, combined with critical TEK of the Inuit, can identify which key resources should be of conservation priority to maximize the chances for polar bear survival beyond the end of the 21st century.

APPENDICES

Appendix I. Summary of the pure-collagen Lancaster Sound polar bears including sex, data of collection, location of collection, $\delta^{13}\text{C}$ value obtained directly from isotopic analyses, $\delta^{13}\text{C}$ value corrected for the Suess effect, and $\delta^{15}\text{N}$ value

Sample ID	Sex	Date collected	Location	$\delta^{13}\text{C}_{\text{raw}}$ (‰)	$\delta^{13}\text{C}_{\text{Suess effect}}$ (‰)	$\delta^{15}\text{N}$ (‰)
CMNMA 4883	Male	1923	Ellesmere Island	-15.47	-15.37	21.84
CMNMA 21828	-	1950	Dundas Harbour, Devon Island	-16.19	-15.98	22.08
CMNMA 25828	Male	1959	Barrow Strait	-16.35	-16.09	23.30
CMNMA 25830	Female	1959	Barrow Strait	-16.10	-15.84	22.82
CMNMA 26410	Male	1958	Cornwallis Island	-16.12	-15.86	22.82
CMNMA 32737	Female	1959	Barrow Strait	-16.70	-16.43	22.84
CMNMA 32738	Male	1959	Barrow Strait	-15.34	-15.08	20.47
CMNMA 33657	Female	1960	Cornwallis Island	-15.96	-15.69	21.77
CMNMA 33661	Male	1963	Beechy Island, Wellington Channel	-15.97	-15.67	22.95
CMNMA 33662	Male	1962	Cornwallis Island	-15.96	-15.67	22.41
CMNMA 33670	Male	1963	Cornwallis Island	-15.31	-15.02	21.55
CMNMA 33672	Female	1963	Cornwallis Island	-16.50	-16.21	23.06
CMNMA 33678	Male	1963	Wellington Channel	-14.97	-14.67	22.40
CMNMA 36165	Male	1963	McDougall Sound	-16.21	-15.91	21.89
CMNMA 36928	Female	1968	Limestone Island (near Somerset Island)	-16.02	-15.68	23.06
CMNMA 36930	Male	1968	Ellesmere Island	-15.09	-14.75	21.88
CMNMA 36933	Male	1968	Barlow Inlet, Cornwallis Island	-15.36	-15.02	22.90
CMNMA 36965	Male	1968	Resolute Bay,	-15.89	-15.55	21.20

			Cornwallis Island			
CMNMA 36978	Female	1962	Barrow Strait	-16.20	-15.92	22.34
CMNMA 36993	Male	1967	Devon Island	-15.93	-15.60	22.39
CMNMA 36994	Female	1967	Wellington Channel	-15.58	-15.25	22.35
CMNMA 36995	Male	1967	Wellington Channel	-16.16	-15.83	21.96
CMNMA 36996	Female	1967	Devon Island	-14.58	-14.25	21.61
CMNMA 38357	Female	1959	Griffith Island	-14.36	-14.10	22.09
CMNMA 38416	Male	1971	Somerset Island	-15.87	-15.51	23.29
CMNMA 38458	Male	1969	Grise Fiord, Ellesmere Island	-16.07	-15.72	21.98
CMNMA 38465	Female	1971	Grise Fiord, Ellesmere Island	-14.91	-14.55	21.66
CMNMA 38472	Male	1970	Grise Fiord, Ellesmere Island	-15.22	-14.86	21.89
CMNMA 38473	Female	1971	Grise Fiord, Ellesmere Island	-15.76	-15.39	21.41
CMNMA 38484	Female	1971	Grise Fiord, Ellesmere Island	-14.82	-14.45	22.26
CMNMA 38485	Male	1971	Grise Fiord, Ellesmere Island	-15.06	-14.69	22.11
CMNMA 38490	Male	1970	Grise Fiord, Ellesmere Island	-15.48	-15.12	22.33
CMNMA 38496	Female	1971	Grise Fiord, Ellesmere Island	-15.35	-14.99	21.59
CMNMA 38550	Male	1971	Grise Fiord, Ellesmere Island	-15.50	-15.13	22.52
CMNMA 39607	Female	1972	Resolute Bay, Cornwallis Island	-15.52	-15.14	23.31
CMNMA 39616	Male	1972	Assistance Bay, Resolute	-15.10	-14.73	21.14
CMNMA 39633	Female	1972	Devon Island	-15.94	-15.56	21.67

CMNMA 39946	Male	1972	Grise Fiord, Ellesmere Island	-15.70	-15.32	21.91
CMNMA 39957	Female	1972	Grise Fiord, Ellesmere Island	-15.29	-14.91	21.14
CMNMA 42607	Female	1973	Cape Sparbo, Devon Island	-15.92	-15.54	23.68
CMNMA 42679	Male	1975	Resolute Bay, Cornwallis Island	-16.32	-15.91	23.60
CMNMA 42691	Male	1975	Somerset Island	-14.79	-14.38	22.36
CMNMA 42692	Male	1975	Resolute Bay, Cornwallis Island	-15.92	-15.51	22.87
CMNMA 54150	Male	1973	Arctic Bay	-14.71	-14.33	22.73
CMNMA 54182	Male	1973	Resolute Bay, Cornwallis Island	-15.86	-15.47	23.92
CMNMA 54185	Female	1969	Devon Island	-15.51	-15.16	21.94
CMNMA 54186	Female	1972	Devon Island	-14.97	-14.60	22.45
CMNMA 54188	Female	1975	Devon Island	-14.89	-14.48	21.54
CMNMA 54218	Female	1975	Somerset Island	-15.00	-14.59	22.13

Appendix II. Summary of the lipid-normalized Lancaster Sound polar bears including sex, data of collection, location of collection, $\delta^{13}\text{C}$ value obtained directly from isotopic analyses, lipid-corrected $\delta^{13}\text{C}$ value, $\delta^{13}\text{C}$ value corrected for the Suess effect, and $\delta^{15}\text{N}$ value

Sample ID	Sex	Year Collected	Location	$\delta^{13}\text{C}_{\text{raw}}$ (‰)	$\delta^{13}\text{C}_{\text{lipid}}$ correction (‰)	$\delta^{13}\text{C}_{\text{Suess}}$ effect (‰)	$\delta^{15}\text{N}$ (‰)	C:N
CMNMA 4883	Male	1923	Ellesmere Island	-15.47	–	-15.37	21.84	3.30
CMNMA 21828	-	1950	Dundas Harbour, Devon Island	-16.19	–	-15.98	22.08	3.49
CMNMA 23327	Male	1958	Resolute Bay, Cornwallis Island	-18.88	-16.94	-16.68	21.62	5.31
CMNMA 23328	Male	1958	Resolute Bay, Cornwallis Island	-16.56	-16.06	-15.81	22.12	3.86
CMNMA 23329	Male	1958	Resolute Bay, Cornwallis Island	-19.83	-16.56	-16.30	22.82	6.65
CMNMA 23332	Female	1958	Resolute Bay, Cornwallis Island	-17.19	-16.90	-16.64	23.15	3.65
CMNMA 25828	Male	1959	Barrow Strait	-16.35	–	-16.09	23.30	3.48
CMNMA 25829	Female	1959	Barrow Strait	-17.93	-17.14	-16.87	23.17	4.16
CMNMA 25830	Female	1959	Barrow Strait	-16.10	–	-15.84	22.83	3.35
CMNMA 25831	Male	1959	Barrow Strait	-17.84	-17.21	-16.94	23.78	3.99
CMNMA 25835	Female	1959	Barrow Strait	-17.82	-17.31	-17.04	22.98	3.87
CMNMA 26409	Female	1958	Cornwallis Island	-16.87	-16.51	-16.25	22.23	3.72
CMNMA 26410	Male	1958	Cornwallis Island	-16.12	–	-15.86	22.82	3.20
CMNMA 32734	Female	1959	Barrow Strait	-16.81	-16.34	-16.08	22.37	3.83
CMNMA 32735	Female	1959	Barrow Strait	-17.73	-16.63	-16.36	21.76	4.46
CMNMA 32736	Female	1959	Barrow Strait	-16.32	-16.06	-15.80	22.55	3.61
CMNMA 32737	Female	1959	Barrow Strait	-16.70	–	-16.43	22.84	3.45

CMNMA 32738	Male	1959	Barrow Strait	-15.34	–	-15.08	20.47	3.15
CMNMA 32739	Female	1959	Barrow Strait	-19.91	-17.11	-16.84	22.25	6.18
CMNMA 32741	Female	1959	Barrow Strait	-16.92	-16.46	-16.19	22.48	3.82
CMNMA 32742	Male	1960	Barrow Strait	-20.24	-17.24	-16.96	23.25	6.39
CMNMA 32757	Male	1959	Barrow Strait	-17.38	-16.61	-16.34	22.80	4.14
CMNMA 32770	Female	1961	Resolute Bay, Cornwallis Island	-19.43	-17.37	-17.09	22.22	5.43
CMNMA 32772	Female	1961	Cornwallis Island	-16.75	-16.18	-15.90	22.02	3.93
CMNMA 32773	Male	1961	Cornwallis Island	-18.06	-17.29	-17.01	23.50	4.13
CMNMA 32774	Female	1961	Cornwallis Island	-20.67	-18.39	-18.11	23.24	5.66
CMNMA 32777	Male	1961	Barrow Strait	-18.49	-16.77	-16.49	22.80	5.09
CMNMA 32778	Female	1961	Barrow Strait	-16.45	-16.18	-15.90	22.49	3.63
CMNMA 32779	Male	1961	Barrow Strait	-18.79	-17.21	-16.93	24.08	4.95
CMNMA 33657	Female	1960	Cornwallis Island	-15.96	-15.80	-15.52	21.77	3.51
CMNMA 33661	Male	1963	Beechy Island, Wellington Channel	-15.97	–	-15.67	22.95	3.27
CMNMA 33662	Male	1962	Cornwallis Island	-15.96	–	-15.67	22.41	3.26
CMNMA 33664	Female	1963	Bathurst Island	-18.44	-17.69	-17.40	22.77	4.11
CMNMA 33669	Female	1963	Cornwallis Island	-16.38	-16.02	-15.73	21.75	3.71
CMNMA 33670	Male	1963	Cornwallis Island	-15.31	–	-15.02	21.55	2.91
CMNMA 33672	Female	1963	Cornwallis Island	-16.50	–	-16.21	23.06	3.13
CMNMA 33678	Male	1963	Wellington Channel	-14.97	–	-14.67	22.40	2.93
CMNMA 36165	Male	1963	McDougall Sound	-16.21	–	-15.91	21.89	3.38
CMNMA 36928	Female	1968	Limestone Island	-16.02	–	-15.68	23.06	3.24
CMNMA 36930	Male	1968	Ellesmere Island	-15.09	–	-14.75	21.88	3.02
CMNMA 36933	Male	1968	Cornwallis Island	-15.36	–	-15.02	22.90	3.22

CMNMA 36935	Male	1967	Cape Hardy, Devon Island	-17.58	-16.80	-16.47	22.45	4.14
CMNMA 36965	Male	1968	Resolute Bay, Cornwallis Island	-15.89	–	-15.55	21.20	3.27
CMNMA 36978	Female	1962	Barrow Strait	-16.20	–	-15.92	22.34	3.19
CMNMA 36993	Male	1967	Devon Island	-15.93	–	-15.60	22.39	3.45
CMNMA 36994	Female	1967	Wellington Channel	-15.58	–	-15.25	22.35	3.26
CMNMA 36995	Male	1967	Wellington Channel	-16.16	–	-15.83	21.96	3.34
CMNMA 36996	Female	1967	Devon Island	-14.58	–	-14.25	21.61	2.94
CMNMA 38357	Female	1959	Griffith Island	-14.36	–	-14.10	22.09	3.02
CMNMA 38416	Male	1971	Somerset Island	-15.87	–	-15.51	23.29	3.09
CMNMA 38458	Male	1969	Grise Fiord, Ellesmere Island	-16.07	–	-15.72	21.98	3.37
CMNMA 38465	Female	1971	Grise Fiord, Ellesmere Island	-14.91	–	-14.55	21.66	3.15
CMNMA 38472	Male	1970	Grise Fiord, Ellesmere Island	-15.22	–	-14.86	21.89	3.17
CMNMA 38473	Female	1971	Grise Fiord, Ellesmere Island	-15.76	–	-15.39	21.41	3.45
CMNMA 38484	Female	1971	Grise Fiord, Ellesmere Island	-14.82	–	-14.45	22.26	3.12
CMNMA 38485	Male	1971	Grise Fiord, Ellesmere Island	-15.06	–	-14.69	22.11	3.13
CMNMA 38486	Female	1971	Grise Fiord, Ellesmere Island	-16.37	-16.13	-15.76	22.45	3.60
CMNMA 38490	Male	1970	Grise Fiord,	-15.48	–	-15.12	22.33	3.36

CMNMA 38495	Female	1971	Ellesmere Island Grise Fiord, Ellesmere Island	-17.08	-16.53	-16.17	22.33	3.90
CMNMA 38496	Female	1971	Grise Fiord, Ellesmere Island	-15.35	–	-14.99	21.59	3.22
CMNMA 38550	Male	1971	Grise Fiord, Ellesmere Island	-15.50	–	-15.13	22.52	3.31
CMNMA 39607	Female	1972	Resolute Bay, Cornwallis Island	-15.52	–	-15.14	23.31	3.11
CMNMA 39615	Female	1972	Assistance Bay, Resolute	-15.64	-15.24	-14.86	21.93	3.76
CMNMA 39616	Male	1972	Assistance Bay, Resolute	-15.10	–	-14.73	21.14	3.29
CMNMA 39619	Female	1972	Devon Island	-16.30	-15.79	-15.42	22.08	3.86
CMNMA 39620	Male	1972	Devon Island	-18.42	-16.66	-16.28	20.55	5.13
CMNMA 39624	Male	1972	Grise Fiord, Ellesmere Island	-16.90	-16.60	-16.22	22.24	3.66
CMNMA 39633	Female	1972	Devon Island	-15.94	-15.76	-15.38	21.67	3.53
CMNMA 39946	Male	1972	Grise Fiord, Ellesmere Island	-15.70	–	-15.33	21.91	3.33
CMNMA 39957	Female	1972	Grise Fiord, Ellesmere Island	-15.29	–	-14.91	21.14	3.06
CMNMA 42607	Female	1973	Cape Sparbo, Devon Island	-15.92	–	-15.54	23.68	3.14
CMNMA 42679	Male	1975	Resolute Bay, Cornwallis Island	-16.32	–	-15.91	23.60	3.07
CMNMA 42691	Male	1975	Somerset Island	-14.79	–	-14.38	22.36	3.04

CMNMA 42692	Male	1975	Resolute Bay, Cornwallis Island	-15.92	–	-15.51	22.87	3.29
CMNMA 54150	Male	1973	Arctic Bay	-14.71	–	-14.33	22.73	3.26
CMNMA 54182	Male	1973	Resolute Bay, Cornwallis Island	-15.86	–	-15.47	23.92	3.02
CMNMA 54185	Female	1969	Devon Island	-15.51	–	-15.16	21.94	3.36
CMNMA 54186	Female	1972	Devon Island	-14.97	–	-14.60	22.45	3.23
CMNMA 54188	Female	1975	Devon Island	-14.89	–	-14.48	21.54	2.95
CMNMA 54218	Female	1975	Somerset Island	-15.00	–	-14.59	22.13	3.12

Appendix III. Climate data from Resolute Cars, Nunavut, from 1950 to 1975

Year	Mean annual temperature (°C)	Total annual precipitation
1950	-16.8	167.5
1951	-16.1	122.4
1952	-15.2	99.4
1953	-16.1	133.9
1954	-16.0	130.0
1955	-16.7	126.7
1956	-17.5	135.9
1957	-16.8	146.5
1958	-15.7	95.7
1959	-16.4	144.7
1960	-15.7	166.1
1961	-17.4	167.7
1962	-15.7	81.5
1963	-16.2	144.8
1964	-17.5	132.2
1965	-16.1	114.0
1966	-17.1	112.5
1967	-17.5	184.5
1968	-16.5	144.8
1969	-15.6	189.5
1970	-16.6	100.2
1971	-16.2	140.4
1972	-19.1	78.2
1973	-16.1	136.4
1974	-17.8	139.5
1975	-16.9	149.7

Appendix IV. Summary of the six prey species included in the Bayesian stable isotope mixing models, including $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values obtained directly from the publication, the $\delta^{13}\text{C}$ value corrected for the Suess effect in this study, the date of collection, and source publication

Species	Sample ID	$\delta^{13}\text{C}$ (‰)	$\delta^{13}\text{C}_{\text{corrected}}$ (‰; Suess effect)	$\delta^{15}\text{N}$ (‰)	Date collected	Source
<i>Balaena mysticetus</i>	453	-16.10	-15.58	14.10	Unknown – before 1984	Schoeninger and DeNiro, 1984
<i>Balaena mysticetus</i>	455	-16.40	-15.88	15.40	Unknown – before 1984	Schoeninger and DeNiro, 1984
<i>Balaena mysticetus</i>	456	-15.30	-14.78		Unknown – before 1984	Schoeninger and DeNiro, 1984
<i>Delphinapterus leucas</i>	461	-13.90	-13.38	15.90	Unknown – before 1984	Schoeninger and DeNiro, 1984
<i>Delphinapterus leucas</i>	462	-14.20	-13.68	17.80	Unknown – before 1984	Schoeninger and DeNiro, 1984
<i>Erignathus barbatus</i>	3496	-15.35	–	15.37	2000 – 2001	Szpak et al., 2018
<i>Erignathus barbatus</i>	3518	-15.81	–	15.24	2000 – 2001	Szpak et al., 2018
<i>Odobenus rosmarus</i>	2666	-14.76	–	13.40	2000 – 2001	Szpak et al., 2018
<i>Odobenus rosmarus</i>	UAM 3382	-12.60	-11.66	11.20	2005 – 2006	Clark et al., 2017
<i>Odobenus rosmarus</i>	UAM 7377	-12.90	-11.96	13.00	2005 – 2006	Clark et al., 2017
<i>Odobenus rosmarus</i>	UAM 11512	-12.60	-11.66	14.50	2005 – 2006	Clark et al., 2017
<i>Odobenus rosmarus</i>	UAM 11517	-14.00	-13.06	14.00	2005 – 2006	Clark et al., 2017
<i>Odobenus rosmarus</i>	UAM 11519	-12.60	-11.66	14.30	2005 – 2006	Clark et al., 2017
<i>Odobenus rosmarus</i>	UAM 11684	-12.80	-11.86	12.80	2005 – 2006	Clark et al., 2017
<i>Odobenus rosmarus</i>	UAM 11689	-14.20	-13.26	12.40	2005 – 2006	Clark et al., 2017
<i>Odobenus rosmarus</i>	UAM 11699	-13.30	-12.36	12.70	2005 – 2006	Clark et al., 2017
<i>Odobenus rosmarus</i>	UAM 12079	-13.30	-12.36	12.60	2005 – 2006	Clark et al., 2017
<i>Odobenus rosmarus</i>	UAM 16593	-13.70	-12.76	13.40	2005 – 2006	Clark et al., 2017
<i>Odobenus rosmarus</i>	134	-14.10	-13.58	12.10	Unknown – before 1984	Schoeninger and DeNiro, 1984

<i>Odobenus rosmarus</i>	425	-13.90	-13.38	12.50	Unknown – before 1984	Schoeninger and DeNiro, 1984
<i>Odobenus rosmarus</i>	426	-13.60	-13.08	12.40	Unknown – before 1984	Schoeninger and DeNiro, 1984
<i>Pusa hispida</i>	3484	-15.32	–	18.95	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3485	-14.89	–	17.56	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3488	-14.21	–	17.77	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3489	-15.55	–	16.90	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3490	-15.17	–	17.87	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3491	-15.29	–	17.35	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3492	-15.73	–	17.53	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3493	-16.59	–	17.84	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3494	-15.22	–	17.68	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3495	-18.24	–	17.57	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3497	-14.98	–	18.38	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3498	-15.21	–	18.39	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3499	-18.31	–	17.67	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3503	-15.01	–	17.99	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3504	-13.35	–	17.75	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3505	-15.40	–	18.05	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3506	-15.63	–	18.59	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3507	-15.61	–	18.09	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3508	-15.49	–	18.09	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3510	-15.48	–	18.91	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3514	-15.59	–	18.51	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3515	-15.95	–	18.11	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3519	-16.06	–	17.79	2000 – 2001	Szpak et al., 2018

<i>Pusa hispida</i>	3521	-15.28	–	17.50	2000 – 2001	Szpak et al., 2018
<i>Pusa hispida</i>	3522	-15.80	–	17.39	2000 – 2001	Szpak et al., 2018
<i>Rangifer tarandus pearyi</i>	BNK-7	-20.20	-19.84	3.20	1970	Drucker et al., 2012
<i>Rangifer tarandus pearyi</i>	BNK-18	-20.20	-19.84	3.50	1970	Drucker et al., 2012
<i>Rangifer tarandus pearyi</i>	BNK-4	-20.70	-20.29	3.70	1975	Drucker et al., 2012
<i>Rangifer tarandus pearyi</i>	BNK-11	-21.00	-20.59	3.10	1975	Drucker et al., 2012
<i>Rangifer tarandus pearyi</i>	BNK-15	-21.10	-20.69	3.60	1975	Drucker et al., 2012

Appendix V. Calculated trophic levels for individual polar bears from the Lancaster Sound

Sample ID	Sex	Year Collected	$\delta^{15}\text{N}$ (‰)	Trophic Level
CMNMA 4883	Male	1923	21.84	5.18
CMNMA 21828	–	1950	22.08	5.24
CMNMA 23327	Male	1958	21.62	5.12
CMNMA 23328	Male	1958	22.12	5.25
CMNMA 23329	Male	1958	22.82	5.45
CMNMA 23332	Female	1958	23.15	5.54
CMNMA 25828	Male	1959	23.30	5.58
CMNMA 25829	Female	1959	23.17	5.55
CMNMA 25830	Female	1959	22.83	5.45
CMNMA 25831	Male	1959	23.78	5.72
CMNMA 25835	Female	1959	22.98	5.50
CMNMA 26409	Female	1958	22.23	5.29
CMNMA 26410	Male	1958	22.82	5.45
CMNMA 32734	Female	1959	22.37	5.32
CMNMA 32735	Female	1959	21.76	5.15
CMNMA 32736	Female	1959	22.55	5.37
CMNMA 32737	Female	1959	22.84	5.45
CMNMA 32738	Male	1959	20.47	4.80
CMNMA 32739	Female	1959	22.25	5.29
CMNMA 32741	Female	1959	22.48	5.36
CMNMA 32742	Male	1960	23.25	5.57
CMNMA 32757	Male	1959	22.80	5.44
CMNMA 32770	Female	1961	22.22	5.28
CMNMA 32772	Female	1961	22.02	5.23
CMNMA 32773	Male	1961	23.50	5.64
CMNMA 32774	Female	1961	23.24	5.57
CMNMA 32777	Male	1961	22.80	5.44
CMNMA 32778	Female	1961	22.49	5.36
CMNMA 32779	Male	1961	24.08	5.80
CMNMA 33657	Female	1960	21.77	5.16
CMNMA 33661	Male	1963	22.95	5.49
CMNMA 33662	Male	1962	22.41	5.34
CMNMA 33664	Female	1963	22.77	5.43
CMNMA 33669	Female	1963	21.75	5.15
CMNMA 33670	Male	1963	21.55	5.10
CMNMA 33672	Female	1963	23.06	5.52
CMNMA 33678	Male	1963	22.40	5.33
CMNMA 36165	Male	1963	21.89	5.19
CMNMA 36928	Female	1968	23.06	5.52
CMNMA 36930	Male	1968	21.88	5.19
CMNMA 36933	Male	1968	22.90	5.47
CMNMA 36935	Male	1967	22.45	5.35
CMNMA 36965	Male	1968	21.20	5.00
CMNMA 36978	Female	1962	22.34	5.32
CMNMA 36993	Male	1967	22.39	5.33
CMNMA 36994	Female	1967	22.35	5.32
CMNMA 36995	Male	1967	21.96	5.21
CMNMA 36996	Female	1967	21.61	5.11
CMNMA 38357	Female	1959	22.09	5.25

CMNMA 38416	Male	1971	23.29	5.58
CMNMA 38458	Male	1969	21.98	5.22
CMNMA 38465	Female	1971	21.66	5.13
CMNMA 38472	Male	1970	21.89	5.19
CMNMA 38473	Female	1971	21.41	5.06
CMNMA 38484	Female	1971	22.26	5.29
CMNMA 38485	Male	1971	22.11	5.25
CMNMA 38486	Female	1971	22.45	5.35
CMNMA 38490	Male	1970	22.33	5.31
CMNMA 38495	Female	1971	22.33	5.31
CMNMA 38496	Female	1971	21.59	5.11
CMNMA 38550	Male	1971	22.52	5.37
CMNMA 39607	Female	1972	23.31	5.58
CMNMA 39615	Female	1972	21.93	5.20
CMNMA 39616	Male	1972	21.14	4.98
CMNMA 39619	Female	1972	22.08	5.25
CMNMA 39620	Male	1972	20.55	4.82
CMNMA 39624	Male	1972	22.24	5.29
CMNMA 39633	Female	1972	21.67	5.13
CMNMA 39946	Male	1972	21.91	5.20
CMNMA 39957	Female	1972	21.14	4.98
CMNMA 42607	Female	1973	23.68	5.69
CMNMA 42679	Male	1975	23.60	5.67
CMNMA 42691	Male	1975	22.36	5.32
CMNMA 42692	Male	1975	22.87	5.46
CMNMA 54150	Male	1973	22.73	5.42
CMNMA 54182	Male	1973	23.92	5.76
CMNMA 54185	Female	1969	21.94	5.20
CMNMA 54186	Female	1972	22.45	5.35
CMNMA 54188	Female	1975	21.54	5.09
CMNMA 54218	Female	1975	22.13	5.26

Appendix VI. Results of the Bayesian stable isotope mixing models for individual polar bears from the Lancaster Sound

Sample ID	<i>Balaena mysticetus</i>	<i>Delphinapterus leucas</i>	<i>Erignathus barbatus</i>	<i>Odobenus rosmarus</i>	<i>Pusa hispida</i>	<i>Rangifer tarandus pearyi</i>
CMNMA 4883	0.172 ± 0.158	0.204 ± 0.155	0.156 ± 0.140	0.086 ± 0.085	0.299 ± 0.215	0.082 ± 0.083
CMNMA 21828	0.174 ± 0.166	0.188 ± 0.151	0.153 ± 0.142	0.076 ± 0.078	0.309 ± 0.227	0.099 ± 0.102
CMNMA 25828	0.170 ± 0.164	0.227 ± 0.161	0.151 ± 0.139	0.078 ± 0.081	0.237 ± 0.210	0.137 ± 0.124
CMNMA 25830	0.167 ± 0.162	0.218 ± 0.161	0.151 ± 0.139	0.080 ± 0.080	0.270 ± 0.221	0.113 ± 0.110
CMNMA 26410	0.172 ± 0.164	0.224 ± 0.161	0.148 ± 0.139	0.078 ± 0.076	0.266 ± 0.222	0.113 ± 0.109
CMNMA 32737	0.173 ± 0.172	0.205 ± 0.161	0.149 ± 0.143	0.071 ± 0.071	0.277 ± 0.237	0.126 ± 0.127
CMNMA 32738	0.177 ± 0.151	0.181 ± 0.140	0.180 ± 0.151	0.098 ± 0.094	0.289 ± 0.189	0.075 ± 0.068
CMNMA 33657	0.175 ± 0.164	0.191 ± 0.149	0.157 ± 0.143	0.077 ± 0.078	0.311 ± 0.221	0.088 ± 0.092
CMNMA 33661	0.172 ± 0.160	0.228 ± 0.160	0.153 ± 0.140	0.081 ± 0.079	0.251 ± 0.207	0.114 ± 0.106
CMNMA 33662	0.169 ± 0.160	0.213 ± 0.157	0.152 ± 0.139	0.079 ± 0.079	0.287 ± 0.222	0.100 ± 0.102
CMNMA 33670	0.169 ± 0.151	0.214 ± 0.159	0.158 ± 0.138	0.090 ± 0.086	0.295 ± 0.205	0.074 ± 0.070
CMNMA 33672	0.176 ± 0.171	0.219 ± 0.159	0.151 ± 0.145	0.074 ± 0.074	0.251 ± 0.221	0.130 ± 0.124
CMNMA 33678	0.169 ± 0.154	0.258 ± 0.168	0.148 ± 0.132	0.095 ± 0.088	0.255 ± 0.202	0.075 ± 0.073
CMNMA 36165	0.177 ± 0.170	0.187 ± 0.151	0.154 ± 0.140	0.075 ± 0.076	0.315 ± 0.227	0.092 ± 0.097
CMNMA 36928	0.168 ± 0.160	0.230 ± 0.162	0.153 ± 0.140	0.082 ± 0.082	0.248 ± 0.214	0.118 ± 0.112
CMNMA 36930	0.168 ± 0.150	0.235 ± 0.163	0.154 ± 0.133	0.093 ± 0.087	0.280 ± 0.202	0.071 ± 0.069
CMNMA 36933	0.171 ± 0.153	0.259 ± 0.166	0.152 ± 0.134	0.089 ± 0.086	0.235 ± 0.196	0.094 ± 0.087
CMNMA 36965	0.180 ± 0.166	0.180 ± 0.145	0.161 ± 0.144	0.088 ± 0.086	0.311 ± 0.211	0.079 ± 0.080
CMNMA 36978	0.168 ± 0.163	0.205 ± 0.156	0.160 ± 0.147	0.077 ± 0.076	0.284 ± 0.227	0.106 ± 0.108
CMNMA 36993	0.170 ± 0.159	0.217 ± 0.159	0.154 ± 0.142	0.080 ± 0.078	0.282 ± 0.218	0.097 ± 0.098
CMNMA 36994	0.175 ± 0.160	0.232 ± 0.160	0.147 ± 0.135	0.085 ± 0.082	0.271 ± 0.208	0.090 ± 0.087
CMNMA 36995	0.172 ± 0.164	0.199 ± 0.156	0.156 ± 0.144	0.077 ± 0.079	0.304 ± 0.227	0.093 ± 0.095

CMNMA 36996	0.171 ± 0.151	0.258 ± 0.170	0.150 ± 0.129	0.109 ± 0.102	0.253 ± 0.192	0.060 ± 0.058
CMNMA 38357	0.159 ± 0.144	0.278 ± 0.167	0.145 ± 0.126	0.110 ± 0.103	0.246 ± 0.189	0.061 ± 0.058
CMNMA 38416	0.171 ± 0.161	0.241 ± 0.159	0.159 ± 0.144	0.085 ± 0.083	0.225 ± 0.200	0.118 ± 0.104
CMNMA 38458	0.171 ± 0.161	0.198 ± 0.153	0.153 ± 0.142	0.076 ± 0.073	0.309 ± 0.224	0.093 ± 0.096
CMNMA 38465	0.167 ± 0.145	0.242 ± 0.162	0.153 ± 0.132	0.101 ± 0.095	0.272 ± 0.194	0.065 ± 0.064
CMNMA 38472	0.177 ± 0.158	0.229 ± 0.161	0.153 ± 0.132	0.096 ± 0.088	0.273 ± 0.203	0.073 ± 0.072
CMNMA 38473	0.170 ± 0.158	0.197 ± 0.152	0.159 ± 0.138	0.090 ± 0.088	0.303 ± 0.208	0.080 ± 0.078
CMNMA 38484	0.166 ± 0.146	0.271 ± 0.169	0.151 ± 0.132	0.098 ± 0.090	0.244 ± 0.193	0.071 ± 0.067
CMNMA 38485	0.167 ± 0.148	0.248 ± 0.162	0.150 ± 0.133	0.094 ± 0.090	0.270 ± 0.200	0.071 ± 0.070
CMNMA 38490	0.173 ± 0.159	0.233 ± 0.162	0.150 ± 0.135	0.088 ± 0.086	0.272 ± 0.208	0.083 ± 0.082
CMNMA 38496	0.170 ± 0.152	0.222 ± 0.160	0.158 ± 0.137	0.093 ± 0.090	0.286 ± 0.203	0.071 ± 0.068
CMNMA 38550	0.175 ± 0.158	0.244 ± 0.163	0.152 ± 0.139	0.088 ± 0.086	0.253 ± 0.204	0.088 ± 0.087
CMNMA 39607	0.169 ± 0.156	0.249 ± 0.159	0.156 ± 0.138	0.095 ± 0.091	0.229 ± 0.194	0.103 ± 0.094
CMNMA 39616	0.172 ± 0.151	0.221 ± 0.157	0.165 ± 0.142	0.099 ± 0.090	0.279 ± 0.192	0.064 ± 0.060
CMNMA 39633	0.180 ± 0.167	0.189 ± 0.151	0.156 ± 0.142	0.080 ± 0.080	0.310 ± 0.217	0.085 ± 0.087
CMNMA 39946	0.175 ± 0.161	0.213 ± 0.156	0.153 ± 0.136	0.084 ± 0.081	0.293 ± 0.211	0.081 ± 0.081
CMNMA 39957	0.174 ± 0.150	0.208 ± 0.152	0.163 ± 0.143	0.098 ± 0.092	0.287 ± 0.196	0.069 ± 0.066
CMNMA 42607	0.165 ± 0.156	0.254 ± 0.163	0.159 ± 0.141	0.087 ± 0.084	0.209 ± 0.185	0.126 ± 0.110
CMNMA 42679	0.166 ± 0.161	0.232 ± 0.157	0.157 ± 0.143	0.080 ± 0.079	0.222 ± 0.201	0.143 ± 0.122
CMNMA 42691	0.166 ± 0.148	0.276 ± 0.171	0.146 ± 0.129	0.103 ± 0.096	0.238 ± 0.188	0.071 ± 0.066
CMNMA 42692	0.171 ± 0.159	0.234 ± 0.160	0.154 ± 0.139	0.083 ± 0.081	0.252 ± 0.207	0.105 ± 0.100
CMNMA 54150	0.157 ± 0.142	0.284 ± 0.166	0.151 ± 0.134	0.104 ± 0.094	0.231 ± 0.186	0.072 ± 0.068
CMNMA 54182	0.167 ± 0.155	0.256 ± 0.162	0.164 ± 0.144	0.088 ± 0.084	0.196 ± 0.175	0.129 ± 0.108
CMNMA 54185	0.172 ± 0.159	0.226 ± 0.164	0.154 ± 0.137	0.089 ± 0.088	0.279 ± 0.207	0.081 ± 0.080
CMNMA 54186	0.167 ± 0.150	0.260 ± 0.166	0.153 ± 0.135	0.099 ± 0.092	0.248 ± 0.198	0.073 ± 0.069

CMNMA 54188	0.168 ± 0.148	0.247 ± 0.165	0.155 ± 0.134	0.102 ± 0.097	0.262 ± 0.194	0.066 ± 0.064
CMNMA 54218	0.168 ± 0.150	0.259 ± 0.168	0.150 ± 0.132	0.097 ± 0.092	0.256 ± 0.198	0.070 ± 0.068

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