

Spatiotemporal Variation in the Foraging Ecology, Habitat Use, and Distribution of Arctic Marine Mammals in Relation to Sea Ice

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Thesis Abstract

The Arctic is shifting under climate change, with loss of sea ice altering marine ecosystem structure. This thesis examined two Arctic marine mammals: Bowhead whales (*Balaena mysticetus*) and ringed seals (*Pusa hispida*), both being at risk of the effects of sea ice loss. Using biomarker analysis for bowhead whales ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, fatty acids) and observations from aerial surveys for ringed seals, this study investigated spatiotemporal variability in (1) foraging of bowheads from 1993-2023 in the eastern Canadian Arctic and (2) density and distribution of ringed seals from 1994 to 2024 in Western Hudson Bay, Canada.

The biomarker results indicated spatiotemporal shifts in bowhead whale diet, including a nonlinear relationship between $\delta^{13}\text{C}$ and sea ice concentration, declining $\delta^{15}\text{N}$ values, narrowing of isotopic niche widths, and shifts in fatty acid profiles- especially in Hudson Bay. Ringed seal density declined from 1994-2024, with sea ice and distance to shore as key predictors.

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1. Chapter 1: General Introduction

The Arctic has changed more significantly in recent decades than most regions on Earth, with temperatures warming roughly four times faster than the global average (Rantanen et al. 2022).

The Arctic is defined by sea ice, which shapes the physical seascape along with food web structure and function. Temperate and Arctic-associated species are subsequently shifting or expanding their ranges northward in response to habitat loss and redistributing prey resources tied to systematic changes from sea ice decline (Florko et al. 2021; Gulland et al. 2022; Noel et al. 2022). Summer sea ice could be absent in the high Arctic by the middle of this century, with regions in the lower latitudes seeing either greatly reduced sea ice extents and concentrations, or complete open water (Kwok 2018; Kim et al. 2023). The rapid loss of sea ice, in addition to being a direct abiotic stressor through the absence of ice acting as a hunting and shelter medium, has far reaching consequences on its influence in trophic interactions and habitat use of predators. Reduction in sea ice extent and the resulting change in phenology is also impacting marine primary productivity and food web dynamics (Lewis et al. 2020).

Trophic mismatch theory describes an environmental occurrence in which the timing of peak resource availability of a consumer species no longer aligns with the phenology of the consumer (Post & Forchhammer, 2007). Temporal changes in the cyclical processes that dictate the presence of primary producers or prey become misaligned with the presence of their respective consumers (Edwards & Richardson et al. 2004; Donnelly 2011). This is of particular relevance in polar environments where there is a high seasonality associated in primary productivity and a short window of peak occurrence which takes place in the spring and summer (Durant et al.

2019). Thinning sea ice and eventual breakup, paired with the abundance of daylight in the spring/summer months in contrast to the months-long polar night in winter, induces a pulse of marine productivity (Ardyna et al. 2020). Earlier ice melt and breakup have been shown to shift the timing of primary and secondary production in the Arctic, potentially impacting the availability of resources for when Arctic consumers such as marine mammals and seabirds require greater energetic demands during their breeding or moulting periods, resulting in a trophic mismatch. This decoupling can have downstream effects on further accessibility, quantity, and quality of prey for consumers (Pratte et al. 2019). If a consumer's greatest need for a prey or primary producer species occurs prior to or after the peak availability of the food source, there will be less prey available to the consumer. Likewise, the nutritional quality of a food item can vary significantly throughout the season, with a change in phenology resulting in a peak nutritional mismatch (Søreide et al. 2010).

1.1 Sea Ice as an Ecological Driver

There are two major marine blooms that occur annually in the Arctic: the ice algae bloom that takes place in spring underneath sea ice, followed by a larger phytoplankton bloom that is associated with open water (Koch et al. 2023). The high concentration of polyunsaturated fatty acids originating in ice algae provide important lipids and calories for marine species in the Arctic (Lewis et al. 2020). However, climate change and the subsequent loss of sea ice is altering the cycles of producers in the Arctic marine environment (Vancoppenolle et al. 2013). The complex amalgamation of factors influencing overall primary productivity is difficult to predict, with current models having conflicting outcomes. While increased open water has been

suggested to increase pelagic-derived carbon and an increase in phytoplankton productivity, it will lead to a decrease in sympagic, or sea-ice associated, productivity (Arrigo et al. 2008; Arrigo et al. 2015; Lewis et al. 2020; Soreide et al. 2010). Under-ice algal blooms will likely be diminished, and the response of understudied under-ice phytoplankton bloom occurrence is unknown (Ardyna et al. 2020; Park et al. 2020). The greater likelihood of increased phytoplanktonic productivity may have a positive effect on the Arctic food web (Renaud et al. 2018), though an increased presence of phytoplankton may not equate to sea ice algae in terms of nutritional value or bioavailability (Duerksen et al. 2014).

Zooplankton, Arctic cod (*Boreogadus saida*), and seabird foraging success have all been tied to the spring algal bloom (Provencher et al. 2011; Steiner et al. 2019). Sympagic activity is similarly tied to the life cycles of certain zooplankton species, such as copepods (which graze on diatoms) that reach maturation during peak spring productivity under ice. Sea ice algae are also closely aligned to the Arctic benthic environment, where "marine snow" is the organic particulate matter and detritus that falls down to the ocean floor, sustaining the food web of the benthos. The sloughing of ice algae during the spring breakup highly contributes to this organic matter in ice-covered regions, supporting a rich Arctic benthic community (Oleszczuk et al. 2021).

Additionally, bacteria and microorganisms in this detritus are consequentially responsible for the decomposition and release of vital nutrients back into the water column, further supporting the broader food web (Niemi et al. 2024). There are numerous studies that currently suggest that Arctic consumers, such as marine mammals, are subsequently shifting or expanding their ranges northward in response to redistributing prey resources tied to systematic changes from sea ice decline (Kovacs et al. 2010; Florko et al. 2021; Gulland et al. 2022; Noel et al. 2022).

1.2 Marine Mammals as Indicators of Arctic Change

Marine mammals such as cetaceans, pinnipeds, and polar bears (*Ursus maritimus*) occupy mid- to top-level trophic positions in the Arctic food web and are impacted by underlying shifts in food web structure or functioning (Møller et al. 2019; Siddiqui et al. 2024). Marine mammals are both sensitive to anthropogenic climate change and highly integral in the top-down control of populations of prey species, given their status as higher-level consumers (Laidre et al. 2008). Marine mammals, who possess long life spans and life histories that reflect changes across wide spatial and temporal scales, are sentinels of change in the Arctic by acting as gauges of ecological alteration through space and over time (Moore 2008). Therefore, examining shifts in marine mammal feeding, habitat use and their distribution can reveal important insights on how the loss of sea ice affects the Arctic ecosystem (Laidre et al. 2015).

1.3 Bowhead Whales

Bowhead whales (*Balaena mysticetus*) are the longest living mammals on Earth, with lifespans exceeding 200 years and are the only baleen whale endemic to the Arctic and sub-Arctic (George et al. 1999; Berta et al. 2006). The distribution of the East Canada-West Greenland stock (ECWG) of bowheads extends from Baffin Bay across the Canadian Arctic Archipelago, ranging southward into Hudson Bay (Biddlecombe et al. 2023). Bowhead whales migrate across the Arctic to accommodate foraging on seasonal aggregations of zooplankton, as well as seasonally prioritize areas of open water such as polynyas to presumably reduce the risk of ice entrapment during the winter (Ferguson et al. 2010; Fortune et al. 2020).

Northern zooplankton are comprised of diverse taxa including cnidarians, ctenophores, mollusks, arthropods, and meroplankton in their larval/immature stages. Of these, some zooplankton have a stronger association to sea ice than others. Arctic calanoid copepods such as *Calanus hyperboreus* and *Calanus glacialis* are herbivorous, with their lifecycles closely following the under-ice algae bloom in spring (Søreide et al. 2010). Both species, being rich in lipids and calories, represent key components of the bowhead whale diet. Additionally, the closely related boreal species of copepod, *Calanus finmarchicus*, is becoming more prominent in bowhead diets as it expands northward in response to warming ocean temperatures. This northward range shift is predicted to continue with ongoing sea ice loss and warming ocean temperatures, potentially supplanting Arctic copepods as a primary bowhead prey species (Fortune et al. 2020; Fortune et al. 2023; Kimmel et al. 2023). Other prey items include omnivorous and carnivorous mysids, amphipods, and euphausiids, which have traditionally represented a lower percentage of overall diet in the ECWG population (Pomerleau et al. 2014; Pontbriand et al. 2023). The examination of bowhead whale diets can reveal trends in prey base shifts in the foundation of the Arctic food web in relation to interannual variability in sea ice dynamics and the progressive loss in sea ice concentration.

1.4 Ringed Seals

Ringed seals (*Pusa hispida*) are a small pinniped with a circumpolar distribution who are arguably the most widespread Arctic marine mammal, found throughout a large range in the north that extends into the subarctic, as well as some specialized locales such as freshwater lakes (Reeves 1998). Due to their abundance, range, and sensitivity to changes in sea ice conditions,

ringed seals are an excellent indicator of ecosystem functioning under climate change (Laidre et al. 2008; Reimer et al. 2019). Ringed seals have a close relationship with sea ice throughout their lives, depending on it both directly as a platform and habitat as well as indirectly as the base substrate from which their prey relies (Yurkowski et al. 2016). They rest, moult, and pup on sea ice, as well as build subnivean lairs under the snow for shelter and hiding from predators (Kovacs et al. 2024).

Adult ringed seals prefer landfast ice, though certain situations may drive adult and subadult ringed seals to select for ice floes farther from shore (Kingsley et al. 1985; Lone et al. 2019). Predation pressure from polar bears, their main predator, and arctic foxes (*Vulpes lagopus*) can influence the selection of habitat by ringed seals (Furgal et al. 1996). Polar bears favor consolidated pack ice, utilizing the platform when ambushing seals near breathing holes, which in turn may drive ringed seals to select for more sheltered ice features (Pagano 2021). Ringed seals may also select locations based on proximity to their migration routes, with juveniles routinely choosing locations farther offshore as they follow the ice edge (Lone et al. 2019; Von Duyke et al. 2020).

Ringed seals are generalist feeders, with their foraging areas hosting a wide variety of prey species ranging from crustaceans, benthic invertebrates, and a wide array of fish species (Insley et al. 2021). Ringed seals are notably adaptable and will target various species depending on seasonal and regional availability, often dictated by sea ice cover and prey availability (Yurkowski et al. 2015; Yurkowski et al. 2016). In addition to primary ice type preferences (ex. landfast, loose floes, pack ice, etc.) and overall ice concentration, ringed seals are also shown to select habitat based on snow type/coverage and ice texture (Iacozza et al. 2014). Snow provides the material for building subnivean lairs in the spring, with total amount and composition being

important for structural integrity (Kovacs et al. 2024). Ice texture, with differences ranging from smooth, interrupted/unbroken ice sheets to rubble ice has a large impact on susceptibility to polar bear predation (Pilfold et al. 2013). The reliance on sea ice for their survival and breeding success is especially magnified in Hudson Bay, which has a high seasonality associated with sea ice presence, being completely ice-free from approximately July to October before freezing over for most of the winter and spring (Gagnon & Gough 2005; Young et al. 2015; Young et al. 2019). As a result, progressive sea ice loss and longer open-water periods will likely impact habitat suitability for ringed seals in Western Hudson Bay, potentially reducing population density and abundance (Ferguson et al. 2017).

1.5 Studying Marine Mammal Density and Habitat Use Through Surveys and Biomarker Analysis

Large scale abundance surveys and biomarker analysis are two widely used methods for studying animal populations. Field surveys offer a means to assess abundance, habitat use, and changes in range or density at a population or regional level (Buckland et al. 2000). Aerial surveys are an efficient means of observing animal locations and overall density across broad geographic areas and are useful for identifying key environmental characteristics associated with animal presence. Biomarker analysis, through both stable isotope and fatty acid analysis, can elucidate responses to environmental conditions, and generally indicate population-level changes to prey availability and composition (Norris et al. 2007; Scott, Falk-Petersen & Sargent 2008; Boecklen et al. 2011; Golikov et al. 2024). The methods utilized in this study are aerial surveys, conducted in the Western Hudson Bay region over the course of approximately 30 years, and

complementary stable isotope and fatty acid analysis of bowhead whale tissue over a nearly identical time period, collected from various regions across the Canadian mid-Arctic.

1.6 Stable Isotope Analysis

Stable isotope analysis is a powerful method to determine the characteristics of diet and prey selection by measuring ratios of stable isotopes incorporated into animal tissue, with ratios of heavy to light isotopes, commonly $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$, indicating aspects of an organism's environment and life history (Lee et al. 2005). Stable isotope ratios are denoted through the following δ notation, where ratio values are expressed in per mil (‰):

$$\delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \cdot 1000$$

Nitrogen stable isotopes are expressed in the atmospheric nitrogen standard. The ratio of $^{15}\text{N}/^{14}\text{N}$ is compared to the ratio found in atmospheric nitrogen, being expressed as $\delta^{15}\text{N}$ where “ δ ” represents the deviation from the standard. Higher $\delta^{15}\text{N}$ values in the sample indicate an enrichment in ^{15}N when compared to the atmospheric nitrogen standard. $\delta^{15}\text{N}$ values typically indicate the trophic level an organism feeds at because $\delta^{15}\text{N}$ increases in consumer tissues up the food chain (Minagawa & Wada 1984; Hobson & Welch 1992). The ratio of the stable isotopes $^{13}\text{C}/^{12}\text{C}$ in a given sample is compared to the ratio found in the Pee Dee Belemnite standard. This comparison is then expressed as $\delta^{13}\text{C}$ where “ δ ” represents the deviation from the standard. Positive $\delta^{13}\text{C}$ values imply enrichment in ^{13}C when compared to the reference standard. Negative $\delta^{13}\text{C}$ values indicate depletion in ^{13}C as compared to the Pee Dee Belemnite reference standard (Leavitt 2009).

1.7 Fatty Acid Profile Analysis

Fatty acids are the building blocks of adipose tissue in living organisms. Adipose tissue is primarily composed of triacylglycerols (triglycerides) which consist of a single glycerol unit and three fatty acids attached by ester bonds (Uphoff et al. 2008). In monogastric carnivores, fatty acids are predictably assimilated into adipose stores, allowing researchers to reconstruct the composition of the predator's diet (Iverson et al. 2004; Thiemann et al. 2007; Budge et al 2008; Thiemann et al. 2009; Iverson 2009). Lipids are typically extracted from a blubber sample, followed by esterification into fatty acid methyl esters (FAMES) and dissolution in an organic solvent (Hewavitharana et al. 2020). This prepared sample is then injected into the gas chromatograph, in which the chromatographic column is coated with a stationary phase. A carrier gas flowing through the column will cause the various fatty acids in the sample to interact differently with the stationary phase, with each eluting from the column at different rates (Forgács & Cserhádi, 2003).

1.8 Fatty Acid Ratios

The ratios 16:1n-7/16:0, 18:1n-9/18:1n-7, 20:5n-3/22:6n-3, and 22:1n-11/20:1n-9 have been identified in previous studies as indicators of dietary sources and ecosystem processes, reflecting variation in sea-ice-associated primary production and prey composition. The first denotes proportionality of diatom- vs dinoflagellate-sourcing in prey items (Auel et al. 2002; Dalsgaard et al. 2003), whereas the second is a proxy for trophic level/carnivory (Graeve et al. 1997; Dalsgaard et al. 2003), and the third is an additional measure of diatom vs dinoflagellate

dietary sourcing (Mayzaud et al. 1990; Dalsgaard et al. 2003), and 22:1n-11/20:1n-9 is a marker of proportionality for copepod species: *C. glacialis* (<0.7), *C. finmarchicus* ($\approx$ 1.1) and *C. hyperboreus* (>1.8) (Falk-Petersen et al. 1990; Falk-Petersen et al. 2009). Fatty acid analysis of bowhead blubber tissue reflects the overall composition of the zooplankton prey that is the basis of their diet. FAs predictably and conservatively transfer from diet to blubber with limited modification (Iverson et al. 2004). Bowhead whales occupy a low trophic level, resulting in a lower degree of baseline modification of fatty acids from their sea ice derived sourcing (Pomerleau et al. 2014; Pomerleau et al. 2017). Fatty acid analysis has been used in bowheads previously to elucidate both differences in FA structure between blubber layers of individual whales and to examine dietary differences between groups in different regions (Budge et al. 2008; Pomerleau et al. 2014). There is a degree of stratification between blubber layers, with the innermost layers containing the most metabolically active and recently assimilated FAs, becoming less metabolically active and more thermoregulatory as it grows outward (Strandberg et al. 2008; Ball et al. 2015). However, outer blubber has been shown to still retain a profile of dietary fatty acids, and has been used in previous studies, allowing for the accurate determination of dietary FAs (Budge et al. 2008; Pomerleau et al. 2014). FAs sourced from diet are assimilated into blubber tissue at the most metabolically active inner layer which reflects recent diet. Tissue grows outward progressively over time, meaning that the structural outer blubber layers, while more inert, may reflect a more integrated, long-term FA profile of diet (Koopman et al. 1996; Pomerleau et al. 2014; Remili et al. 2023).

1.9 Aerial Surveys

Aerial surveys are an effective survey methodology used for measuring the abundance or density of numerous species and their habitat (Buckland et al. 2000; Lunn et al. 1997). Plane or UAS (unmanned aerial system) surveys are particularly useful for covering large areas of remote environments, making them especially useful for seabirds and marine life (Ferguson et al. 2018). Marine mammals inhabit territories that cover large expanses of water, with detection being more unlikely if limited to a smaller study area. Frequent movement, paired with longer timespans spent underwater further contributes to issues with detection. Aerial surveys are particularly useful in polar environments, where sea ice can make ship-based transect surveys difficult to impossible.

Planned transects also allow for systematic, repeatable survey coverage across a varied environment, with continued effort over time providing a timeline of population trends. The combination of strip transects, and distance sampling techniques allows for a robust coverage of the survey area and lends to the long-term monitoring of density and distribution changes of the study species when repeated over years (Buckland et al. 2000; Lunn et al. 1997; Young et al. 2015; Young et al. 2019).

1.10 Thesis Structure and Objectives

The goal of my thesis is to identify the degree and extent of dietary and distributional changes in two species of Arctic marine mammal that are closely associated with sea ice. Both chapter datasets cover an extensive temporal range of approximately three decades, meaning that this study is in a unique position to inform climate change policy and management decisions in the Arctic.

The specific objectives of my MSc thesis were to investigate: 1) the spatial and temporal variability of bowhead whale foraging ecology in relation to sea ice concentration over time through dietary biomarkers ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, fatty acid profiles) and 2) the spatial and temporal variability of ringed seal density, habitat use, and distribution in relation to sea ice concentration in Western Hudson Bay over the span of the aerial surveys (1994 to 2024). This thesis is formatted as two independent manuscripts (Chapter 2 and Chapter 3).

Chapter 2

First, I investigated regional (Hudson Bay Complex; Baffin Bay-Davis Strait) and temporal variation in stable isotopes from bowhead whale skin ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) and fatty acid composition from blubber. I also estimated isotopic niche widths to determine the degree of dietary and trophic variability across the Hudson Bay Complex group and the Baffin Bay-Davis Strait group in response to spatial and temporal differences in relation to sea ice concentration.

Second, I examined the effects of spring sea ice concentration on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, fatty acid composition, and isotopic niche metrics of bowhead whales using principal component analysis (PCA), PERMANOVA on CLR-transformed FAs, and generalized additive models (GAMs) on identified FA ratios of interest.

Chapter 3

First, I determined spatial and temporal variation in ringed seal habitat use and distribution by estimating segment-level densities (ringed seals per km^2) with buffered transect

areas from aerial surveys conducted in Western Hudson Bay. I estimated approximate ringed seal locations from recorded aircraft speed, animal sighting time, and personnel notes for years 1994-2000 where no GPS/recorded animal locations exist. Secondly, I calculated kernel density estimations (KDEs) and isopleth areas (50%, 95%) to determine key areas of ringed seal habitat use and higher densities, over the course of the survey years (1994 to 2024) as well as examined overall ringed seal densities over space and time. Lastly, I examined how potential predictor variables, year, spring sea-ice concentration, distance to shore, and bathymetry influenced ringed seal density using generalized additive models (GAMs).

2. Chapter 2: Stable Isotope and Fatty Acid Analysis of Bowhead Whales

Abstract

The Arctic has changed more significantly in recent decades than most regions on Earth due to climate change, with ongoing sea ice loss impacting the northern food web. Bowhead whales are a zooplanktivorous cetacean, with sea ice being a significant driver of their foraging ecology. I investigated shifts in bowhead whale diets using a comprehensive dietary biomarker dataset spanning 30 years across their range in the eastern Canadian Arctic to determine the effects of spring sea ice concentration, region, and year on bowhead foraging and food web dynamics. Overall, my findings indicate spatiotemporal shifts in bowhead whale diets in relation to prey availability and changing habitats. Stable isotope analysis of bowhead skin revealed that average spring sea ice concentration was the most significant predictor of $\delta^{13}\text{C}$ values, with the relationship being strongly nonlinear and variable. $\delta^{13}\text{C}$ values were higher in Hudson Bay, supporting greater use of sympagic (ice-associated) carbon sources. Region and collection year were the most significant predictors for $\delta^{15}\text{N}$ values. $\delta^{15}\text{N}$ values declined over time, particularly in Baffin Bay-Davis Strait. Isotopic niche widths narrowed over time in both regions, possibly indicating dietary specialization. Fatty acid profiles shifted over decades, especially in Hudson Bay, with more recent samples showing greater copepod and ice-associated contributions. Region and collection year were significant predictors of fatty acid ratios: 16:1n-7/16:0, 18:1n-9/18:1n-7, and 22:1n-11/20:1n-9 in outer blubber samples. The trophic FA ratio

(18:1n-9/18:1n-7) increased, suggesting changing zooplankton composition or greater carnivory. The diatom marker FA ratio (16:1n-7/16:0) showed conservative decline, with variation likely driven by nutrient conditions and spring bloom dynamics, rather than sea ice alone. The EPA/DHA ratio (20:5n-3/22:6n-3) was weakly linked to sea ice, region, or year, implying influence from producer type, temperature, and seasonal zooplankton stages. The copepod FA ratio (22:1n-11/20:1n-9) showed only slight temporal variation, with a mid-2010s peak, suggesting moderate shifts in *Calanus* input but no strong long-term trend. Together, these results suggest that the bowhead prey base has undergone compositional shifts in response to ongoing climate change and sea ice loss.

2.1 Introduction

In the Arctic, foraging opportunities are constrained by extreme seasonality in environmental conditions. Shifts between temperatures and daylight hours throughout the year mean ‘boom and bust’ for productivity and prey availability. High quality prey species in the Arctic are generally lipid-rich and energy-dense. The processes that lend to nutritionally valuable prey are shown to be inextricably linked to sea ice (Søreide et al. 2010). The ice algal and phytoplankton blooms are heavily influenced by sea ice dynamics which largely dictate the zooplankton diversity that larger predators rely upon (Ramírez et al. 2017; Baird 2022; Ershova et al. 2021). Copepods are a key species of primarily herbivorous zooplankton and are crucial to the breeding success of many species of fish and seabirds (Bouchard et al. 2020). Other zooplankton species can be carnivorous or omnivorous, predating on other zooplankton species as part of a broader ecological food web on a near-microscopic scale (Arctic Council - *Life Linked to Ice* 2013).

Bowhead whales, especially the East Canada-West Greenland (ECWG) population in the eastern Arctic, are reliant on copepods as a rich source of fats and calories in the energetically demanding polar environment. Spring primary productivity, largely in the form of the under-ice algal bloom, contributes to the fat content in these copepods (Mayzaud et al. 2015). While bowhead whales can be seen as generalist feeders, the overall composition of their prey conglomerations is crucial to their nutritional quality and the health of the species (Simon et al. 2009; Fortune et al. 2020). Because of this specialization in feeding style and small-scale prey, habitat selection is fluid and largely dependent on transient conglomerations of zooplankton.

Highly variable oceanographic conditions, such as currents, can continually alter the location of energetically profitable zooplankton patches. Other environmental factors influencing the presence of these aggregations include temperature, salinity, intermixing, and sea ice- all of which are greatly influenced by climate change (Ershova et al. 2021). Environmental changes caused by Arctic warming are likely to alter the size, timing, composition, and predictability of zooplankton patches with the potential to impact animals that forage upon them (Mackas et al. 2012; Grémillet & Descamps 2023; Kuletz et al. 2024). Photogrammetry and energetic modelling determined that adult bowhead whales require 102-218 kg of lipid-rich calanoid copepods per day during spring foraging (March-June) (Christiansen et al. 2024; McLennon et al. 2025). The loss or redistribution of adequate aggregations could have deleterious effects on a species which depend so heavily on peak foraging seasons for survival.

Bowheads have slow metabolisms compared to other cetaceans, relying on their stores of blubber during scarce winter months while foraging extensively during summer to accumulate adipose reserves for the rest of the year (Ball et al. 2016; George et al. 2020). Changes in primary productivity linked to climate change and sea ice loss may impact the availability of prey during key foraging windows (Szesciorka et al. 2023). Dietary analysis is a useful tool to gauge the response of trophic base to a progressively reduced concentration in sea ice over time (De La Vega et al. 2019; Carlyle et al. 2022). Analysis of biomarkers in bowhead blubber and skin may provide an indication of regional foraging conditions and systemic shifts in the environment in relation to the loss of sea ice (Budge et al. 2008). Biochemical markers are integrated and assimilated into tissues in a predictable manner over time and potentially reveal patterns in foraging over months to years (Iverson et al. 2004).

The months of June through October are shown to be the key foraging period (Ferguson et al. 2010). The increase in daylight after the polar night in winter, alongside warming spring temperatures cause sea ice thinning and the subsequent associated algal blooms that are nutritionally integral to the Arctic ecosystem, providing a rich source of calories and long-chain polyunsaturated fatty acids, while the open-water period post-ice breakup is coupled with the phytoplankton blooms (Koch et al. 2023). While the aforementioned processes occur throughout the Arctic, there are regional differences that dictate their timing and characteristics. Bowhead whale summer foraging areas of importance (Wheeler et al. 2011; Nielson et al. 2015) were identified as belonging to three major ecoregions in the Canadian Arctic: The Baffin Bay-Davis Strait (BBDS) Complex, Hudson Bay Complex (HBC), and The Canadian Arctic Archipelago. These ecoregions have unique geographic and systemic traits that influence their biogeochemical compositions (Ahmed et al. 2019; Lukovich et al. 2021; Hamilton and Wu 2013).

Foxe Basin, a key bowhead foraging and congregation area, is shallow and has more extensive ice cover that remains into the summer season- providing shelter which lends to being an important calving area during the late spring to early summer months (Cosens et al. 2006; Ferguson et al. 2010; Higdon et al. 2011). The entrance to Fury and Hecla Strait is located in the northwest corner of the basin and serves as an important migration corridor for bowhead whales traveling into the Gulf of Boothia (Ferguson et al. 2010). Cumberland Sound is another important region for bowhead whales and is located on the eastern side of Baffin Island which receives an influx of zooplankton prey carried up by Atlantic currents during all seasons, making it a key feeding area for bowheads year-round (Heide-Jørgensen et al. 2010; Fortune et al. 2020). Whales will travel throughout their range during the open water peak foraging months, with individuals potentially crossing Davis Strait to the coast of Greenland, west through Hudson

Strait to the Canadian Arctic Archipelago, or north along the coast of Baffin Island (Ferguson et al. 2010; Pomerleau et al. 2011).

2.1.1 Dietary Biomarkers in Bowhead Whales

Biochemical markers can serve as powerful indicators of feeding habits in free-ranging animals. Stable isotopes are widely used for determining dietary sourcing through tissue analysis. $\delta^{13}\text{C}$ baselines are environmentally variable and can reveal insights on a species habitat use (Peterson and Fry, 1987; Kelly 2000; Ben-David & Flaherty 2012). $\delta^{13}\text{C}$ is also a useful indicator of sympagic dietary sourcing, with higher $\delta^{13}\text{C}$ values generally indicating a more sea ice-derived diet than phytoplankton-derived in polar ecosystems (Søreide et al. 2006; Kohlbach et al. 2016). $\delta^{15}\text{N}$ is used to estimate relative trophic position, with values increasing at higher levels in the food web in a process known as trophic enrichment (Post 2002). Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ can be used to estimate isotopic niche size, which is indicative of changes in habitat use and diet when examined over time (Bearhop et al. 2004).

Long-chain dietary fatty acids tend to undergo minimal modification and predictable tissue assimilation in the consumer, which means that the composition of blubber in marine mammals is a reflection of its dietary sources (Iverson et al. 2004; Strandberg et al 2008). Fatty acid analysis via gas chromatography is an important tool in determining the diets of marine mammals (Iverson et al 2004). By comparing their overall percentages across groups, it is possible to identify biomarkers of interest linked to environmental conditions and subsequently predict ice-associated fluctuations in prey availability. Sea ice loss and warmer temperatures is causing population restructuring of zooplankton communities in much of the Arctic, with temperate species expanding into new regions and regionally occurring native species moving

farther north (Ratnarajah et al. 2023). Certain fatty acids have been identified as markers of trophic level, diatomic vs. dinoflagellate origin, or a copepod-heavy diet (Kohlbach et al. 2021; Dalsgaard et al. 2003). Bowhead whale diets can reliably be studied through qualitative fatty acid compositional analysis. Outer blubber samples obtained through biopsy sampling provide a proven means of diet determination (Pomerleau et al. 2014; Remili et al. 2023). While outer blubber is less metabolically active than inner blubber and stratification is present between layers, outer blubber fatty acids can still yield robust and informative insights (Koopman et al. 1996; Budge et al. 2008; Remili et al. 2023). Examination of total fatty acid composition of blubber and ratios has been used previously in bowhead whale blubber and found distinct regional dietary differences between populations. The degree of reliance on copepods has been found to be greater in the East Canada West Greenland (ECWG) population of bowheads, as opposed to Bering Chukchi Beaufort (BCB) whales, suggesting that they are a more important prey item for the study population (Budge et al. 2008; Pomerleau et al. 2014; Pontbriand et al. 2023). Previous findings similarly found that ECWG whales fed in a more diatomic-influenced food web when compared to the western population, possibly suggesting a system more responsive to changing sea ice dynamics (Kohlbach et al. 2023). It can be predicted that as sea ice dynamics change in the Canadian Eastern Arctic, a change in zooplankton dietary markers will be reflected in bowhead whale fatty acids.

In the ratio, 16:1n-7/16:0, a ratio higher in 16:1n-7 indicates more diatom-dominated diet (with diatoms typically being associated with sea ice in the Arctic) while 16:0 is a ubiquitous fatty acid uniformly prevalent in marine adipose tissue. For the ratio, 20:5n-3/22:6n-3, 20:5n-3 is similarly indicative of a diatom-sourced diet, while 22:6n-3 is an indicator of a dinoflagellate diet more associated with open water (Auel et al. 2002; Stübing & Hagen 2003; Dalsgaard et al.

2003). The 18:1n-9/18:1n-7 ratio highlights dietary trends in relation to trophic level, with 18:1n-9 indicating carnivory while 18:1n-7 is a proxy for herbivory (Graeve et al. 1997; Kohlbach et al. 2021). Lastly, 22:1n-11/20:1n-9 is a ratio of two long-chain monounsaturated fatty acids that are synthesized de novo by *Calanus* copepods (Scott et al. 2002; Dalsgaard et al. 2003; Graeve et al. 2005; Falk-Petersen et al. 2009; Kohlbach et al. 2021). The relative abundance of these fatty acids can therefore indicate the contribution of Arctic (*C. hyperboreus*, *C. glacialis*) versus boreal (*C. finmarchicus*) zooplankton consumer diets: a higher 22:1n-11/20:1n-9 ratio indicates greater contribution from Arctic-resident copepods, while a lower ratio suggests a shift toward boreal or Atlantic copepods. Each copepod species exhibits varying 22:1n-11/20:1n-9 ratios; *C. glacialis* (<0.7), *C. finmarchicus* ($\approx$ 1.1) and *C. hyperboreus* (>1.8) (Scott et al. 2002; Falk-Petersen et al. 2009; Pontbriand et al. 2023).

Research objectives in Chapter 2

The objective of my research is to examine spatial and temporal variations in $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, fatty acid composition, and isotopic niche size in bowhead whale skin/blubber samples collected from separate regions of the Canadian Arctic and examine the influence of sea ice concentration.

Hypotheses and predictions in Chapter 2:

- 1) Bowhead whale dietary profiles will show progressively lower $\delta^{13}\text{C}$ values over time, indicating a lower dietary sourcing from sympagic/sea-ice derived carbon.
- 2) Stable isotope results will show higher $\delta^{15}\text{N}$ values over the course of the sampling time frame. $\delta^{15}\text{N}$ increases progressively with each trophic level and will indicate an

increasing reliance on omnivorous and carnivorous zooplankton species as sea ice loss contributes to zooplankton redistribution and decline of herbivorous *Calanus* species.

- 3) I hypothesized that loss of spring sea ice concentration will diminish spring algal blooms and large-bodied copepod species, leading to shifts in bowhead whale fatty acid profiles. Copepod markers (22:1n-11/20:1n-9) and ice-diatom markers (16:1n-7, 20:5n-3) were hypothesized to decrease over time with lower sea ice concentrations, resulting in lower 20:5n-3/22:6n-3 and 16:1n-7/16:0 ratios, and increased trophic (18:1n-9/18:1n-7) ratios, reflecting greater carnivory. Isotopic niche widths are hypothesized to expand as a result of the targeting a broader range of zooplankton species.

2.2 Methods

2.2.1 Sample Collection and Processing

Between 1994 and 2023, a total of 456 skin and 148 blubber samples were collected from bowhead whales across three regional complexes in the Canadian Arctic: Hudson Bay Complex (skin: n = 285; blubber: n = 91), Baffin Bay-Davis Strait Complex (skin: n = 171; blubber: n = 44), and Arctic Archipelago Complex (blubber only: n = 13).

Samples were obtained through a combination of Inuit subsistence harvests, collection from stranded individuals, and biopsy darting from living whales conducted by Fisheries and Oceans Canada (DFO). Biopsy collection uses a hollow-tipped dart designed to remove a small “plug” of skin and outer blubber from an individual, usually from the posterior dorsal surface. Sample breakdown by sourcing were as follows: hunted (skin: n = 12; blubber: n = 23), stranded (skin: n = 1; blubber: n = 10), biopsy (skin: n = 436; blubber: n = 111), and source unspecified in

record (skin: $n = 7$; blubber: $n = 4$). Biopsy sampling was primarily undertaken in offshore areas near Igloodik and Pangnirtung, where bowhead whales are predictably present during summer foraging months and represent key areas of bowhead foraging range and to capture variability in regional and environmental conditions (Heide-Jørgensen et al. 2006). Samples were collected during the summer/early fall open water period (July-September) which allows for sampling accessibility in boats and encompasses the subsistence hunt period.

Blubber tissue from deceased individuals was collected in portions encompassing the innermost layer to the skin, though only the outermost layer was sampled in the lab to maintain consistency across sampling procedures. Though there is a degree of stratification in blubber layers, reliable inferences can still be made from outer blubber fatty acid analysis alone (Pomerleau et al. 2014; Remili et al. 2023). A previous study approximated an average isotopic turnover time of six months in blue whales (Busquets-Vass et al. 2017). This turnover rate may be longer in bowhead whales, due to their hypometabolic rate, though direct estimates are currently unavailable (George & Thewissen 2020). Whales were assigned age classes based on size ranges, with calves being < 8 m long; juveniles being ≥ 8 m for males, ≥ 10 m for females; subadults being ≥ 8 m for males and ≥ 10 for females; and ≥ 12.5 m for males and ≥ 13 m for females (Pontbriand et al. 2023). Age class and sex was ultimately omitted from the analysis due to the high prevalence of ‘unknown’ individuals for both categories due to incomplete metadata. Previous studies have yielded mixed results in suggesting that there is definite segregation between both age class and sex in most instances (Heide-Jørgensen et al. 2010; Fortune et al. 2020).

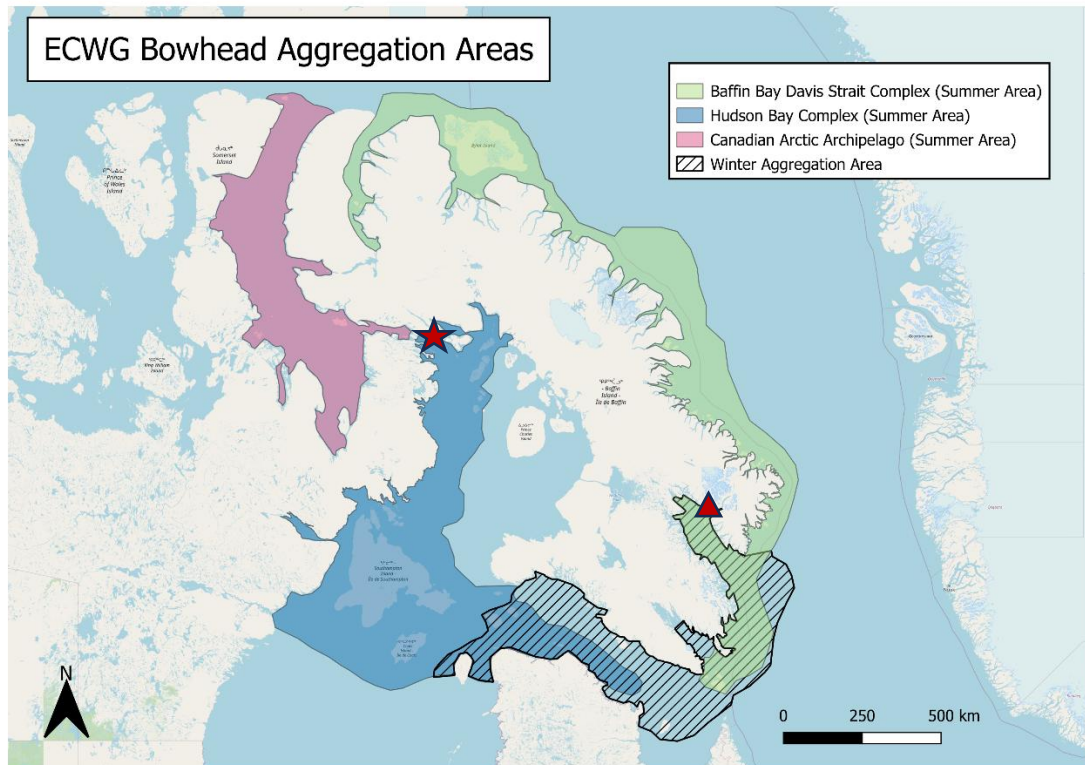


Figure 2-1: Map of primary bowhead aggregation areas in eastern Canada. The map and areas were recreated from Ferguson *et al.* 2021; NWMB (2000), COSEWIC (2009), Heide-Jørgensen *et al.* (2021). Igloolik (the sampling location for Hudson Bay Complex samples) is represented by the star symbol and Pangnirtung (sampling location for Baffin Bay-Davis Strait samples) by the triangle symbol.

2.2.2 Stable Isotope (Skin) Sample Preparation

All biopsy samples were collected during the open water field season (summer), while samples from harvested individuals were collected in the late summer/fall hunting season, and samples from stranded animals were collected opportunistically from recently deceased individuals not in an advanced state of decomposition. All tissues were stored in -80°C freezers at the Freshwater Institute in Winnipeg, Manitoba, with biopsy samples stored in vials and tissues from deceased animals stored as muktuk (i.e. pieces of skin and blubber). I first finely diced skin samples with a scalpel before freeze-drying samples for at least 48 hours in

preparation for lipid extraction. Lipid-extraction was completed using a 2:1 chloroform:methanol (C:M) solution according to the Folch Method (Folch et al. 1957) with C:M solution being added directly to cryovials to minimize loss. Capped vials were placed in a tube rack, incubated in a 30°C water bath for 24 hours, and then centrifuged for 5 minutes at 3000 rpm. Solvent liquid was then decanted, and fresh C:M solution added to the vials for additional lipid extraction. Vials were vortexed and centrifuged for another 5 minutes at 3000 rpm before being decanted and dried in a fume hood for 24 to 48 hours (Folch et al. 1957). Lipid extracted and dried samples were sent for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis at the Great Lakes Institute for Environmental Research at the University of Windsor. The University of Windsor instrumentation for mass spectroscopy uses an Elemental Analyzer (Costech) - Isotope Ratio Mass Spectrometer (Thermo Delta V) (EA-IRMS) for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %N and %C analysis.

The most recent stable isotope samples received in August and November of 2024 from the University of Windsor had accompanying precision and accuracy values: For $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, instrumentation accuracy was checked throughout analysis by the lab and based on U.S. National Institute of Standards and Technology (NIST) standards. Precision, assessed by the standard deviation of replicate analyses of four standards (NIST1577c, internal lab standard (tilapia muscle), USGS 40 and Urea (n=30 for all), measured $\leq 0.17\text{‰}$ for $\delta^{15}\text{N}$ and $\leq 0.20\text{‰}$ for $\delta^{13}\text{C}$ for all the standards. Analytical accuracy for $\delta^{13}\text{C}$ was assessed using USGS 40 and NIST reference materials (NIST 8542, 8573, 8574) and was within -0.17 to 0.19‰ of certified values. Analytical accuracy for $\delta^{15}\text{N}$ was assessed using USGS 40 and NIST standards 8573, 8547 and 8574 and was within -0.20 to 0.00‰ of certified values.

2.2.3 Fatty Acid (Blubber) Preparation

Blubber samples were prepared for gas chromatography using the applicable standard of procedure for adipose tissues (Folch et al. 1957; DFO Freshwater Institute Fatty Acid Standard of Procedure 2023). A scalpel was used to remove the exposed surface of the blubber sample to remove any oxidized tissue. Lipids were extracted from a portion of outer blubber weighing ~0.5 g using the Folch method (Folch et al. 1957) as modified for marine mammal tissues (Iverson et al. 2001). Fatty acid methyl esters (FAMES) were prepared via transesterification using sulfuric acid as a catalyst. Prepared samples were sent to the Marine Lipids Lab at Dalhousie University for analysis. FAME analysis was conducted via temperature-programmed gas-liquid chromatography (Budge et al. 2006), analyzed in duplicate on an FID gas chromatograph (flame ionization detector (GC-FID)) fitted with a 30 m × 0.25 mm ID column coated with 50% cyanopropyl polysiloxane (0.25 µm film thickness) (Dodds et al. 2005). Duplicate runs were conducted approximately every 10 samples by the lab to ensure precision and accuracy. Individual FA were identified based on retention times and manually verified and corrected using Compass CDS software (Version 3.9, Bruker Daltonics Inc., Germany). Standard nomenclature for fatty acids is denoted as: A:Bn-x, where A is the number of carbon atoms, B is the number of double bonds, and n-x is the position of the first double bond from the methyl (ω) end of the fatty acid chain.

2.2.4 Sea Ice Data Extraction

Sea ice concentration indicates ice persistence and partial cover in an area (Barbraud et al. 2015; Pratte et al. 2019). While sea ice breakup date is commonly used as a proxy for overall

sea ice conditions, I chose to use mean sea ice concentration, averaged for the spring to early summer period reflecting ice-associated primary productivity between March and July, by region as a predictor variable. To determine annual spring sea ice concentration for each year in the dataset (1993-2023), I extracted monthly sea ice concentration values for March-July of the prior year from NSIDC. To represent seasonal spring ice conditions for each year, I calculated the average of the five monthly means (March-July). Each monthly mean is based on 30-31 daily values, so the difference in underlying sample size across months is minimal (at most one day). Because of this, a simple unweighted mean across the five months introduces only a negligible difference compared to a weighted average using daily values. Sea ice data were obtained from the National Snow and Ice Data Center (NSIDC) and reprojected to match the NSIDC Polar Stereographic projection. Regional sampling polygons followed bowhead foraging areas defined in Ferguson et al. (2021). Raster values for land and intercoastal zones were extracted from within polygons (`exactextractr` package, R version 4.5.1) and were filtered out within R using `dplyr` (`tidyverse` package, R version 4.5.1)

My decision to use mean spring sea ice concentration values (March-July) from the year prior to collection was based on ecological and physiological considerations related to cetacean tissue assimilation and metabolic dynamics. The spring sea ice window is ecologically pivotal due to the return of sunlight after polar winter, paired with thinning ice that enables under-ice diatom blooms (Perrette et al. 2011; Lange et al. 2019). Using sea ice from the same year risks incorporating conditions that post-date or only narrowly overlap with the period of tissue assimilation, particularly given suspected slower (likely between 6 to 12 months) turnover rates for isotopes and fatty acids in mysticete skin and blubber. In contrast, referencing the prior year's spring conditions offers a temporally appropriate predictor for tissues assimilated leading up to

the midsummer biopsy period. Although exact turnover rates in bowheads remain unknown, studies in blue whales estimate ~6 months for skin (Busquets-Vass et al. 2017), with fatty acid turnover likely to be slower. Bowheads, given their thick tissues and hypometabolic rates, are likely to have tissue turnover times slower than other similarly sized large whales (George & Thewissen 2020; George et al. 2021; Pontbriand et al. 2023) supporting a potential year-long integration window in this species. Under a conservative 6-month estimate, whales sampled in July would reflect diet from January onward, meaning the peak spring bloom (April-June) may be only partially assimilated by the time of sampling.

To evaluate whether the choice of sea ice concentration year (prior year or collection year) affected model results, a sensitivity analysis was conducted on parallel GAMs for each biomarker ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, 16:1n-7/16:0, 18:1n-9/18:1n-7, 20:5n-3/22:6n-3, and 22:1n-11/20:1n-9) comparing prior year and collection year spring (March-July) sea ice concentrations. Results were similar, if not slightly improved in prior-year ice across models- with AIC/AICc rankings, deviance explained, and smooth term significance suggesting that model performance was robust to the temporal window (Tables S2-1 through S2-12, in appendix). These results, paired with the low metabolism and unknown nature of bowhead tissue turnover times, support the retention of prior-year sea ice in the final models.

2.2.5 Pre-processing of stable isotopes

For $\delta^{13}\text{C}$, the Suess Effect describes the progressive shift in the $\delta^{13}\text{C}/\delta^{12}\text{C}$ ratio of atmospheric carbon. Since the advent of the industrial revolution, yearly influx of CO_2 is depleted in ^{13}C , has caused a gradual decrease in atmospheric ^{13}C (Keeling 1979; de la Vega et

al. 2019). The oceanic Suess effect ^{13}C change in the Arctic is generally accepted as ~ 0.011 per year (de la Vega et al. 2019) as per the following equation:

$$\delta^{13}\text{C}_{\text{base, aligned}} = \delta^{13}\text{C}_{\text{base}} - 0.011(\text{Year}_{\text{bowhead}} - \text{Year}_{\text{base}})$$

A Suess Effect correction was not applied for $\delta^{13}\text{C}$, as observed decadal shifts in values exceeded the expected atmospheric depletion rate of $\sim 0.3\text{‰}$ over the 30-year period. Prey baseline corrections were required for ^{15}N to account for spatiotemporal variations in primary consumer isotopic ratios. The correction was done by subtracting the isotopic ratios of primary consumers from the isotopic ratios of the bowhead ^{15}N values to account for differences between sampling regions (Post 2002; Black & Armbruster 2021). Copepods (*Calanus spp.*) are the herbivorous primary consumer and main species preyed upon by bowhead whales in the Canadian Arctic (Fortune et al. 2020). Copepod prey samples were not collected at the time of bowhead tissue collection, so literature values were used to correct for primary consumer baseline. Copepod ^{15}N studies are relatively sparse for both Foxe Basin and the Baffin Bay-Davis Strait regions, with the literature value for Foxe Basin being sourced from *Calanus hyperboreus* samples ($^{15}\text{N} = 9.5 \pm 0.4$) collected from around Southampton Island (Amiriaux et al. 2023) and the literature value for the Baffin Bay-Davis Strait region being sourced from an average of *Calanus hyperboreus* and *Calanus glacialis* samples ($^{15}\text{N} = 6.9 \pm 0.4$; 7.4 ± 1.1) collected in Davis Strait (Pomerleau et al. 2011).

2.2.6 Pre-processing of Fatty Acids

Fatty acids were separated to those known to be informative dietary biomarkers in connection with sea ice and environmental conditions, excluding FAs ubiquitous across marine

lipids that contribute little to dietary discrimination. The resulting FAs were chosen from literature based on their relation to sea ice: 16:0, 16:1n-7, 16:3n-4, 16:4n-1, 18:0, 18:1n-9, 18:1n-7, 18:4n-3, 20:1n-9, 20:1n-7, 22:1n-11, and 22:1n-9. The FAs 20:1n-9, 20:1n-7, 22:1n-11, and 22:1n-9 are long-chain monounsaturated markers indicative of calanoid copepods and are consistently used as indicators of copepod-based diets in Arctic marine food web studies; 16:0, 16:1n-7, 16:3n-4, 16:4n-1, and 18:4n-3 are markers of phytoplankton, sea ice algae/diatoms; 18:1n-9 and 18:1n-7 are trophic markers of carnivory (Iverson et al. 2002; Budge et al. 2008, Dalsgaard et al. 2003, Falk-Petersen et al. 2000).

2.2.7 Isotopic Niche Width

To test my hypothesis that bowhead whale dietary diversity and trophic niche width have changed over time and differ between regions (as expected under shifting prey communities due to sea ice loss), Bayesian standard ellipses were generated using the SIBER package in R. Bayesian ellipses capture the core isotopic niche space of a species, with a larger ellipse representing a broader diet and a narrower ellipse representing a more specialized diet (SIBER package, R core team). Ellipses were fitted using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each decade and regional complex to quantify temporal shift in isotopic niche width and ellipses were only generated for region-decade combinations with more than 10 samples. Samples were binned by approximate decades spanning the span of sample collection using the following intervals: 1993-2003; 2004-2013; 2014-2023. Sampling effort in the Canadian Arctic Archipelago was not extensive enough for adequate sample sizes and was totally omitted. The 1993-2003 time period only had two usable samples collected from Baffin Bay-Davis Strait and were consequentially

omitted from analysis. Standard Ellipse Area, corrected for small sample size (SEAc) is a quantitative and robust measurement that is not influenced by outliers and smaller sample sizes compared to total area and offers insights into dietary changes and diversity. Stable Isotope Bayesian Ellipses in R (*SIBER*) package in R was used to determine isotopic niche overlap between regions and decades and calculate isotopic niche breadth (Standard Ellipse Area, SEAb). Posterior distributions were generated using Markov Chain Monte Carlo (MCMC) with 2 chains of 20,000 iterations each, a burn-in of 1,000, and thinning interval of 10, resulting in 3,800 posterior draws per group. Pairwise differences in SEAb between groups (region, decade) were estimated as the proportion of posterior draws where one group's SEAb exceeded another's.

2.2.8 Generalized Additive Models (GAMs)

To test my hypothesis that $\delta^{13}\text{C}$ values will decrease over time and higher $\delta^{15}\text{N}$ values over time reflecting sea ice-related shifts in bowhead whale diets, I modeled $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values as a function of year of collection, mean spring sea ice concentration from the previous year, and region. To first test for long-term trends in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values over the 1993-2023 sampling period, linear regressions were performed with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values as the response variable and year as the predictor, with outliers removed using the interquartile range (IQR) rule, as were years with sparse sampling ($n < 3$, and $\delta^{15}\text{N}$ values corrected for prey baseline. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were subsequently fitted as responses in generalized additive models (GAMs) with mean regional sea ice concentration for the prior year March-July as well as 'year' and 'region' as the explanatory variables.

GAMs are a commonly used statistical approach to modeling non-linear relationships between predictor and response variables. GAMs utilize a link function and smoothing parameters (λ) that mediate the degree of model complexity, with a larger λ denoting a more linear response and stronger penalization while a comparatively smaller λ represents more curves that allow increasingly more flexible, nonlinear relationships in the model (Wood 2017). In interpretation, the effective degrees of freedom (EDF) display the degree of smooth curvature with ~ 1 being approximately linear. GAMs are ideal in a range of ecological studies due to their flexibility to model variable and complex biological responses to multiple predictor types in the model (region, sea ice concentration, bathymetry, etc.) (Jansen et al. 2012; Ruiz-Cooley & Gerrodette 2012; Deschutter et al. 2019). Model selection was based on both AIC and AICc values to identify the most parsimonious (“best”) models, while deviance explained was used as an indicator of each model’s explanatory power (Jackson et al. 2011; Wood 2017).

Fatty acid (FA) ratios were used as a means of assessing spatial and temporal dietary shifts (Pontbriand et al 2023). The fatty acid ratios were modeled using GAMs as functions of collection year, prior year spring sea ice concentration (for months March to July), and regional complex. This approach enabled testing whether bowhead whale diets have shifted temporally and spatially with declining sea ice and whether these shifts differ regionally. ‘Deviance explained’ was used as the primary metric of fit, ‘concurvity’ was calculated in the *mgcv* package in R for each predictor variable smooth term, with an output of 0.8 or greater denoting an unacceptable degree of concurvity that warrants avoiding pairing concurred predictor sets in the same model (Wood 2017).

2.2.9 Principal Component Analysis (PCA)

To address my hypothesis that environmental shifts linked to sea ice loss would influence prey assemblage and, in turn, impact overall fatty acid composition of bowhead whale blubber—particularly the proportion of copepod- and diatom-derived biomarkers that are closely aligned with sea ice, I conducted a PCA to identify dominant dietary gradients that reflect changes in underlying prey communities. Two PCAs, one for the Hudson Bay Complex and one for the Baffin Bay-Davis Strait Complex, were performed on a subset of centered log-ratio (CLR) transformed fatty acids associated with sea ice and dietary markers, following Aitchison, 1986, Budge et al. (2008), and Iverson et al. (2002), with the transformation converting the compositional data to log-ratios relative to the geometric mean of all the fatty acid components. The PCAs were then conducted to assess broad-scale temporal shifts in bowhead whale blubber composition. Only data from the Hudson Bay Complex and Baffin Bay-Davis Strait complexes were compared in the PCAs, as data from the Arctic Archipelago Complex were omitted due to low sample size across years. FAs included in subset were: 16:0, 16:1n-7, 16:3n-4, 16:4n-1 (diatom and ice-algae markers), 18:1n-7 (carnivory marker), 18:4n-3 (flagellate marker), 20:5n-3 (EPA), 20:1n-7, 22:1n-11, 22:1n-9 (copepod markers).

The first two principal components (PC1 and PC2) were retained for each region, explaining 76.9% of the variance in Hudson Bay and 76.4% in Baffin Bay-Davis Strait. To evaluate decade-based shifts in FA composition, a multivariate analysis of variance (MANOVA) was performed on PC1 and PC2 scores. This PCA-to-MANOVA approach was selected to reduce multicollinearity among the original variables, yield uncorrelated axes robust to overfitting, and enable the detection of broad multivariate shifts in FA profiles over time. By capturing more than

75% of the total variance, the retained components provided an ecologically interpretable framework for assessing long-term dietary changes in bowhead whales.

2.2.10 PERMANOVA

To further test my hypothesis that bowhead whale fatty acid composition varies across regions and over time in response to changes in sea ice conditions, I used a permutational multivariate analysis of variance (PERMANOVA) on Euclidean distance matrices derived from the CLR-transformed fatty acid subset outlined above. PCA provides an unconstrained ordination to visualize dominant dietary gradients, and PERMANOVA allows for a formal multivariate hypothesis test of overall compositional differences in response to predictors (region, ice, year). The regional complexes (Hudson Bay Complex; Baffin Bay Davis Straight Complex), year of sample collection, and average spring sea ice concentration were chosen as explanatory variables, with permutations limited within year strata. Homogeneity of multivariate dispersion was assessed with the `betadisper()` function from the ‘vegan’ package in R (Oksanen et al. 2022) to assess that results were not influenced by differences in dispersion among groups. Conducting the PERMANOVA on the previously described FA subset ensures that the potentially meaningful ecological variance between groups wouldn’t be lost in the dimensionality reduction of the principal component analysis. The marginal effects were tested using ‘by = margin’ in the `adonis2` R package with permutations stratified by year to evaluate the contributions of region and sea ice to the data variation. A multivariate homogeneity of group dispersion (PERMDISP) was run for year and region to test the distributional differences between groups.

2.3 Results

2.3.1 Stable Isotope Results

Across all samples (1993-2023), $\delta^{13}\text{C}$ values in bowhead whale skin ranged from -22.11 to -17.92‰, while $\delta^{15}\text{N}$ values ranged from 10.81 to 15.06‰ (Table 2-1). Linear regressions indicated significant temporal declines in both isotopic values over the 1993-2023 sampling period (Figure 2-2). $\delta^{13}\text{C}$ values decreased at a rate of -0.032‰ per year ($p < 0.001$, $R^2 = 0.07$), while $\delta^{15}\text{N}$ values declined at -0.043‰ per year ($p < 0.001$, $R^2 = 0.13$). In the Baffin Bay-Davis Strait Complex, $\delta^{13}\text{C}$ values increased significantly over time (0.042‰ per year, $p < 0.001$, $R^2 = 0.09$), while $\delta^{15}\text{N}$ values declined (-0.033‰ per year, $p < 0.001$, $R^2 = 0.09$). In contrast, the Hudson Bay Complex showed a modest decline in $\delta^{13}\text{C}$ (-0.015‰ per year, $p = 0.023$, $R^2 = 0.02$), a pattern that is consistent with the expected rate of decline from the Suess effect, while $\delta^{15}\text{N}$ values remained statistically unchanged over the 30-year period ($p = 0.68$, $R^2 < 0.001$).

Decade	Site Complex	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C:N
1993-2003	Baffin Bay-Davis Strait Complex	2	-20.16 ± 0.81	13.25 ± 0.12	NA
1993-2003	Hudson Bay Complex	19	-20.20 ± 1.13	13.01 ± 0.78	3.46 ± 0.30
2004-2013	Baffin Bay-Davis Strait Complex	59	-20.81 ± 0.56	12.41 ± 0.56	3.69 ± 0.23
2004-2013	Hudson Bay Complex	228	-19.79 ± 0.60	13.10 ± 0.65	3.81 ± 0.39
2014-2023	Baffin Bay-Davis Strait Complex	110	-20.62 ± 0.59	12.14 ± 0.52	3.76 ± 0.28
2014-2023	Hudson Bay Complex	38	-20.10 ± 0.54	12.86 ± 0.49	3.80 ± 0.40

Table 2-1: Mean $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and C:N values ($\pm\text{SD}$) of bowhead whales in the Hudson Bay and Baffin Bay-Davis Strait complexes.

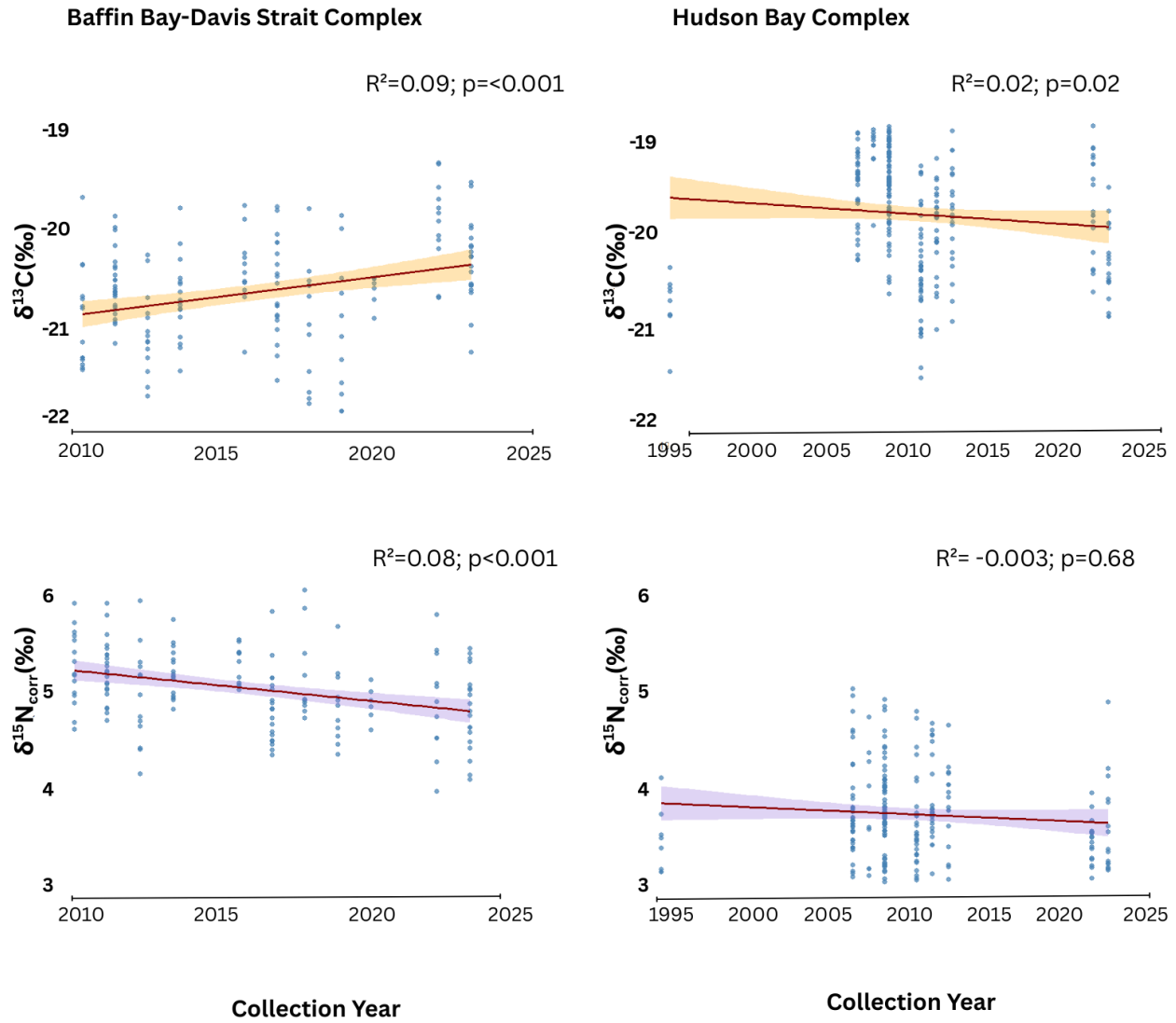


Figure 2-2: Linear regressions of stable isotope values ($\delta^{13}\text{C}$; $\delta^{15}\text{N}$ is corrected for baseline) over the sampling period for bowhead whales in the Baffin Bay-Davis Strait and Hudson Bay Complexes. To reduce the influence of extreme values and sparse-year effects, outliers were removed using the interquartile range (IQR) method, and all years with fewer than 3 samples were excluded from the analysis. Trend lines represent linear fits with 95% confidence intervals.

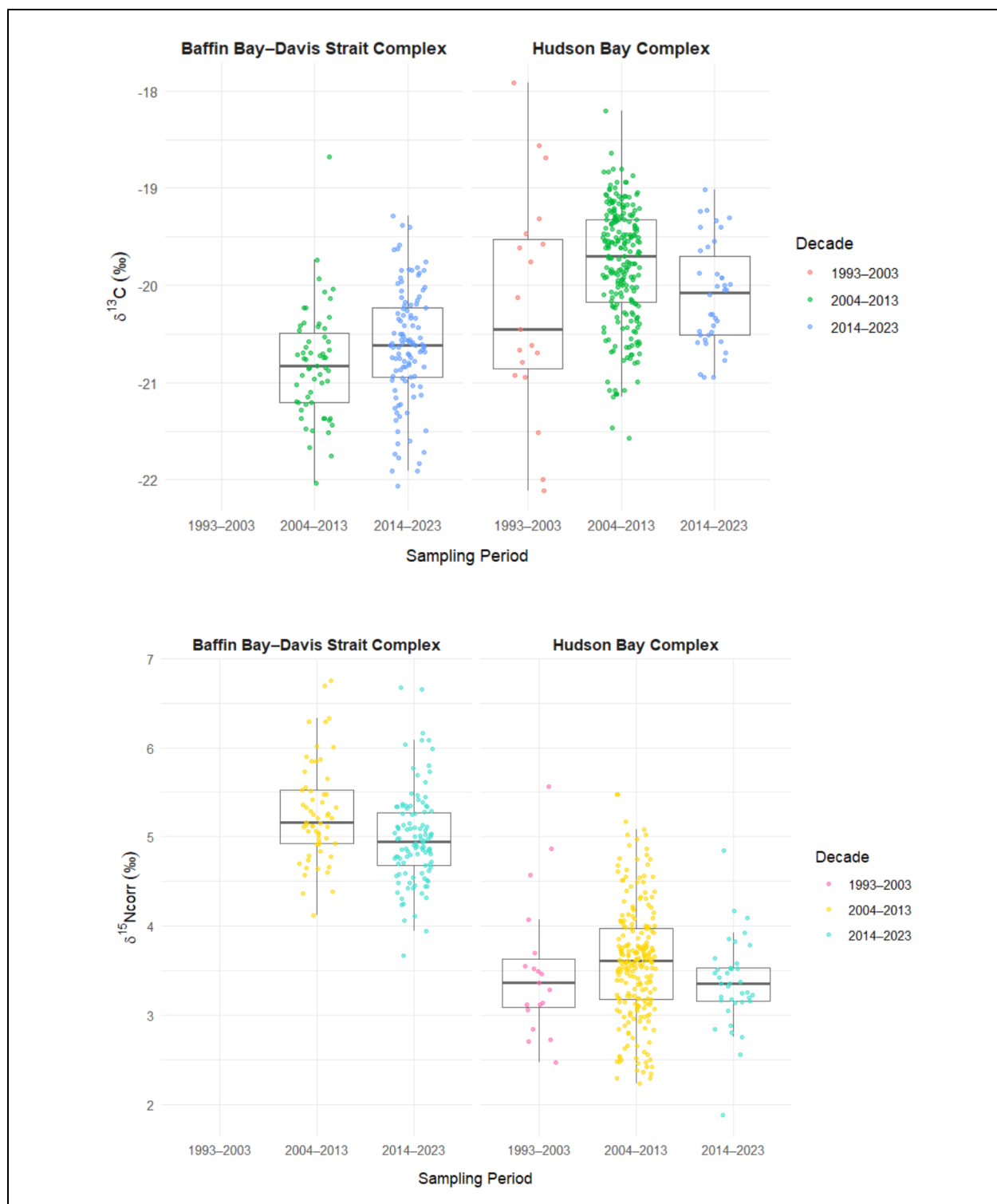


Figure 2-3: Boxplots showing decadal variation in stable isotope values ($\delta^{13}\text{C}$, top; $\delta^{15}\text{N}$, bottom) in bowhead whale skin samples collected from 1993 to 2023 across two regions: the Baffin Bay-Davis Strait Complex (left panels) and Hudson Bay Complex (right panels). Each point represents an individual sample, color-coded by sampling decade: 1993–2003 (red), 2004–2013 (green/blue), and 2014–2023 (yellow/cyan). $\delta^{13}\text{C}$ values were generally higher in the Hudson Bay Complex, consistent with greater reliance on sympagic production, while $\delta^{15}\text{N}$ values were higher in the Baffin Bay-Davis Strait Complex.

2.3.2 Isotopic Niche Width

Only the Hudson Bay Complex (HBC) had sufficient sample size to support a separate isotopic niche analysis for the 1993-2003 period; Whales exhibited a broad $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ spread during this period. In 2004-2013, both regions showed significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Bowheads in the Hudson Bay Complex displayed higher $\delta^{13}\text{C}$ values while BBDS individuals had slightly lower $\delta^{13}\text{C}$ values on average and marginally higher $\delta^{15}\text{N}$ (corrected) values. In recent decades (2004-2023), bowheads in BBDS exhibited slightly broader isotopic niche widths than HBC.

Bayesian standard ellipse area (SEAb) estimates revealed temporal and regional variation in isotopic niche breadth of bowhead whales. In the Hudson Bay Complex (HBC), SEAb declined markedly over time, with posterior mode estimates decreasing from 2.57‰^2 (1993-2003) to 1.21‰^2 (2004-2013) and 0.84‰^2 (2014-2023). In contrast, SEAb in the Baffin Bay-Davis Strait Complex remained relatively stable, with posterior modes of 0.90‰^2 and 0.95‰^2 in the 2004-2013 and 2014-2023 periods, respectively. When comparing isotopic niche breadths between regions within each decade, I found a 100% posterior probability that SEAb was greater in HBC than BBDS during 2004-2013, but only a 50% probability during the 2014-2023 decade. These posterior probabilities indicate support for greater trophic variability in HBC during 2004-2013, but no evidence for regional differences in the most recent decade. Collectively, the results indicate a broader and more variable isotopic niche in HBC bowheads in earlier decades,

followed by a contraction over time, consistent with potential dietary shifts or ecosystem changes in the region.

<i>Decade</i>	Complex	SEAc (‰²)	SEAb (‰²)
1993-2003	Hudson Bay Complex (n=19)	2.72	2.57
2004-2013	Baffin Bay-Davis Strait Complex (n=59)	1.21	0.90
2004-2013	Hudson Bay Complex (n=228)	0.92	1.21
2014-2023	Baffin Bay-Davis Strait Complex (n=110)	0.96	0.95
2014-2023	Hudson Bay Complex (n=38)	0.85	0.84

Table 2-2: Standard ellipse area corrected for small sample size (SEAc) and Bayesian standard ellipse area (SEAb) for bowhead whale stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) by region (Hudson Bay Complex and Baffin Bay-Davis Strait Complex) and decade.

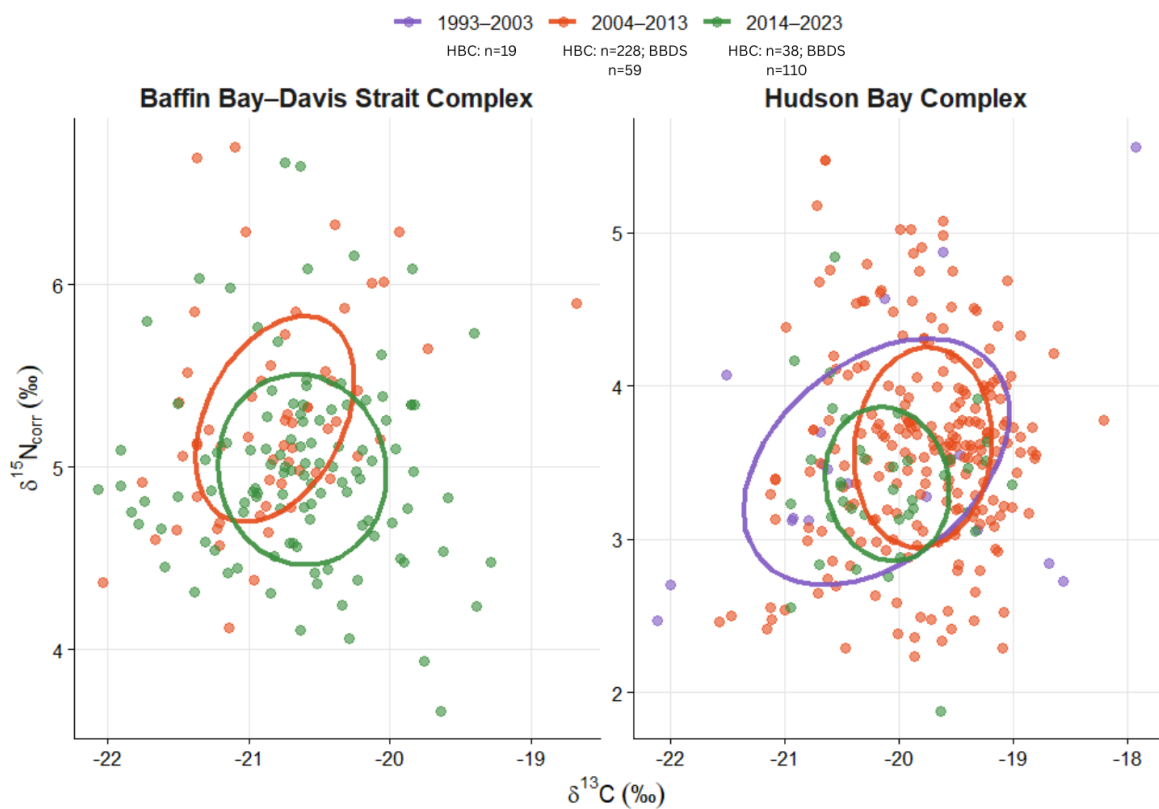


Figure 2-4: Bayesian standard ellipses (SEAc) representing isotopic niche widths of bowhead whale skin samples from the Baffin Bay-Davis Strait Complex (left) and Hudson Bay Complex (right), separated by decade (1993–2003: purple; 2004–2013: orange; 2014–2023: green). Ellipses are based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values corrected for prey baseline ($\delta^{15}\text{N}_{\text{corr}}$). Ellipse area reflects isotopic niche width, with larger ellipses indicating greater dietary or foraging variability within each decade-region group.

2.3.3 Generalized Additive Model (GAM) Results for Stable Isotopes

2.3.4. $\delta^{13}\text{C}$

A Pearson correlation on predictors showed no strong collinearity ($r = 0.31$; $p < 0.001$) with all predictors being retained initially. Models were subsequently tested for concurvity between predictors, from which GAMs with predictor combinations that exhibited severe concurvity were excluded from further analysis. These included the full model and those combining sea ice with region or year, all of which showed high ‘worst’ concurvity estimates (≥ 0.8) in both parametric and smooth terms. In contrast, models including only sea ice, only year, or year with region passed concurvity checks. A region-only model and a null model were also retained, as they contained no smooth terms.

The best-fitting GAM for $\delta^{13}\text{C}$ in bowhead whale skin included a smooth term for prior-year sea ice concentration (Table 2-3). The model explained 56.8% of the deviance, with an adjusted R^2 of 0.548 and a REML score of 382.94. The smooth term had an estimated degrees of freedom (edf) of 19.75, a reference df of 21.94, an F-statistic of 25.04, and was highly significant ($p < 0.001$), indicating a strong non-linear relationship between sea ice concentration and $\delta^{13}\text{C}$ values. As shown by the partial effects plots (Figure 2-5), $\delta^{13}\text{C}$ values started at intermediate levels at a 0.5 proportion of sea ice, showing fluctuations until rising up until peak high values at a 0.65 proportion of sea ice. Peak low values occurred at an approximate proportion of 0.75 sea ice. The partial effects plot is defined by a strong oscillations across sea ice concentrations, with confidence intervals widening significantly during periods of low sampling.

$\delta^{13}\text{C}$ Model Selection

Rank	Selected variables	AIC	ΔAIC	AICc	ΔAICc	Adj R^2	Dev. explained
1	Prior Year Average Spring Sea Ice	686.32	0	688.92	0	0.55	56.8%
2	Year Collected + Region	694.04	7.72	695.45	6.53	0.53	54.8%
3	Year Collected	732.43	46.11	733.72	44.80	0.49	50.7%
4	Region	871.53	185.21	871.58	182.66	0.29	29.1%
5	Null (intercept only)	1026.44	340.12	1026.46	337.54	0	0.0%

Table 2-3: Summary of top selected generalized additive models (GAMs) predicting $\delta^{13}\text{C}$ values in bowhead whale skin. Models were ranked using $\Delta\text{AICc} < 2.0$ (AICc = Akaike's Information Criterion corrected for small sample size). The best-supported model included average spring sea ice concentration and explained 56.8% of the deviance in $\delta^{13}\text{C}$ values. Smooth terms are denoted as $s()$ in the model formula.

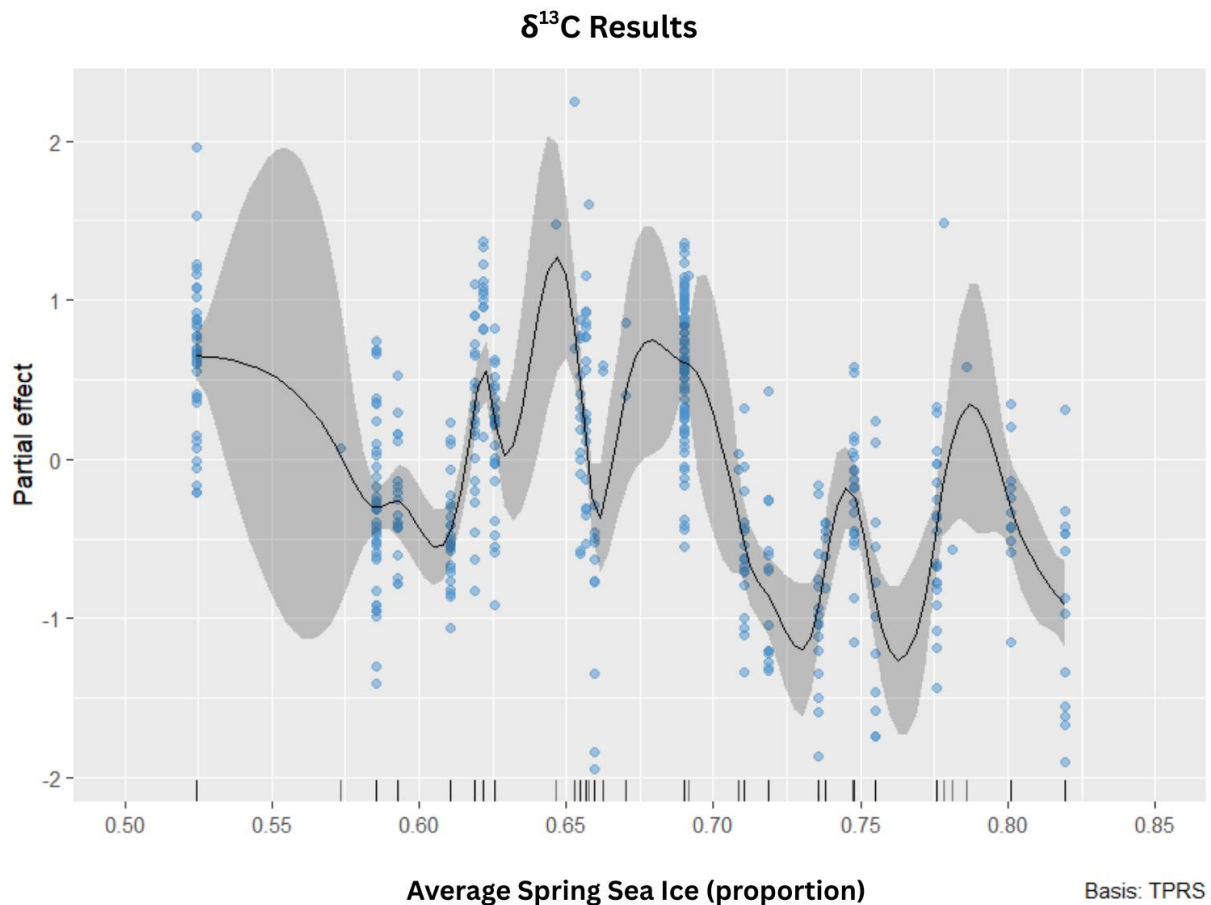


Figure 2-5: Partial effects plot from the top-ranked generalized additive model (GAM) predicting bowhead whale $\delta^{13}\text{C}$ values as a function of average spring sea ice concentration (proportion). The plot illustrates the smooth term effect of sea ice ($\pm 95\%$ CI), with region included as a fixed parametric effect. This model was selected as the best fit based on ΔAICc and explained 56.8% of the deviance in $\delta^{13}\text{C}$ values. Basis: Thin Plate Regression Spline (TPRS).

2.3.5. $\delta^{15}\text{N}$

A Pearson correlation on predictors showed no strong collinearity ($r = 0.31$) with all predictors being retained initially. Following this, concurvity testing of smooth term interactions showed that several models should be excluded due to high concurvity, including the full model and all others combining sea ice with region or year (high ‘worst’ concurvity estimates ≥ 0.8). In contrast, models containing only sea ice, only year, and year with region passed all concurvity checks. A region-only model was also retained, as concurvity is not applicable when no smooth terms are present.

The GAMs for $\delta^{15}\text{N}$ explained a comparable proportion of variation to those for $\delta^{13}\text{C}$ (Table 2-4). The best-fitting model, as determined by AICc, included year and region, explaining 61.5% of the deviance with an adjusted R^2 of 0.612 and a REML score of 419.6.. Year had an estimated degrees of freedom (edf) of 2.25, a reference df of 2.75, and was statistically significant ($F = 6.63$, $p = 0.00075$), indicating a moderate non-linear trend over time. The parametric effect of region was also highly significant (estimate = -1.63 , $SE = 0.068$, $t = -24.07$, $p < 0.001$). As shown by the partial effects plots, $\delta^{15}\text{N}$ values showed a steady decrease over time, beginning very gradually in the years prior to 2000 and continuing a steady decline until the most recent collection year (Figure 2-6).

$\delta^{15}\text{N}$ Model Selection

Rank	Selected variables	AIC	ΔAIC	AICc	ΔAICc	Adj R^2	Dev. explained
1	Year Collected + Region	833.01	0	833.18	0	0.61	61.5%
2	Region	846.07	13.06	846.12	12.94	0.60	59.9%
3	Average prior-year Spring Sea Ice	859.84	26.83	862.25	29.07	0.60	62.0%
4	Year Collected	1139.44	306.43	1139.84	306.66	0.25	25.7%
5	Null (intercept only)	1260.69	427.68	1260.72	427.54	0.00	0%

Table 2-4: Generalized additive model (GAM) selection results for $\delta^{15}\text{N}$ values in bowhead whale skin, ranked by ΔAICc . Models included various combinations of smooth terms ($s()$) for year of collection and average spring sea ice concentration, with region included as a parametric factor.

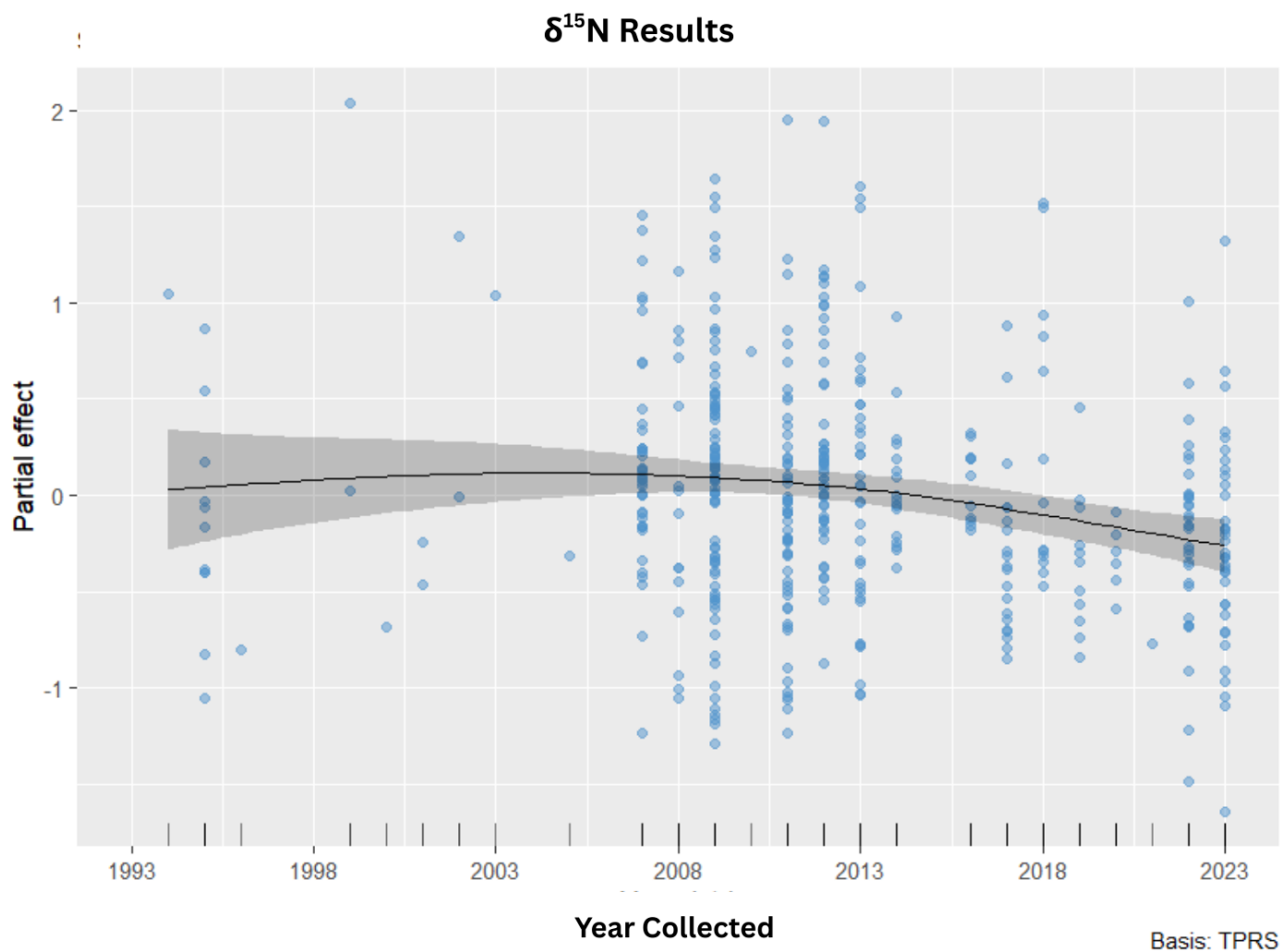


Figure 2-6: Partial effects plot of the top-performing GAM for $\delta^{15}\text{N}$ in bowhead whale skin, showing the smooth term for year of collection. Region was included as a fixed parametric effect. The fitted smooth is shown with 95% confidence intervals (gray shading). The model used a thin plate regression spline (TPRS) basis

2.3.6. Fatty Acid and Principal Components Analysis (PCA) Results

PC1 for the Hudson Bay Complex accounted for 64.3% of the total variance and PC2 accounted for 12.6% of the total variance (76.9% total). PC1 was positively driven by 16:1n-7, 16:0, 18:1n-7, 22:1n-9, 22:1n-11, and 20:1n-7, while it was negatively driven by 20:5n-3, 18:4n-3, and 16:4n-1. Loadings for PC2 were positive for 18:1n-7, 16:1n-7, and 16:0, and negative for 22:1n-9, 22:1n-11, and 18:4n-3. The PCA biplot showed moderate separation along PC1 when grouped by decade (2004-2013 vs 2014-2023) (Figure 2-8).

A multivariate analysis of variance (MANOVA) was conducted on PC1 and PC2 for the Hudson Bay Complex to test for temporal differences across decades in the FA subset of the blubber compositions. The results indicated a strong overall effect of decade (2004-2013 vs 2014-2023) on the multivariate FA signature (Pillai's Trace = 0.350, $F(2, 86) = 23.20$, $p < 0.001$). Following ANOVAs showed that this effect was driven primarily by PC1 ($F = 46.83$, $p < 0.001$). By comparison, PC2 did not differ significantly between decades ($p = 0.84$).

PC1 for the Baffin Bay-Davis Strait Complex accounted for 50.9% of the variance, while PC2 accounted for 25.5%, explaining 76.4% of the total variance. PC1 was positively driven by 22:1n-9, 22:1n-11, 16:0, 18:1n-7, 16:1n-7, and 16:3n-4, and negatively driven by 20:5n-3 (EPA), 18:4n-3, and 16:4n-1. PC2 was positively influenced by 20:1n-7, 16:3n-4, 22:1n-9, and 22:1n-11, while negatively influenced by 16:0, 16:1n-7, and 18:1n-7. Decadal groupings in the PCA biplot (2004-2013 vs. 2014-2023) showed moderate separation along PC1, suggesting temporal shifts in fatty acid composition and sea-ice-associated dietary inputs in this region.

A MANOVA for Baffin Bay-Davis Strait on PC1 and PC2 indicated a marginal multivariate effect of decade (2004-2013 vs. 2014-2023) on PCA scores (Pillai's trace = 0.115,

$F_{2,41} = 2.66$, $p = 0.082$), suggesting moderate evidence for temporal shifts in fatty acid composition. The separation of decadal groups along PC1 was driven by increased 22:1n-9, 22:1n-11, and 16:1n-7 in more recent samples, consistent with greater contributions of ice-associated and copepod-derived prey. An ANOVA for the region showed marginal separation along PC1 ($F_{1,42} = 3.88$, $p = 0.056$), and no significant effect for PC2 ($F_{1,42} = 1.32$, $p = 0.26$).

A PERMANOVA on centered log-ratio transformed fatty acid compositions across all samples ($n = 148$) for the subset indicated significant effects of average spring sea ice ($R^2 = 0.03$, $F = 5.70$, $p = 0.004$), year of collection ($R^2 = 0.118$, $F = 22.35$, $p = 0.001$), and region ($R^2 = 0.034$, $F = 3.27$, $p = 0.014$). These results highlight both temporal and spatial structure in bowhead whale fatty acid profiles, with year explaining the largest proportion of variance (11.8%).

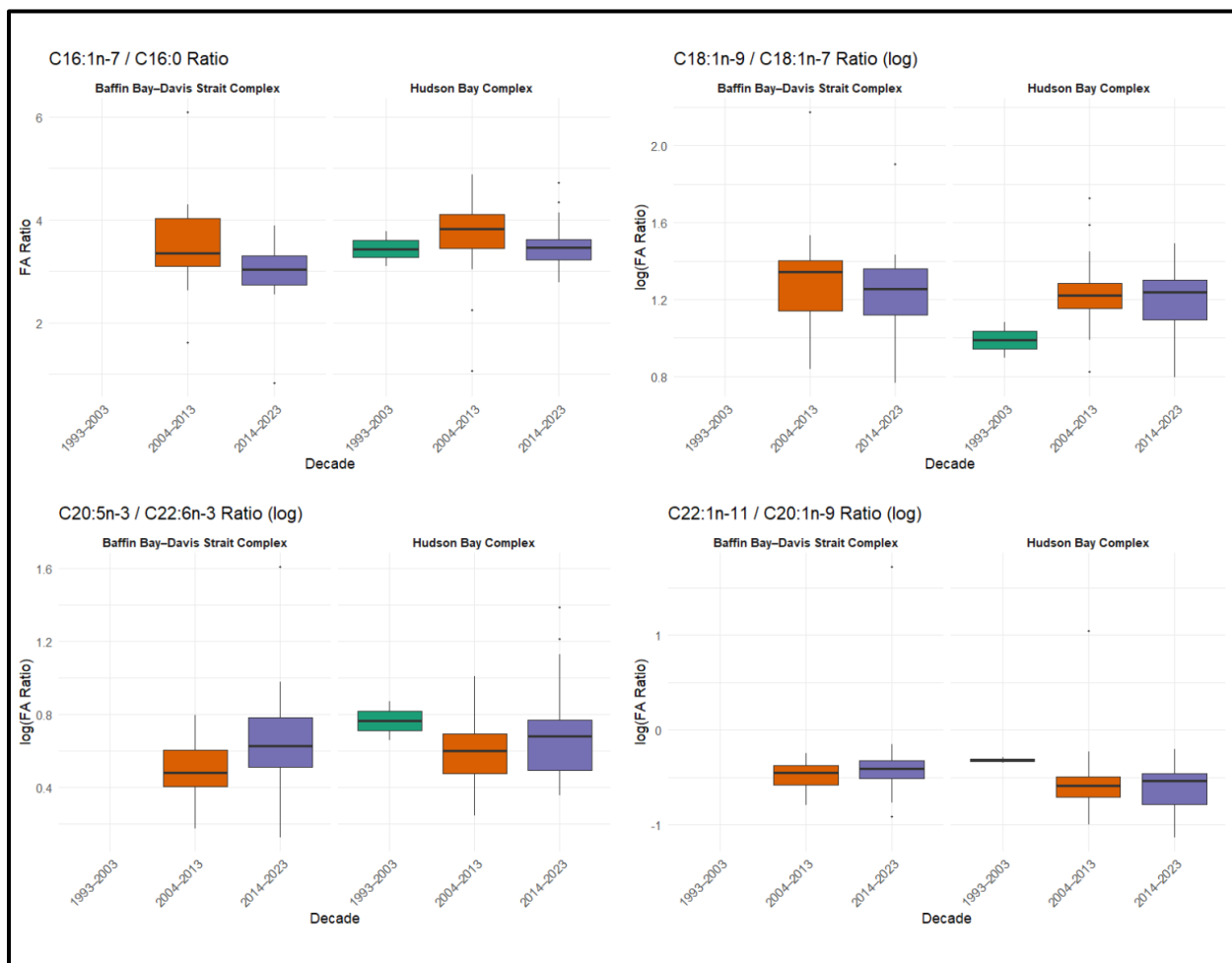


Figure 2-7: Boxplots of four fatty acid (FA) ratios of interest in bowhead whale blubber across three decadal bins (1993-2003, 2004-2013, 2014-2023) and two regions: Baffin Bay-Davis Strait Complex (left) and Hudson Bay Complex (right). The four FA ratios include: **(A)** 16:1n-7/16:0 (diatom/ice-associated marker); **(B)** log-transformed 18:1n-9/18:1n-7 (trophic/carnivory indicator); **(C)** log-transformed 20:5n-3/22:6n-3, and **(D)** log-transformed 22:1n-11/20:1n-9 (copepod fatty acid marker). Data was binned by decade to increase sample sizes and enable temporal comparisons.

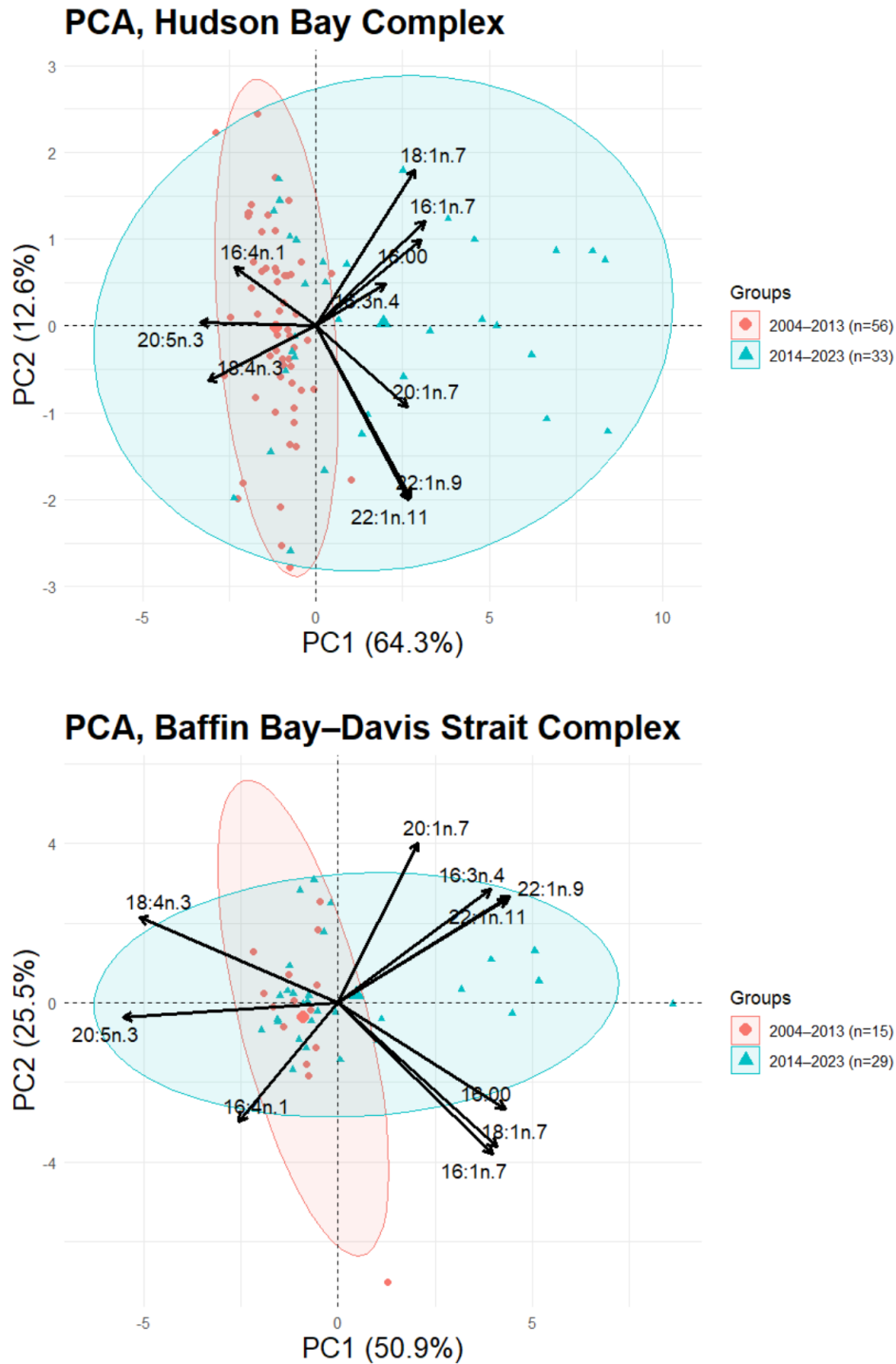


Figure 2-8: Principal component analysis (PCA) biplots of bowhead whale blubber fatty acid (FA) composition, grouped by decade (2004–2013, 2014–2023) for the Hudson Bay Complex (top) and Baffin Bay–Davis Strait Complex (bottom). PCA was performed on a centered log-ratio (CLR) transformed subset of fatty acids associated with sea ice and dietary markers: 16:0, 16:1n-7, 16:3n-4, 16:4n-1 (diatom and ice-associated markers), 18:1n-7 (carnivory marker), 18:4n-3 (flagellate marker), 20:5n-3 (EPA), 20:1n-7, 22:1n-11, and 22:1n-9 (copepod markers). Arrows represent loadings of each FA on the first two principal components, indicating their contribution to variation in FA composition. Percent variance explained by PC1 and PC2 is shown on respective axes. Ellipses represent 95% confidence intervals for each decade group.

2.3.7. Generalized Additive Model (GAM) Results for Fatty Acid Ratios

Fatty Acid Ratio	Ratio Range	Mean $\pm$ SD	Ecological Indicator
16:1n-7 / 16:0	0.82 - 6.09	3.49 $\pm$ 0.67	Diatom contribution (Auel et al. 2002; Dalsgaard et al. 2003; Sampei et al 2021)
18:1n-9 / 18:1n-7	2.15 - 8.79	3.40 $\pm$ 0.79	Trophic marker (higher C18:1n-9 indicative of carnivory (Graeve et al. 1997; Kohlbach et al. 2021)
20:5n-3 / 22:6n-3	1.13 - 5.00	1.93 $\pm$ 0.48	EPA/DHA proportion (phytoplankton source shift) (Mayzaud et al. 1990; Dalsgaard et al. 2003; Leu et al., 2013)
22:1n-11 / 20:1n-9	0.32 - 5.57	0.64 $\pm$ 0.46	Copepod dominance (<i>Calanus</i> indicator) (Falk-Petersen et al. 1990; Dalsgaard et al. 2003; ICES CM 2008; Falk-Petersen et al. 2009; Pontbriand et al. 2023)

Table 2-5: Fatty acid ratio ranges, mean, standard deviations, and biomarker association for all samples.

2.3.8. 16:1n-7 / 16:0 (Diatom Ratio)

For the diatom-associated ratio 16:1n-7/16:0, the best-fitting GAM included a smooth term for year and a parametric term for region (Table 2-6), explaining 26.6% of the deviance (adjusted $R^2 = 0.235$, REML = 140.13). The smooth term for year was statistically significant ($edf = 3.89$, $F = 5.66$, $p = 0.00016$), indicating moderate non-linear temporal variation in diatom signal strength. The effect of region was marginal ($p = 0.054$), with the Hudson Bay Complex showing slightly higher diatom ratios than the reference region (estimate = 0.368 ± 0.189). The ratio increased during the early 2000s, reaching a broad peak around 2008, followed by a gradual decline until approximately 2015, after which it remained relatively stable (Figure 2-9).

16:1n-7 / 16:0 (diatom ratio): Model Selection

Rank	Selected variables	AIC	ΔAIC	AICc	$\Delta AICc$	Adj R^2	Dev. explained
1	Year Collected + Region	273.28	0	274.41	0	0.24	26.6%
2	Year Collected + Avg Spring Sea Ice	276.24	2.96	277.15	2.74	0.22	24.2%
3	Year Collected	278.57	5.29	279.24	4.83	0.20	21.8%
4	Avg Spring Sea Ice	292.08	18.80	292.41	17.99	0.12	14%
5	Region	292.73	19.45	292.36	17.95	0.11	11.5%
6	Null	306.19	32.91	306.28	31.87	0	0%

Table 2-6: Generalized additive model (GAM) selection results for the fatty acid ratio 16:1n-7/16:0 (diatom marker) in bowhead whale blubber, ranked by $\Delta AICc$. Models included various combinations of smooth terms $s()$ for year of collection and average spring sea ice concentration, with region included as a parametric factor.

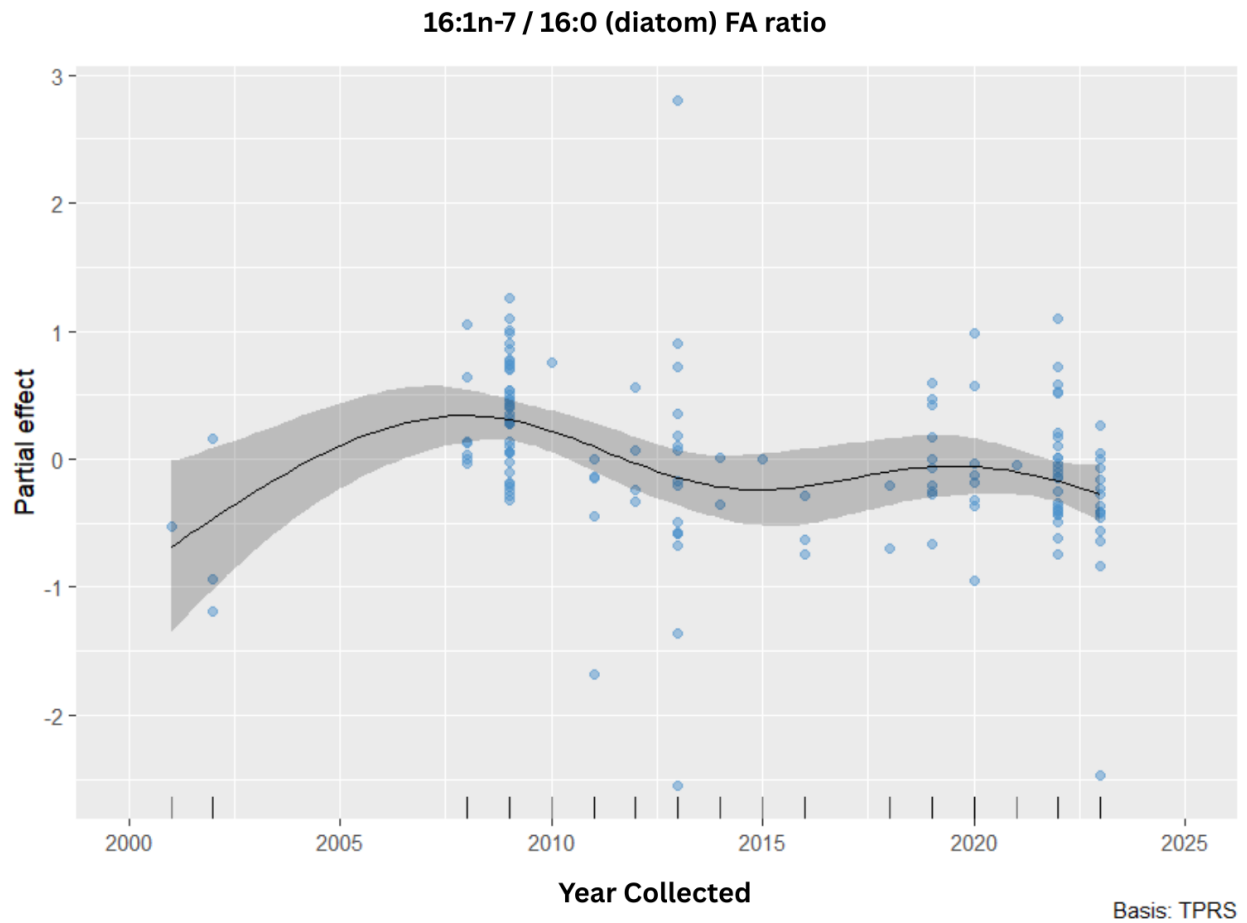


Figure 2-9: Partial effects plot from the top-performing generalized additive model (GAM) for the fatty acid ratio 16:1n-7/16:0 (diatom marker) in bowhead whale blubber. The model included a smooth term for year of collection and a parametric term for region. The plot shows the partial effect of year on the diatom ratio, with shaded ribbons indicating 95% confidence intervals.

2.3.9. 18:1n-9 / 18:1n-7 (Trophic Ratio)

For the trophic fatty acid ratio 18:1n9 / 18:1n7, the top-performing GAM included a smooth for year and a parametric term for region (Table 2-7). The model explained 27.8% of the deviance (adjusted $R^2 = 0.246$, REML = -31.27). Year had a statistically significant non-linear effect (edf = 4.36, $F = 5.39$, $p < 0.001$), while both regions also showed significant differences from the reference category (Baffin Bay-Davis Strait: $\beta = 0.21 \pm 0.06$, $p < 0.001$; Hudson Bay: $\beta = 0.19 \pm 0.06$, $p = 0.001$). The model intercept was 1.02 ± 0.05 . The partial effects plot for year (Figure 2-10) shows a non-linear temporal pattern in the 18:1n9/18:1n7 trophic FA ratio. Values begin relatively low around the year 2000, rise steadily to a peak near 2012, then declining to a relative low in 2016, before increasing again from ~2018 through 2023.

18:1n-9 / 18:1n-7 (trophic ratio): Model Selection

Rank	Selected variables	AIC	ΔAIC	AICc	$\Delta AICc$	Adj R^2	Dev. explained
1	Year collected + Region	-82.21	0	-80.97	0	0.25	27.8%
2	Year Collected + Avg Spring Sea Ice	-82.43	0.22	-80.80	0.17	0.26	29.3%
3	Year Collected	-72.56	9.87	-71.82	9.15	0.18	20.8%
4	Region	-65.06	12.27	-64.78	11.43	0.12	13.6%
5	Avg Spring Sea Ice	-70.16	17.37	-69.54	16.19	0.17	18.9%
6	Null	-47.42	35.01	-47.34	33.63	0	0%

Table 2-7: Generalized additive model (GAM) selection results for the log-transformed fatty acid ratio 18:1n-9/18:1n-7 (trophic marker) in bowhead whale blubber, ranked by $\Delta AICc$. Models included various combinations of smooth terms (s()) for year of collection and average spring sea ice concentration, with region included as a parametric factor.

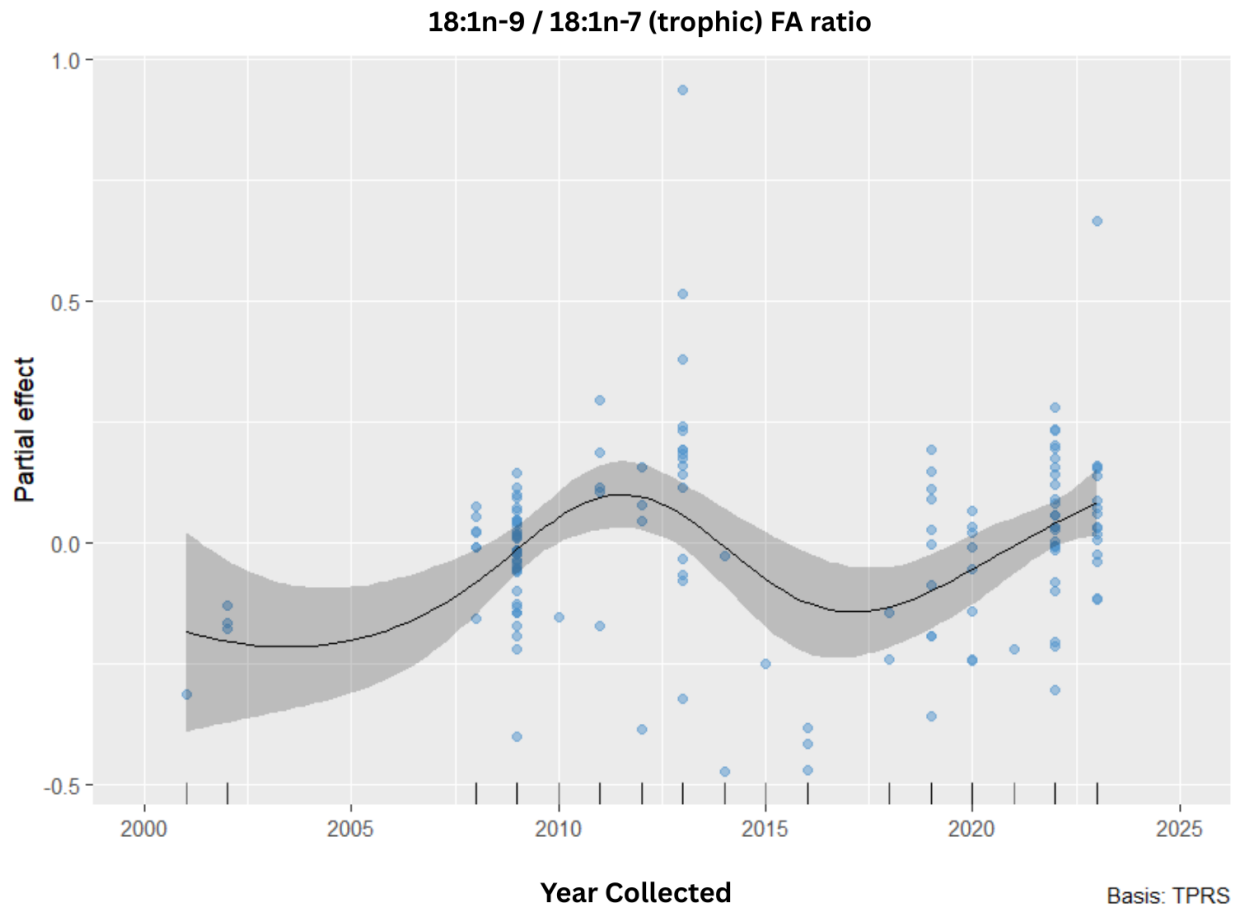


Figure 2-10: Partial effects plot of top-performing model, with 18:1n-9/18:1n-7 (trophic marker) as the response variable to the smooth term predictor of year of collection. The model included region as a parametric factor

2.3.10. 20:5n-3 / 22:6n-3

For the fatty acid ratio 20:5n3/22:6n3, the best-performing GAM included smooth terms for average spring sea ice concentration and year (Table 2-8), explaining 9.8% of the deviance (adjusted $R^2 = 0.071$, REML = -14.90). The effect of sea ice approached significance (edf = 2.39, $F = 2.15$, $p = 0.069$), while the year effect was weaker and non-significant (edf = 1.93, $F = 1.49$). Partial effects plots revealed a shallow non-linear decline in 20:5n3/22:6n3 values from

~0.60 to ~0.75 sea ice proportion, followed by a modest increase at higher ice concentrations. The effect of year remained largely flat across the time series, with wide confidence intervals (Figure 2-11).

20:5n-3 / 22:6n-3: Model Selection

Rank	Selected variables	AIC	Δ AIC	AICc	Δ AICc	Adj R ²	Dev. explained
1	Avg Spring Sea Ice + Year Collected	-40.56	0	-39.69	0	0.07	9.82%
2	Avg Spring Sea Ice	-40.75	0.19	-40.32	0.63	0.05	7.07%
3	Year Collected + Region	-37.72	3.03	-37.01	3.31	0.05	7.16%
4	Year Collected	-37.77	2.98	-37.37	2.95	0.03	4.92%
5	Null	-35.92	4.94	-35.84	4.79	0	0%
6	Regional Complex	-35.81	4.83	-35.53	4.48	0.01	2.61%

Table 2-8: Generalized additive model (GAM) selection results for the log-transformed fatty acid ratio 20:5n-3/22:6n-3 in bowhead whales, ranked by Δ AICc. Models included various combinations of smooth terms ($s()$) for average spring sea ice concentration and year of collection, with region included as a parametric factor where applicable.

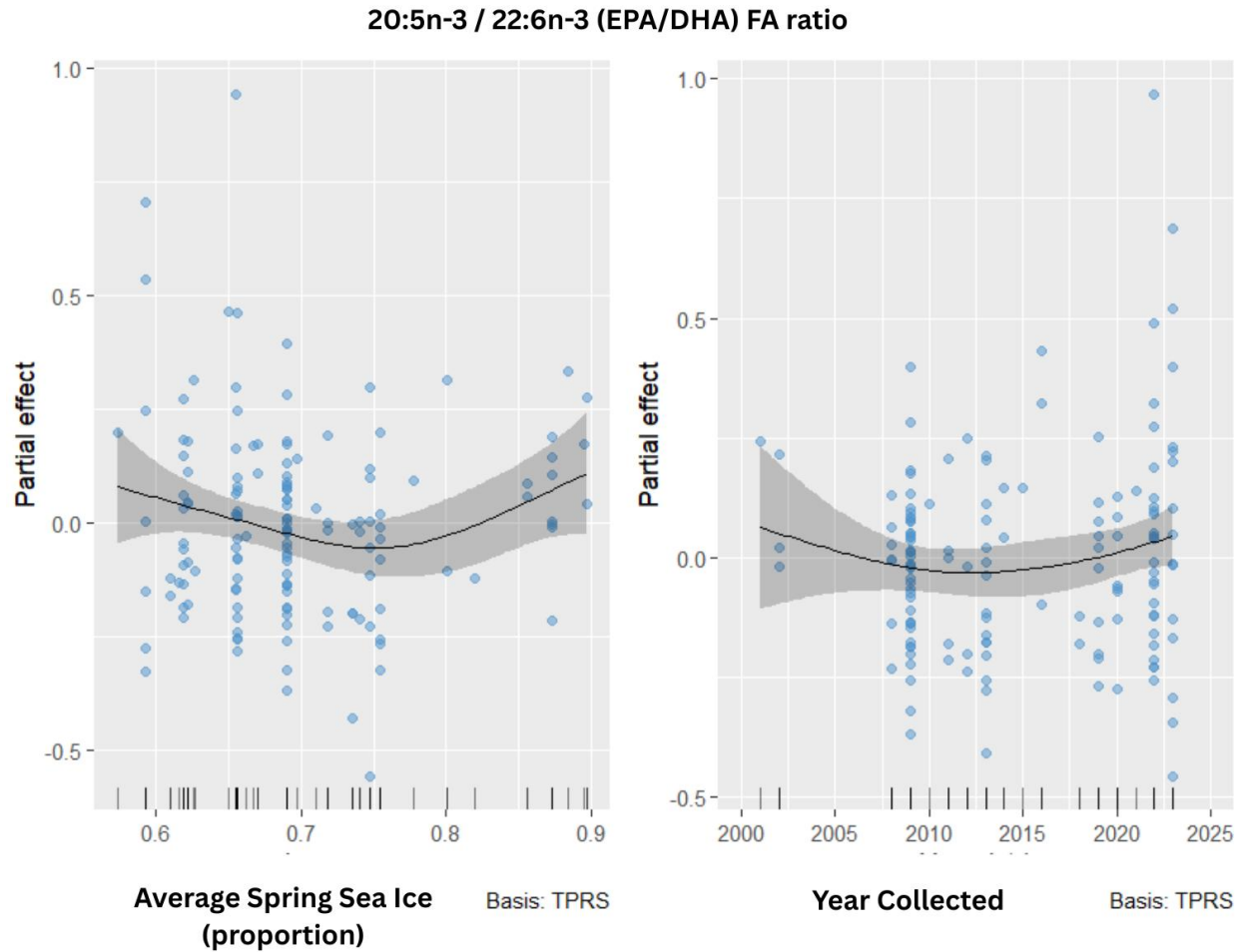


Figure 2-11: Partial effects plot of the top-performing model, with 20:5n-3/22:6n-3 as the response variable to smooth term predictors of average spring sea ice proportion and year of collection.

2.3.11. 22:1n-11 / 20:1n-9 (Copepod markers)

For the log-transformed copepod biomarker ratio (22:1n11/20:1n9), the top-performing GAM included a smooth for year and a parametric term for region (Table 2-9). This model explained 16.1% of the deviance (adjusted $R^2 = 0.128$, REML = 33.38). The year effect was significant (edf = 3.71, $F = 2.65$, $p = 0.0294$), showing a weak non-linear trend: values declined

slightly from 2002 to approximately 2009, rose steadily to a 2016 peak, then declined again through 2023. Regional differences were marginal, with only the BBDS complex approaching significance ($\beta = 0.180 \pm 0.094$, $p = 0.057$). Confidence intervals were narrowest from 2010-2020 and widened at either end due to lower sample sizes (Figure 2-12).

22:1n-11 / 20:1n-9 (Copepod markers): Model Selection

Rank	Selected variables	AIC	Δ AIC	AICc	Δ AICc	Adj R ²	Dev. explained
1	Year Collected + Region	54.78	0	55.88	0	0.13	16.1%
2	Year Collected	59.42	4.64	60.07	4.19	0.09	11.2%
3	Regional Complex	62.08	6.35	62.36	6.10	0.05	6.71%
4	Avg Spring Sea Ice + Year Collected	61.13	7.30	61.98	6.48	0.08	11.3%
5	Avg Spring Sea Ice	63.71	8.93	64.36	8.48	0.06	8.52%
6	Null	68.36	13.58	68.44	12.56	0	0%

Table 2-9: Generalized additive model (GAM) selection results for the log-transformed fatty acid ratio 22:1n-11/20:1n-9 (copepod markers) in bowhead whales, ranked by Δ AICc. Models included various combinations of smooth terms $\{s()\}$ for average spring sea ice concentration and year of collection, with region included as a parametric factor where applicable.

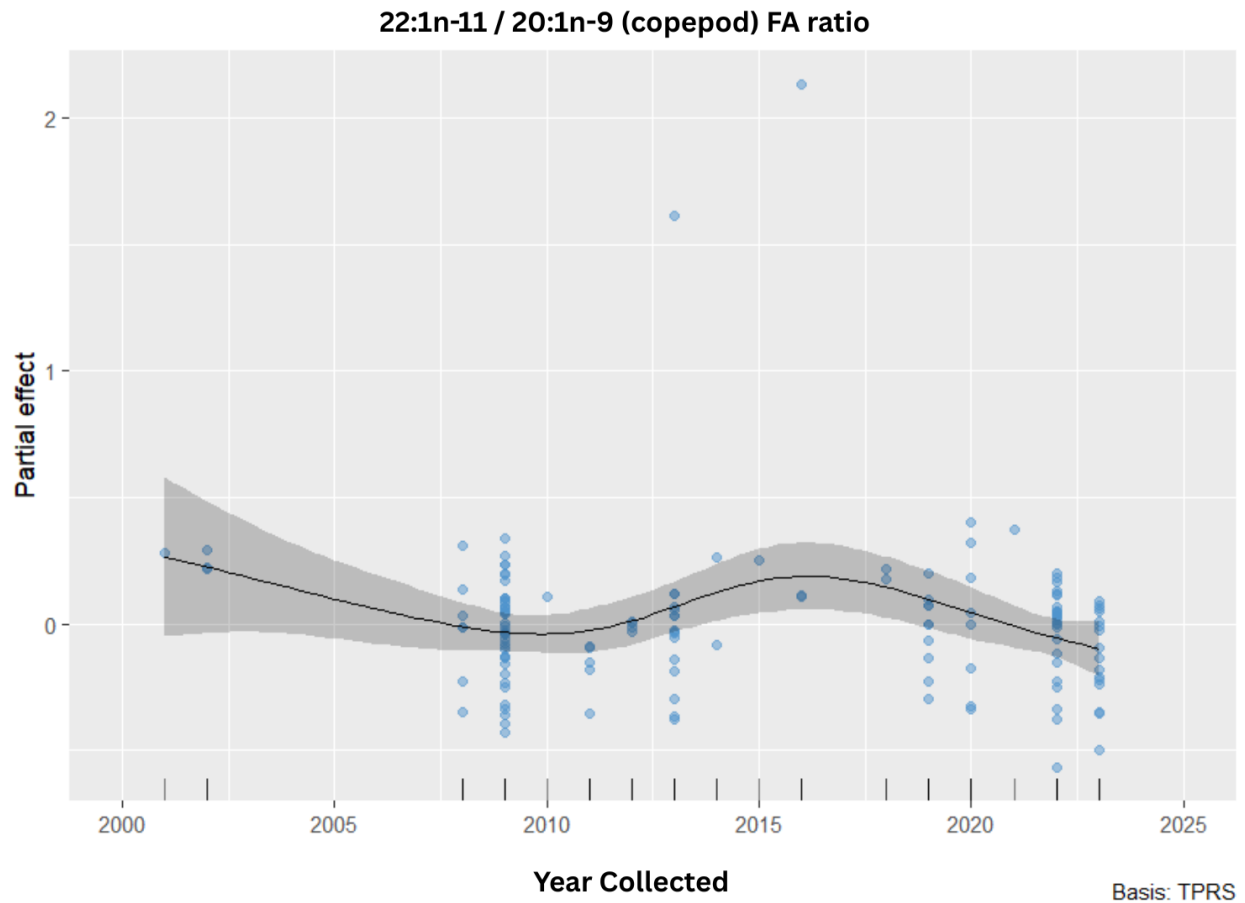


Figure 2-12: Partial effects plot of the top-performing model, with log-transformed 22:1n-11/20:1n-9 (copepod marker) as the response variable to a smooth term predictor of collection year. Shaded bands represent 95% confidence intervals. The model includes region as a parametric term

2.4 Discussion

2.4.1 Spatiotemporal variability of biomarkers

My results indicate a contraction in bowhead niche width over time, with the pattern being consistent with a narrowing prey base and a more pelagically influenced diet, potentially including more contributions from boreal species such as *C. finmarchicus*. ‘Year’ and ‘region’ were the most consistent significant predictors for biomarkers in bowhead whale tissue, with

both being connected to interannual variation in sea ice conditions. $\delta^{13}\text{C}$ values in bowhead whale skin had a strong nonlinear relationship with sea ice, though it was highly variable. $\delta^{13}\text{C}$ values decreased in Hudson Bay and increased in Baffin Bay-Davis Strait, supporting that bowhead diets are responding to region-specific carbon pathways not exclusively tied to sea ice. $\delta^{15}\text{N}$ values declined over time, particularly in Baffin Bay-Davis Strait, which may reflect shifts in nitrate cycling dynamics over time- with greater Atlantic inflow in the north and anthropogenic atmospheric nitrogen deposition due to fertilizer and fossil fuel use causing $\delta^{15}\text{N}$ depletion (de la Vega et al. 2022). Fatty acid analyses revealed greater temporal differentiation in Hudson Bay bowheads than in the Baffin Bay-Davis Strait Complex, possibly suggesting more pronounced changes in local foraging conditions. Fatty acid GAMs indicated increasing 18:1n-9/18:1n-7 trophic ratios indicating carnivory, alongside declining total 16:1n-7/16:0 diatom and 22:1n-11/20:1n-9 copepod ratios. In contrast, the PCA captured broader compositional shifts towards diatom and copepod markers over decades, suggesting that bowhead diets are sustaining systematic, large-scale shifts that are less influenced by short-term variability in foraging habits.

2.4.2 Predictors of spatial variation in bowhead whale dietary biomarkers

The Hudson Bay Complex displayed increasing dietary convergence, while whales in the Baffin Bay-Davis Strait Complex maintained more stable dietary niches over time. This could be due to Baffin Bay-Davis Strait being heavily buffered by Atlantic inflow, currents and oceanographic processes, with environmental changes being less dramatic than enclosed and ice-driven Hudson Bay Complex (Curry et al. 2013; Carmack et al. 2015). Bowhead whales in Hudson Bay showed dietary profiles higher in $\delta^{13}\text{C}$ compared to Baffin Bay-Davis Strait

samples, with this pattern being consistent with previous findings suggesting that bowhead whale diets in Hudson Bay are more sympagically-sourced (Pomerleau et al. 2012; Pontbriand et al. 2023). In contrast, the Atlantic-influenced Baffin Bay-Davis Strait supports more pelagic-dominated phytoplankton blooms, which aligns with the lower $\delta^{13}\text{C}$ values observed there. These findings suggest that bowheads that concentrate foraging effort in the Hudson Bay Complex may be targeting prey more tightly linked to ice-edge environments such as *C. glacialis* and other Arctic *Calanus* species, which tend to have higher $\delta^{13}\text{C}$ signatures (Dunton et al. 1989). This difference may highlight a spatial divergence in foraging strategy and prey quality, with HBC whales feeding on potentially more lipid and calorie-rich prey during the peak foraging months. When considered in tangent with fatty acid composition and isotopic niche contraction, these $\delta^{13}\text{C}$ patterns indicate that Hudson Bay bowheads are increasingly constrained to a narrower trophic position, reflecting differences in how bowhead whales forage on regional prey sources rather than differences in baseline isotope values alone.

While Baffin Bay-Davis Strait bowhead showed higher $\delta^{15}\text{N}$ values overall, which are consistent with a more trophically diverse prey base, $\delta^{15}\text{N}$ values also were shown to be overall declining over time, suggesting that a possible shift toward lower-trophic prey species or a change in baseline nitrogen sourcing due to zooplankton community restructuring (Post 2002). This could be potentially explained by the increased influx of the temperate species, *C. finmarchicus* (Hop et al. 2019; Fortune et al. 2020). The Baffin Bay-Davis Strait may host a more complex food web given the continued influx of boreal species, with bowheads potentially having access to more omnivorous and carnivorous zooplankton species. This could also potentially indicate that bowheads may be foraging in deeper and more stratified waters, which could be offering more prey diversity while showing the increased $\delta^{15}\text{N}$ values indicating higher

trophic levels. Alternatively, bowheads that focus foraging effort in the Hudson Bay Complex may be relying more heavily on primarily herbivorous Arctic copepods such as *C. glacialis* and *C. hyperboreus*, which are more closely associated with sympagic primary production and a shorter trophic pathway. Higher $\delta^{15}\text{N}$ values in the Baffin Bay-Davis Strait Complex, coupled with greater fatty-acid variability and stable niche width, are consistent with bowheads integrating a more trophically complex and heterogeneous prey base, potentially reflecting greater prey diversity associated with boreal species influx and increasingly pelagic habitats (Fortune et al. 2020).

Bowhead fatty acid profiles showed regional differences in bowhead whale diets. In both complexes, profiles were influenced by high concentrations of copepod markers such as 22:1n-11 and 22:1n-9, along with lower contributions from phytoplankton-linked fatty acids such as EPA (20:5n-3) and 18:4n-3. The separation of individual bowheads was more pronounced in Hudson Bay, with whales showing a broader spread in earlier decades and more recent decades showing a stronger indication of positively aligned copepod markers. This temporal convergence toward copepod-associated fatty acid profiles suggests that Hudson Bay bowheads increasingly exploit a narrower and more consistent prey base, whereas bowheads in the Baffin Bay-Davis Strait Complex have targeted a broader range of prey species over time (Fortune et al. 2020; Pontbriand et al. 2023). Zooplankton communities are likely to exhibit diversity in the Atlantic-influenced Baffin Bay-Davis Strait Complex as opposed to Hudson Bay Complex communities that are comparatively contained and undergoing rapid localized shifts (Gagnon and Gough 2005; Schembri et al. 2023). This pattern would align with stable isotopic niche widths in the Baffin Bay-Davis Strait Complex and progressive niche contraction in Hudson Bay.

2.4.3. Predictors of temporal variation in bowhead whale dietary biomarkers

Bowhead $\delta^{13}\text{C}$ values were shown to be decreasing over time in the Hudson Bay Complex while increasing in Baffin Bay-Davis Strait Complex. The decrease in $\delta^{13}\text{C}$ observed in the Hudson Bay Complex aligns with the expectation that ongoing sea ice loss would reduce sympagic contributions to the base of the food web and subsequently to bowheads as secondary consumers. The increase in $\delta^{13}\text{C}$ in the Baffin Bay-Davis Strait Complex may reflect a combination of environmental and behavioral factors. One explanation for the trend could be the more limited sampling window for this region, as samples outside of the 2011-2023 range were omitted from the Baffin Bay-Davis Strait Complex due to low sample sizes and outliers. This would suggest that the more limited time frame (12 years) might be more influenced by biogeochemical and anthropogenic fluctuations that affect $\delta^{13}\text{C}$ in the environment (de la Vega et al. 2019), and subsequently in bowhead tissue. An alternative explanation could be that bowheads are increasingly feeding in areas influenced by North Atlantic Deep Water (NADW), which is formed in the Nordic and Labrador seas and is characterized by notably high $\delta^{13}\text{C}$ values in dissolved inorganic carbon (DIC) (Bouttes et al. 2020). Phytoplankton takes up DIC during primary production, with fractionation causing the uptake of lighter ^{12}C , and the isotopic baseline of the surrounding water influencing the $\delta^{13}\text{C}$ of organic matter entering the food web. Organic material is then taken up by zooplankton, with higher $\delta^{13}\text{C}$ signatures transferring up to higher trophic levels, including bowheads. As the North Atlantic warms, the increase in primary productivity could exacerbate the removal of ^{12}C during photosynthesis, subsequently increasing $\delta^{13}\text{C}$ in marine organic matter (Montoya et al. 2002; Espinasse et al. 2022; Tuerena et al. 2019). This could cause bowhead whale tissue to exhibit increasingly higher $\delta^{13}\text{C}$ signatures as a result of shifts in oceanographic processes and related carbon cycling.

The observed declines in $\delta^{15}\text{N}$ values may be caused by regional differences in baseline nitrate dynamics rather than shifts toward higher trophic-level prey, consistent with prior studies documenting spatial variability in food-web base $\delta^{15}\text{N}$ signatures. Pomerleau et al. 2011 found an increase of almost 3‰ in $\delta^{15}\text{N}$ values in *C. glacialis* and *C. hyperboreus* in the more ice-influenced Gulf of Boothia in contrast to the Atlantic-influenced Davis Strait (Pomerleau et al. 2011; Pontbriand et al. 2023). Anthropogenic changes may also be contributing to long-term declines in $\delta^{15}\text{N}$ values across the North Atlantic. In this context, temporal decreases in $\delta^{15}\text{N}$ suggest that bowhead whales are increasingly integrating prey from lower trophic pathways, contrary to expectations of trophic increases with ongoing sea-ice loss (de la Vega et al. 2022; de la Vega et al. 2023). Long-term declines in $\delta^{15}\text{N}$ values linked to changes in nitrogen cycling have been documented in Arctic marine mammals, including harp seals from the Barents Sea (1951-2012; de la Vega et al. 2022). Such large-scale shifts in nitrogen supply, atmospheric inputs, and Atlantic water influence are likely to propagate through zooplankton prey and may contribute to declining $\delta^{15}\text{N}$ values observed in bowhead whale tissues (de la Vega et al. 2022; de la Vega et al. 2023). More unique to bowheads and their prey, these findings could suggest that whales could be preying more readily on *C. finmarchicus*, which have been shown to have distinctly lower $\delta^{15}\text{N}$ values overall when compared to other copepod species (Sato et al. 2002). Bowheads have been shown to increasingly target *C. finmarchicus* as a prey item, which are becoming more present in the Arctic as they expand their range (Fortune et al. 2020). The narrowing of dietary niches could suggest that bowheads have prioritized foraging effort on *C. finmarchicus*, either due to their increasing abundance, or because they could be displacing other zooplankton species (Møller and Nielson 2019; Ramondenc et al. 2023).

Diatom-sourced prey, generally associated with sea ice-associated primary production, contributed most strongly to bowhead whale diets during the late 2000s, before declining thereafter. Diatoms form much of the base of the sympagic food web, with interannual variability in bloom dynamics cascading upward to directly affect zooplankton composition- particularly *Calanus* species (Gawinski et al. 2024). Consequentially, the temporal variation observed in diatom-associated fatty acid ratios in bowhead blubber may reflect ecosystem-level shifts in nutrient availability and subsequent differences in the characteristics and timing of diatom productivity. Diatom presence is mediated by nitrogen, phosphate, and silicic acid, which are key limiting nutrients in the Arctic system (Codispoti et al. 2013; Krause et al. 2019). Seasonal availability is at its peak during the spring algal bloom and is exhausted afterwards, meaning that nutrient levels need to be rebuilt over the course of the following seasons. A difference in diatomic ratios in relation to 'year' can potentially indicate that diatomic blooms are more affected by conditions controlling nutrient availability (Bi et al. 2021), meaning that bowheads may exhibit lower ratios after years with a depleted nutrient supply for diatom blooms. Studies have shown that certain years have greater producer productivity when there is an influx of meltwater, river runoff, or precipitation (Oksman et al. 2022; Sejr et al. 2022), which could also suggest that warmer years with higher air temperatures could result in bowheads may display greater diatomic ratios as a result of runoff fueling phytoplankton blooms.

As predicted, the trophic-associated FA ratio (18:1n-9/18:1n-7) increased over time, with the partial effects plot showing an overall increasing trend over the sampling years. This pattern, linked to region, suggests potential long-term changes in the prey base available to bowhead whales. Because this FA ratio is associated with higher trophic levels, its increase could suggest shifts in bowhead whale diets toward more carnivorous and omnivorous zooplankton, either due

to changes in prey availability or in bowhead foraging strategy (Lowry et al. 2004; Pomerleau et al. 2014). The observed FA trends may reflect broad shifts in zooplankton community compositions and structure, which are often influenced by oceanographic conditions, such as currents, water temperature, salinity, and nutrient availability (Helenius et al. 2020; Perry et al. 2021). These physical and biological factors shape the composition and dominance of prey fields from year to year, directly impacting what bowheads are able to consume. I originally hypothesized that increasing 18:1n-9/18:1n-7 ratios might signal greater consumption of carnivorous zooplankton like euphausiids and amphipods in response to declining copepod abundance, though it could also suggest a change in the foraging behavior of copepods themselves. Kohlbach et al. 2021 showed that *Calanus finmarchicus*, as a temperate copepod species, exhibits elevated 18:1n-9/18:1n-7 ratios compared to Arctic copepods (*C. glacialis*, *C. hyperboreus*). This is likely due to *C. finmarchicus*'s predisposition to shift towards an omnivorous feeding strategy, including predation on other zooplankton, due to its more boreal origins resulting in its independence from ice-algal blooms (Kohlbach et al. 2021), which could suggest that bowheads would be feeding at a higher trophic level not because their prey species has changes, but rather because *C. finmarchicus* has increased in trophic level. Recent research demonstrates a pronounced northward shift in *C. finmarchicus*, which is now increasingly resident in Arctic regions such as Baffin Bay and Davis Strait as warming conditions facilitate its expansion. (Fortune et al. 2020). The northward expansion of *C. finmarchicus*, largely driven by climate change and Atlantification, means that bowhead whales may be increasingly consuming this species, as opposed to larger bodied copepod species endemic to the Arctic (Fortune et al. 2020; Freer et al. 2022). As such, the observed FA shift may reflect changing copepod composition and dietary habits rather than shift to euphausiids or amphipods.

The temporal variation of the 22:1n-11/20:1n-9 copepod FA ratio in bowhead whale blubber could reflect a decrease in the overall proportion and assimilation of *Calanus*-derived lipids in bowhead whale diets, however, the principal component analysis showed that *Calanus*-derived lipids load strongly on PC1 for both regions, suggesting that diets are still dominated by copepods overall. In this context, the variable, but in some periods decreasing, 22:1n-11/20:1n-9 copepod FA ratio does not fully align with increasing 18:1n-9/18:1n-7 ratios, or the declining $\delta^{15}\text{N}$. These discrepancies may be the results of differences in physiological and temporal integration of biomarkers that aren't in unified alignment, which is indicative of complex and dynamic environments and potential mixed foraging habits across individuals, rather than clear directional changes in dietary copepod compositions (Budge et al. 2006).

Due to beneficial environmental conditions, there may have been an abundance of large, lipid-rich copepods such as *Calanus hyperboreus* during the mid-2010s peak observed in bowhead whale tissue, during which time bowheads may have consumed more. Outside of this peak, there is a degree of interannual variability in this biomarker, which may be explained by several mechanisms. The diversity and abundance of zooplankton species that bowheads prey upon is largely dictated by interannual shifts in zooplankton community composition caused by environmental factors such as interannual shifts in bloom phenology and cyclic climate oscillations such as the North Atlantic Oscillation (NAO) and the Arctic Oscillation (AO) (Piontkovski et al. 2006; Henson et al. 2009; Seip et al. 2019; Fortune et al. 2020; Limoges et al. 2020). Bowhead whales are limited in their selectiveness of targeted species, with the composition of zooplankton aggregations being subject to these environmental influences and directly affecting whale dietary intake. Seasonal changes in the abundance of herbivorous copepods (*C. glacialis*, *C. hyperboreus*) that graze on ice algae may explain why years with

higher sea ice cover could correspond to more sympagic, energy-rich prey in the food web (Søreide et al. 2010; Leu et al. 2015). Conversely, in lower ice years, bowheads may ingest more omnivorous or carnivorous zooplankton (*Metridia longa*, chaetognaths), which occupy higher trophic positions and possess different fatty acid signatures (Lowry et al. 2004). While $\delta^{15}\text{N}$ decreased overall, the mismatch between $\delta^{15}\text{N}$ and 18:1n-9/18:1n-7 ratio results could be caused by trophic enrichment signals being masked/confounded by the aforementioned changes in environmental nitrogen baseline, while not capturing changes in trophic feeding (Buchanan et al. 2022).

The 20:5n-3/22:6n-3 models had a notably weak relationship with all predictors: year, region, and sea ice conditions, suggesting that other factors such as temperature, bloom phenology, and light/nutrient dynamics could play more important roles of EPA/DHA concentrations (Søreide et al. 2010; Helenius et al. 2020). In Arctic primary producers, PUFA content is impacted by regional and seasonal nutrient limitations, which may also indirectly affect whale fatty acid profiles (Jónasdóttir 2019; Calderini et al. 2023). Another potential confounder in the prediction of EPA and DHA in bowhead whale tissue is that zooplankton exhibit different proportions of both depending on life stage. Copepodites and nauplii typically have lower levels of both, with could obscure signal in tissue if bowheads are feeding on a mix of stages (Amparyup et al. 2022; Cavallo et al. 2020). Likewise, copepods coming out from winter diapause in their pre-reproductive state may have elevated EPA/DHA ratios, which could be affected by differing emergence timeframes impacted by sunlight through sea ice and warming water temperatures (McMeans et al. 2012). Altogether, many factors may be obscuring EPA and DHA biomarker signals in bowhead whale blubber, thereby attributing little explanatory power to any of the predictors.

2.5 Conclusion

This study was the first to examine the entire 30-year span of bowhead whale stable isotope data and the over 20-year span of the fatty acid data to study long-term changes in bowhead whale dietary patterns. My results suggested that bowhead whales are feeding on prey lower in $\delta^{15}\text{N}$ and have also narrowed their isotopic niche. The principal component analysis (PCA) and generalized additive models (GAMs) of the diatom and copepod-associated FA ratios suggest fluctuating contributions from both sources in bowhead whale diets, with evidence that this sourcing may be increasing in more recent years. My findings have also indicated that bowheads may targeted prey with a higher ratio of 18:1n-9/18:1n-7, indicating a higher degree of carnivory. These findings altogether strongly support previous studies that bowhead whales may be shifting diets towards boreal zooplankton species, namely *C. finmarchicus*, which displays lower $\delta^{15}\text{N}$ values, higher 18:1n-9/18:1n-7 ratios due to carnivory and is rapidly increasing in the Arctic as sea ice declines. The non-linear relationship between $\delta^{13}\text{C}$ and diatomic FAs may suggest that productivity in the Arctic may be benefiting from a lower concentration of sea ice that allows for advantageous open-water conditions.

This study has added to the knowledge of bowhead foraging ecology in a rapidly changing Arctic defined by the ongoing loss of sea ice, which is a driver of the northern marine food web through its close relationship with marine primary production. This study aims to inform conservation policy and management decisions, as well as preserve bowhead whales as a crucial Inuit subsistence resource.

3. Chapter 3: Spatiotemporal variation in density and habitat use of western Hudson Bay Ringed Seals

Abstract

Climate change is altering the polar seascape significantly, with rising temperatures largely driving the northward retreat of sea ice. Within the Canadian Arctic, Western Hudson Bay is a unique environment characterized by extensive seasonal ice coverage and a rich marine biota. Ringed seals (*Pusa hispida*) are an ice-dependent pinniped species with a circumpolar range that is ubiquitous to Western Hudson Bay and are indicators of the rapidly changing Arctic environment. Examining spatio-temporal shifts in ringed seal density and distribution can reveal important insights about how changing sea ice dynamics impacts ringed seals. A total of 13 aerial surveys have occurred between 1994 and 2024 and our intention is to investigate spatial and temporal variation in their density and habitat use using this unique dataset. Ringed seal density in Western Hudson Bay ranged from 0.215 to 0.958 ringed seals per km² and has declined over time. The most significant predictors of ringed seal habitat use were sea ice concentration and distance to shore, with seals generally preferring greater sea ice coverage (peak density occurred at approximately 70-100% sea ice concentration) and habitat offshore (peak density occurred at roughly ~200km from shore). Kernel density estimations (KDEs) revealed consistent areas of use over the course of survey years, with core density hotspots emerging between 58° and 61° latitude, located approximately 150-200 km from shore. These findings elucidate the importance of both sea ice concentration and offshore habitat characteristics on ringed seals and highlight the ramifications of ongoing sea ice loss and climate change, with implications for future research and policy development.

3.1 Introduction

Habitat characteristics strongly influence the distribution and abundance of a species in a given environment. Given the rapid pace of climate change impacting the Arctic, the habitat qualities selected for by many species are likewise changing across environments, with the availability of preferred habitat potentially being less accessible or is shifting spatially. The contraction of sea ice, warmer water temperatures, and greater influx of meltwater has been changing the seascape of many Arctic regions, causing the redistribution of many prey species and scarcity of shelter in the form of ice and snow (Macias-Fauria & Post 2018). Available resources such as prey and suitable shelter can also vary greatly in quality, while competition for higher-quality resources, as well as predation pressure, can lead to individuals selecting new habitats or those with sub-optimal resource availability (Grand 2002). The evaluation of habitat selection by a species can reveal key insights as to the characteristics sought after in a given environment and is crucial for the development of policies in conservation management under climate change (Morris 2003).

Hudson Bay is a large, inland sea considered to be part of the Arctic Ocean (Stroeve et al. 2024). The western portion of Hudson Bay is characterized by its shallow depth, extreme seasonal ice coverage, extended open-water period for much of the summer and early fall, and influx of freshwater from rivers and wetlands prevalent along the coast. Its unique characteristics allow Hudson Bay to support an extensive array of marine life, including polar bear (*Ursus maritimus*), ice seals (i.e. ringed seals and bearded seals, *Erignathus barbatus*), and beluga (*Delphinapterus leucas*), and is deemed an ecologically significant area of the Canadian Arctic (Stewart and

Barber 2010). The western coastal region generally freezes over completely by December, with sea ice formation generally beginning in October and November but has experienced a marked decline in sea ice over recent decades (Saucier et al. 2004; Tivy et al. 2011). Sea ice concentration in Western Hudson Bay has been declining by an average of 15.1 to 20.4% per decade, with the length of the open-water period increasing 9.9 days per decade (Hochheim et al. 2011; Johnson et al. 2020). The absence of sea ice for more extensive portions of the year can have cascading effects on the region's biota, particularly marine mammals, such that marine mammals may need to alter their migration routes, timing, habitat use, and behavior (Hamilton et al. 2015; Shuert et al. 2022; Hauser et al. 2018). Western Hudson Bay is an excellent study location to examine climate change-associated shifts in marine mammal habitat due to its interconnected relationship with sea ice and the availability of a relative abundance of historical data. Fisheries and Oceans Canada and Environment and Climate Change Canada have conducted regular marine mammal aerial surveys of western Hudson Bay in the spring for 30 years, which provides an extensive long-term dataset of ringed seal observations to determine temporal changes in habitat use and density.

3.1.1. Ringed Seal Habitat Selection and Relevance to Western Hudson Bay

Ringed seals are widely distributed across most of the circumpolar Arctic and sub-Arctic, occupying a wide range of depths, varying sea ice types, and physical features such as polynyas and glaciers (Laidre et al. 2008; Lone et al. 2019; Von Duyke et al. 2020). Ringed seals are an ice-obligate pinniped, relying on sea ice for resting and whelping. Breathing holes are maintained with sharp claws and may be sustained all throughout winter after freeze-up,

allowing seals access to areas and resources that other pinnipeds are unable to utilize (Kelly 2022). Ringed seal habitat use spans landfast ice, drifting pack ice, and seasonally open-water areas, reflecting a high degree of ecological flexibility (Laidre et al. 2008; Kelly 2022). As generalist feeders, ringed seals utilize various foraging areas hosting a wide variety of prey species ranging from crustaceans, benthic invertebrates, and an array of fish species that varies geographically (Insley et al. 2021; Yurkowski 2015, 2016). Ringed seals are known to feed on some benthic invertebrates such as bivalves and amphipods which become increasingly important during the winter season when other food is scarce (Matley et al. 2015) prior to the energetically costly whelping and moulting period. The combined loss of sea-ice-derived nutrient inputs to both benthic and pelagic systems may create increasingly suboptimal foraging conditions for ringed seals (Young et al. 2013; Thometz et al. 2020) and could lead to spatio-temporal changes to their habitat use.

Sea ice selection by ringed seals can be highly variable, ranging from landfast ice, to scattered, drifting floes, to ice conditions influenced by polynyas (Boucher et al. 2020). Sparse ice cover can have negative consequences for pup survival, with early breakup contributing to early weaning when pups are too young and loss of essential shelter. Conversely, excessive sea ice has been linked to poor body conditions and survival rates in ringed seals which may be attributed to less prey availability in these excessive ice years (Chambellant et al. 2012). Ringed seals also prefer landfast ice, though certain situations may drive ringed seals to select for pack ice farther from shore. In a study on the Alaskan population, satellite-tagged adult ringed seals were shown to prefer winter habitat with higher concentrations of sea ice in the Chukchi Sea, while sub-adults moved farther south into the more-open Bering Sea (Von Duyke et al. 2020). Studies in the Barents Sea suggest that ringed seals across all age groups generally preferred

habitat near a 50% sea ice concentration (Laidre et al. 2008; Lone et al. 2019; Von Duyke et al. 2020). More recently, Boveng et al. 2024 was the first study to include snow depth when modelling the Chukchi Sea ringed seal population and found that ringed seal density increased strongly with snow depth, peaking at approximately 20 cm. Predation pressure from polar bears, their main predator, and Arctic foxes (*Vulpes lagopus*) can influence the selection of habitat by ringed seals (Furgal et al. 1996). Polar bears favor consolidated pack ice, utilizing the platform when ambushing seals near breathing holes, which subsequently influences seal habitat selection (Pagano 2021). Ringed seals may also select locations based on proximity to their migration routes, namely as juveniles in certain regions (Lone et al. 2019). In addition to primary ice type preferences (e.g., landfast, loose floes, pack ice, etc.) and overall ice concentration, ringed seals are also shown to select habitat based on snow type/coverage and ice texture (Iacozza et al. 2014). Snow provides the material for building subnivean lairs in the spring, with total amount and composition being important for structural integrity (Kovacs et al. 2024). Ice texture, with differences ranging from smooth, interrupted/unbroken ice sheets to rubble ice has a large impact on susceptibility to polar bear predation (Pilfold et al. 2014).

Sea ice characteristics not only influence the habitat selection of ringed seals but can also influence their physiology and reproductive success (Ferguson et al. 2017; Iacozza et al. 2014). Observed body conditions of ringed seals in Western Hudson Bay decreased and measured stress levels increased in studies spanning survey years 1995 through 2013, during which time ringed seal density progressively decreased (Ferguson et al. 2017). Additionally, the extended open water period in 2010, marked by an earlier breakup and later freeze-up, coincided with the highest measured levels of cortisol between 2003 and 2013. The following year showed a notable

decrease in ovulation rates and new pups, suggesting that longer open water periods are detrimental to the overall health of ringed seals (Ferguson et al 2017).

Research objectives in Chapter 3:

Declining spring sea ice in Western Hudson Bay has been associated with changes in ringed seal distribution and abundance, reflecting the species' reliance on stable ice platforms for breeding and their preference for mid-to-high sea ice concentrations during spring (Laidre et al. 2008; Chambellant et al. 2012; Lydersen et al. 2017; Lone et al. 2019; Carlyle et al. 2022).

The objective of my research aims to 1) quantify long-term trends in ringed seal density spanning the 30-year range of the Western Hudson Bay aerial surveys; 2) characterize the interannual variability in habitat use within the aerial survey area using kernel density estimates/hotspot analysis; and 3) explore the relationship between ringed seal density and environmental characteristics including sea ice concentration, bathymetry, and distance to shore to determine the drivers of habitat selection in a changing environment.

Hypotheses and predictions in Chapter 3:

- 1) I hypothesized that ringed seal densities in Western Hudson Bay will show a long-term decline (1994 to 2024), as well as a distributional shift northward and closer inshore through time in relation to long-term decline of sea ice concentration in the study area. As offshore spring sea ice diminishes and retracts northward, the spatial extent of preferred

ice conditions is expected to shift, with landfast ice persisting longer nearshore and in shallower waters.

- 2) I hypothesized that ringed seal densities will be highest in areas with mid-to-high sea ice concentrations ranging from 40%-80% as well as shallower waters, due to the reliance of ringed seals on stable sea ice habitats during moulting and the persistence of landfast ice in nearshore environments during spring.

3.2 Methods

3.2.1 Study Area

The study region spans the western coast of Hudson Bay from approximately Owl River in Wapusk National Park to north of Chesterfield Inlet, adjacent to Southampton Island, all of which is an ecologically important area for many Arctic marine mammal species (Stewart and Lockhart 2005). The original surveys in the 1990s were designed to encompass the range of the Western Hudson Bay subpopulation of polar bears, with planned transects having a survey design of a latitudinal gradient of transects that run perpendicular to the coastline from north to south (Lunn et al. 1997). Ringed and bearded seals comprise the base of polar bear diets and are ecologically important mesopredators in Hudson Bay.

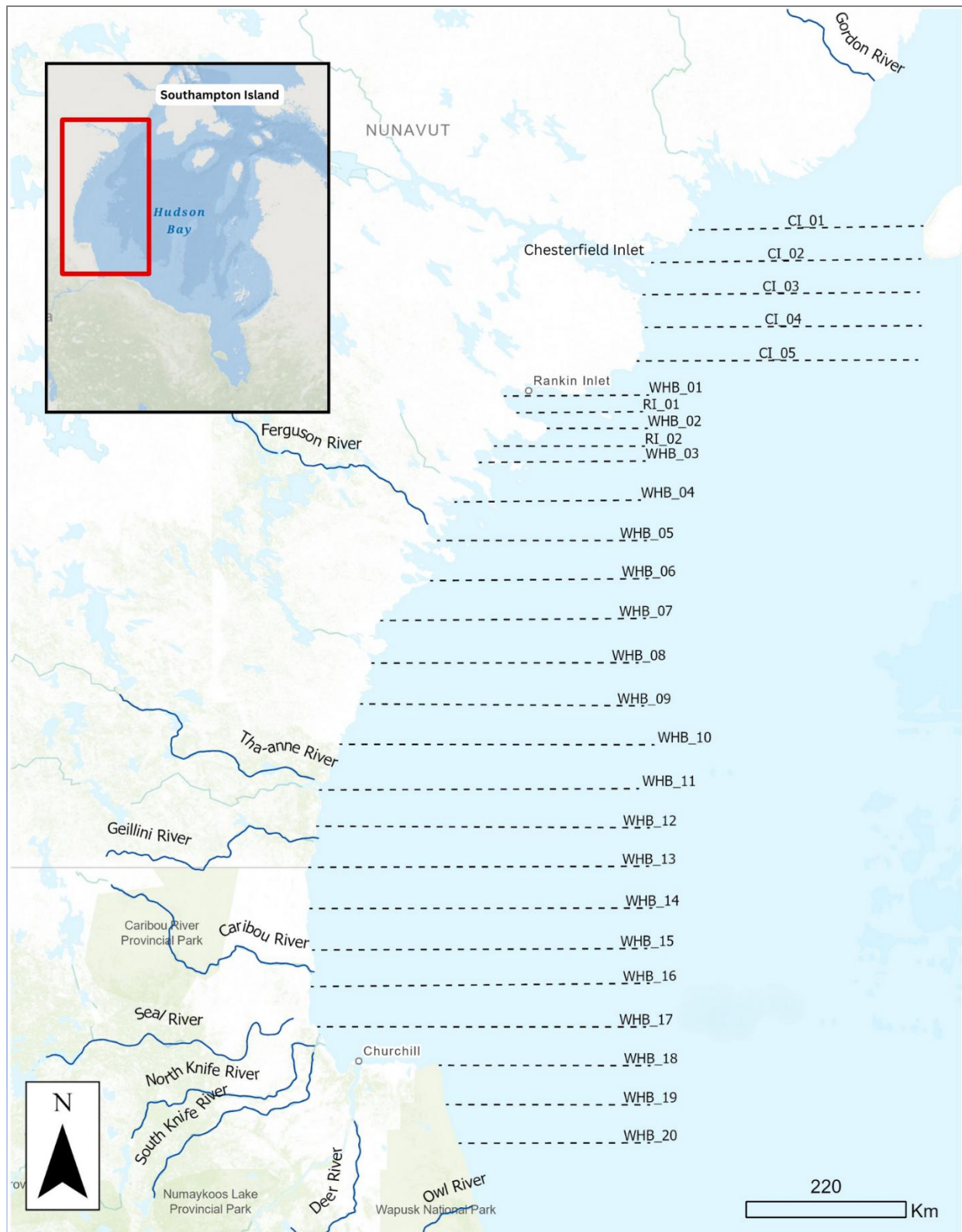


Figure 3-1: Western Hudson Bay Aerial Survey Transects 2024

3.2.2. Survey Design

The survey consisted of east-west transects running perpendicular from the Western Hudson Bay shoreline to 89° W, with approximately 15' latitude between transects (Young et al. 2015). Logistics and poor weather prevented the full set of transects (22 in the first 1994 survey) from being completed for some years (1996, 2010, 2013, 2017) with most of the completed effort being constrained to a core 10 transects in the center of the Western Hudson Bay coast from approximately 61° 06' 30" N to 58° 46' 51" N (Stirling and Derocher, 1993; Lunn et al. 1997; Young et al. 2015). The annual timing of the surveys is intended to coincide with peak haul-out in spring in May through early June, when moulting ringed seals spend the most time basking on the sea ice and are therefore the most likely to be sighted (Stirling and Derocher, 1993; Lunn et al. 1997; Young et al. 2015; Lindsay et al. 2023). It should be acknowledged that the first Western Hudson Bay survey in 1994 was conducted too late in the season, with low observed ringed seal counts due to excessive rotten sea ice and open water. The results of this survey have been excluded from other long-term density analyses due to the reduced detectability relative to other years, with subsequent surveys being more optimally timed for the peak spring haul-out period (Lunn et al. 1997; Young et al. 2015). In the present study, the 1994 survey is retained to preserve the full temporal extent of the dataset but is interpreted cautiously given its non-standard timing. The survey flights were conducted between 8:30 am and 8:00 pm local time in clear conditions with no fog, low clouds, or precipitation to not hinder sighting visibility.

Surveys utilized visual and, starting in later surveys, photographic observation methods- and were flown with 2-3 visual observers for all years, with at least 2 observers actively monitoring through bubble windows on each side of the plane while a third performs data

logging of weather conditions/sea ice concentration/visibility and conducted photographic equipment operation duties (Lunn et al. 1997; Young et al. 2015; Young et al. 2019; Lindsay et al. 2023). Visual aerial surveys were conducted from 1994 to 2013, and digital photographic surveys were conducted in 2017 and 2024. Visual surveys (1994-2008) were flown in a Cessna 337 Skymaster at 150 m altitude and 260 km/hr ground speed and used clinometers with wing strut markings to estimate distance within an 800 m strip width (400 m on each side) (Lunn et al. 1997). The 2017 and 2024 surveys used DSLR and infrared cameras. The infrared was the initial means of animal detection, with digital photography being used to confirm the sighting (Young et al. 2019). This method allows for later review and archiving and reduces the dependence on observers who can be prone to fatigue after long survey days. In 2024, a custom-built frame was mounted in the belly of the DeHavilland Twin Otter plane, and a trio of cameras was positioned in the center of this frame, angled downward. The camera setup consisted of a Nikon D850 with a 25mm focal lens length, a full-frame sensor with a 35.9 mm width and a 23.9 mm height; another Nikon D850 model with a 35mm lens; and a FLIR (forward-looking infrared) camera. A Bad Elf (West Hartford, CT, USA) global positioning system (GPS) unit was mounted in the back window of the aircraft and connected to the Nikon camera through a Foolography Bluetooth unit (Berlin, Germany). This provided automated geotagging for each DSLR photo, with heading, speed, position, and altitude being recorded and linked to each image's metadata. Camera intervals were set for 2 seconds, with an intended overlap of approximately 30% between photo frames for continuity. FLIR video/seq files were reviewed manually, as were DSLR images, using the Picture Reflect photo viewing application usable for raw Nikon 'nef' raw files. I completed review using a two-step methodology, reviewing all FLIR footage, recording hotspots, and then locating animals in the DSLR photos corresponding to the time

stamps in the FLIR footage which follows the method described in Young et al. (2019). Metadata were verified for completeness and consistency across all survey days and transects.

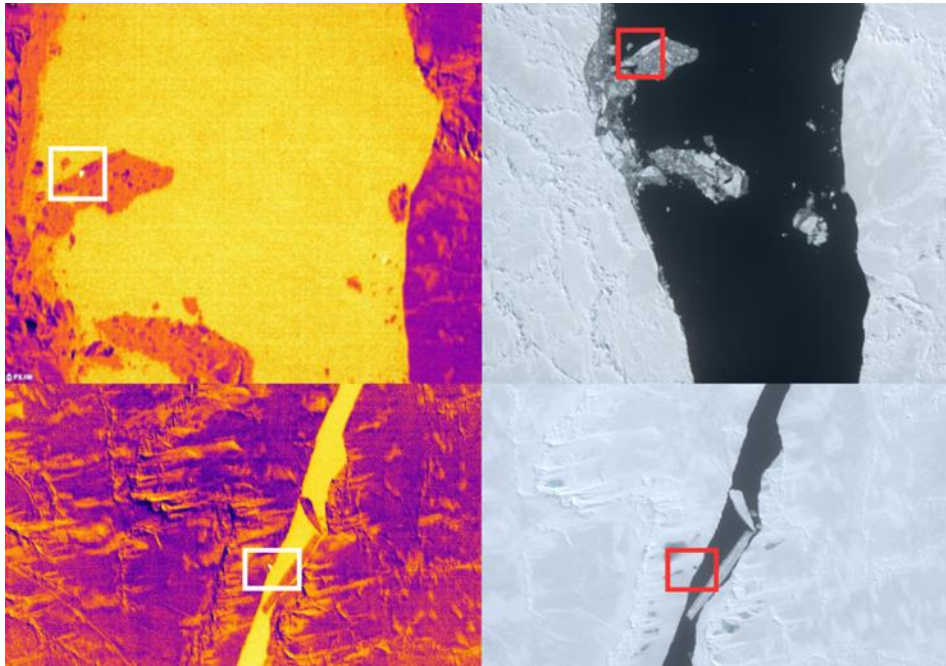


Figure 3-2: Example of a ringed seal detected using FLIR (left panels) and corresponding DSLR imagery (right panels). Red boxes indicate the same individual seal observed across both imaging methods.

3.2.3. Ringed Seal Observation Locations 1994 - 2013

GPS units were not used for earlier surveys (1994-2000), so I used DFO field survey reports and scanned, handwritten pilot and observer survey notes with recorded sighting times to estimate animal locations. I developed a process by which the approximate locations of animals could be determined based on recorded animal sighting times, average plane speed, and transect length/coordinates. Archived data for these years included observer and pilot notes that recorded

- 1) Transect ID, length, start and end times
- 2) Observed ice conditions at regular intervals
- 3)

Average speed of plane per transect 4) Time of animal observations. A spreadsheet with the formula: $\text{Distance} = \text{speed} \times (\text{elapsed min} / 60)$ was used to calculate approximate distances of ringed seal sightings along each transect line based on transect start/end time and the plane speed recorded. Direction of travel was discerned from the sequence of ice observations throughout the course of the transect line, e.g., observations of landfast ice progressing to small, scattered floes indicated the plane was moving away from land. Validation for this methodology was confirmed when the ringed seal shapefiles were overlaid on the sea ice concentration raster files extracted from the National Snow and Ice Data Center.

3.2.4. Covariate Data Extraction

I downloaded daily sea ice concentration data (GeoTIFF image files) from the National Snow and Ice Data Center using the Sea Ice Index Version 3 (<https://nsidc.org/home>). For each survey year, daily files corresponding to the survey dates were acquired. Each survey's transect shapefile-derived either from GPS flight paths or reconstructed based on field notes and approximate routes- was buffered based on the swath width of the observation system (visual or photographic) used that year. Buffered transects were then divided into approximately 25 km segments to match the spatial resolution of the sea ice raster cells. The `exactextractr` package (R version 4.5.1) was applied to extract sea ice concentration values from the GeoTIFFs using these buffered transect segments as polygons. This function enables accurate zonal statistics by weighting raster values based on the proportion of each cell intersecting a polygon. The extracted values within each segment were then averaged to obtain the mean sea ice concentration

corresponding to each segment and survey date, with the ggplot2 R package being used to validate the spatial resolution of the sea ice distribution.

Bathymetric data for the Western Hudson Bay study region was downloaded from the General Bathymetric Chart of the Oceans (GEBCO) 2024 grid, which provides global coverage at 15 arc-second (~500 m) resolution in the WGS 84 geographic coordinate system.

The area selected for the raster file download was chosen to encompass all survey transects for all years. The bathymetry GeoTIFF was re-projected from the original WGS 84 geographic coordinate system to NSIDC polar stereographic projected coordinate system to maintain compatibility with the sea ice concentration data and both the transect and observation shapefiles. Using the same segments created from the buffered transect shapefile, the mean depth (in meters) was extracted from the bathymetry raster with the `exactextract()` function from the `exactextractr` R package. The mean depth (in meters) for each segment was validated using `ggplot2` to confirm the bathymetric gradient across the survey area.

For distance to shore, the centroids, located at the center of each 25 km transect segment unit, were calculated in R as a mean reference. To determine the centroids' relative distance to the coast, the Natural Earth coastline dataset preloaded in R (R package, `rnaturalearth`, R version 4.5.1) was used as a shoreline reference. The coastline shapefile, originally in WGS 84 geographic coordinate system, was transformed in R to NSIDC polar stereographic (EPSG:3413) to ensure compatibility with other data. Euclidean distances from the centroids to their nearest respective coastal point were calculated using the `dist2land()` function from the `ggOceanMaps` R package (R version 4.5.1). Distance-to-shore values were appended to the metadata for the corresponding transect segments as a predictor for analyses.

Predictor Variable	Resolution / Value Range	Reason For Inclusion	Raw Data Source	Processing
Sea Ice Concentration	25 km cell size	Sea ice extent influences habitat accessibility, predator avoidance, and haul-out availability for ice-associated marine mammals.	Sea Ice Index v3 from the National Snow and Ice Data Center (NSIDC)	Monthly sea ice raster files (March-July) reprojected to Polar Stereographic and averaged per year over the Hudson Bay Complex
Bathymetry	500 m	Seafloor depth is a major determinant of marine mammal habitat use, prey availability, and oceanographic processes.	GEBCO 2022 Global Bathymetry Grid	Bathymetry raster reprojected to match study CRS and clipped to survey extent
Distance to Shore	0 to coastal distance (km) '0' would represent shore, with progressive distances being farther offshore	Proximity to shore can influence access to prey, risk from predators, and availability of haul-out or calving sites.	Derived from land polygon edges (Natural Earth, 1:10m) using geodesic distance calculation	Distances from each raster cell to nearest coastline calculated and saved as km-resolution raster

Table 3-1: Predictor variables chosen for ringed seal density models with spatial resolution/values, data source, and processing methods.

3.2.5. Statistical Analysis

Total area (km²) was calculated for each 25 km transect segment, and a spatial join was performed between ringed seal observation points and segment polygons to assign presence, counts, and densities in ringed seals per km². Density (animals/km²), being continuous and standardized for survey effort, is more commonly used as a response variable in marine mammal and seabird transect surveys and was therefore chosen as the response over count (Becker et al.

2010; Becker et al. 2014). The data distribution was checked for normality and homogeneity of variance using histograms and quantile-quantile (QQ) plots. The distribution showed a heavy right skew that corresponded to a higher number of zeros representing transect segments with no ringed seal observations. For environmental predictors such as sea ice, the non-linear response of ringed seal density prompted the selection of a generalized additive model (GAM) using the `mgcv` package in R. Smoothing functions, or splines, are used in lieu of assuming linearity (`mgcv` package, R version 4.5.1). Due to the right-skew, the model was fitted using a Tweedie distribution and a log link function, both well-suited to continuous, positive, and zero-inflated data such as the ringed seal density values. The model used the 'REML' (restricted maximum likelihood) fitting method to estimate smoothing parameters to reduce bias. Predictor variables included mean sea ice concentration (as proportion) per transect segment; mean depth (in meters) per transect segment; distance of individual transect segment to shore (in kilometers) were all fitted inside of smooth terms 's()' to determine suspected non-linear relationships to the response variable. Collinearity of predictor variables was tested for using a Spearman correlation analysis. As an additional check prior to model fitting, VIFs were calculated from a pre-fit model with scaled variables for multicollinearity indicating acceptable [VIF values (≤ 4.0)] for the remaining predictor variables. In addition to collinearity testing, concurvity testing of models passing correlation tests post-model fitting was conducted. A separate linear regression was conducted using the overall annual density of ringed seals per total surveyed area against 'year' as the independent variable to determine broadscale trends from 1994 to 2024.

3.2.6. Kernel density Analysis

Specific areas of higher ringed seal densities between survey years were determined using kernel density estimation (KDEs). Kernel density analysis is a non-parametric statistical method that utilizes a probability density function to create KDEs which was used for 10 Western Hudson Bay aerial survey years: 1994, 1995, 1996, 1997, 1999, 2000, 2010, 2013, 2017, and 2024. Aerial surveys were completed in 2007, 2008, and 2009 however there was insufficient data to approximate ringed seal locations, so these were omitted from analysis. The extent for the calculation was created using a concave polygon (concaveman package, R version 4.5.1) based on the transect line areas, which varied from year to year based on survey design and completion rate. Both the transect and the ringed seal point shapefiles were first transformed from the National Snow and Ice Data Center (NSIDC) polar stereographic projection to WGS84 geographic coordinates (EPSG:4326). Shapefiles were then reprojected to Universal Transverse Mercator (UTM) Zone 15N to allow for distance-based area calculations in meters. Transects were buffered based on swath width and merged into a singular polygon representing the area for the KDE calculation extent. Bandwidth is a smoothing parameter which controls the degree of influence each observation point has on the density surface. The bandwidth was calculated using Silverman's Rule of Thumb (Silverman, 1986):

$$h=0.9\times\min(\sigma,\frac{1.34}{IQR})\times n^{-1/5}$$

with the kernel density estimation completed using the kde2d() function in the R MASS package (R version 4.5.1). Land areas derived from the Natural Earth R suite of data were omitted from KDE bounding boxes to keep the estimates based on marine areas only, with the KDE raster being masked to this portion.

3.3 Results

Surveys were completed for Western Hudson Bay between 1994 to 2024, with total survey transect effort ranging from 1,222 km (2017) to 6,098 km (1994). Total ringed seal counts spanned from 191 (2017) to 4,057 (1995) (Table 3-4) with resulting density estimates ranging from 0.22 to 0.96 seals/km². The lowest density estimates were observed in 2024 (0.22 seals/km²) and 2013 (0.24 seals/km²) and the highest in 1995 (0.96 seals/km²) and 1996 (0.93 seals/km²).

3.3.1. Kernel Density Estimations/Hotspots

The series of kernel density estimates (KDEs) and resulting hotspots created for years 1994-2024 showed that there was inter-annual variability in space use in terms of size and location of higher use areas across the 30-year period. Across 10 surveys spanning from 1994 to 2024, the 50% isopleth ranged between 11,574-44,798 km² (median 26,928 km²), and the 95% isopleth ranged from 35,988-131,407 km² (median 79,119 km²) (Figure S3-2).

A series of core density hotspots emerged generally between 58° and 61° latitude, located approximately 150-200 km from shore. These hotspots were located in the central survey transects that cover the midway portion of Western Hudson Bay region and persisted in roughly the same or adjacent locations across the span of the survey years. The locations remained roughly consistent despite variability in survey effort over the years. Years that included northern survey transects (1994, 1995, 2024) all had relatively lower ringed seal densities in this area. Additionally, it was noticeable that with the exception of 2017 (and 1996 and 2000, to a lesser extent) no prominent density hotspots emerged immediately nearshore. Coastal ringed seal

presence showed a more diffused distribution, with density increasing progressively away from shore.

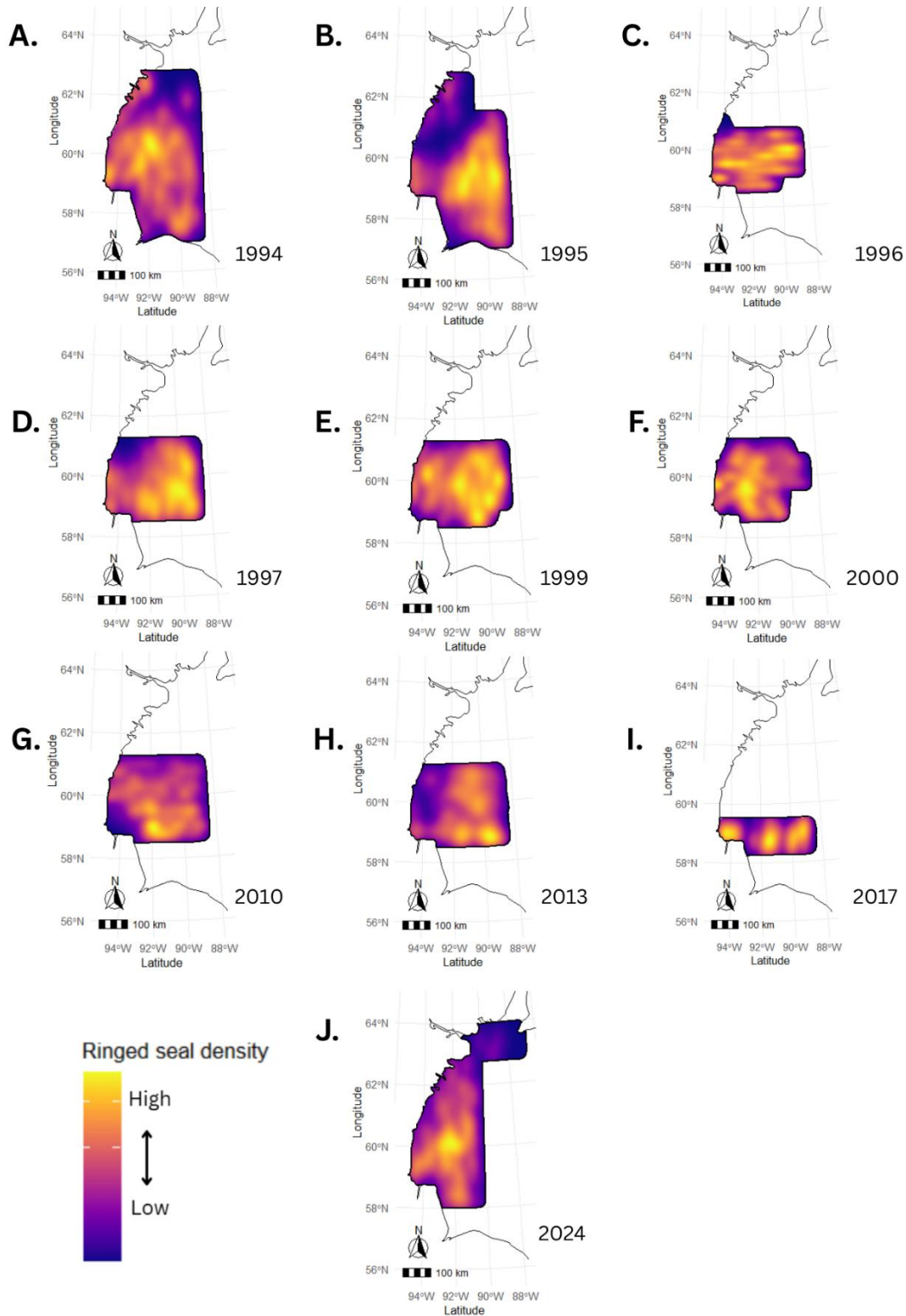


Figure 3-3: Western Hudson Bay aerial survey ringed seal kernel density estimate hotspots by year denoting areas of concentration of observations, 1994-2024

Table 3-2: Summary of ringed seal aerial survey effort, seal counts, and associated ice conditions by year

Year	Date	Method	Effort (km)	50% Isopleth areas (km ²)	95% Isopleth area (km ²)	Number of ringed seal observations	Area (km ²)	Density (animals/k m ²)	Avg. Sea Ice Concentration
1994	June 07-14	Visual Observer	6097.93	44798	131407	1104	4878.344	0.226	0.66
1995	June 01-04	Visual Observer	5294.00	31358	103216	4057	4235.200	0.958	0.67
1996	June 05-06	Visual Observer	2440.40	23831	63814	1823	1952.320	0.934	0.81
1997	May 30-June 01	Visual Observer	3246.52	27092	77979	1666	2597.216	0.641	0.78
1999	May 30-31	Visual Observer	3114.79	29483	80258	1055	2491.832	0.423	0.85
2000	June 01-02	Visual Observer	2776.34	24640	70820	1275	2221.072	0.574	0.99
2010	June 05-09	Visual Observer	3278.58	25555	77050	1917	2622.864	0.731	0.93
2013	May 28-June 05	Visual Observer	3257.25	27242	81273	629	2605.800	0.241	0.82
2017	May 26	Remote sensing	1221.58	11574	35988	191	305.395	0.625	0.76
2024	May 02-15	Remote sensing	4612.18	26763	88465	427	1983.237	0.215	0.95

3.3.2. Ringed Seal Density Generalized Additive Model (GAM) Results

A Spearman correlation analysis showed that bathymetry and distance to shore were highly collinear ($\rho = -0.90$) so were never included in the same model. Additionally, VIFs calculated from a pre-fit model with scaled variables for multicollinearity indicated acceptable VIF values (≤ 4.0) for the remaining predictor variables. In addition to collinearity testing, concavity testing of models passing correlation tests showed that models which included ‘year’ as a random-effect smooth term failed concavity diagnostics (high ‘worst’ concavity estimates ≥ 0.8). Consequently, all models containing year as a random-effect smooth were excluded from

the final set of concurvity-passing models. A final set of candidate models, each passing both collinearity and concurvity screening, was compared using AIC and AICc scores as the primary model selection criteria.

The top-performing GAM for ringed seal density included average spring sea ice concentration and distance to shore as smooth predictors. This model had the lowest AICc (2465.17) among candidate models and explained 20.3% of the deviance, with an adjusted R^2 of 0.13 (Table 3-3). Both smooth terms were statistically significant ($p < 0.001$), supporting non-linear associations with seal density. The smooth for sea ice concentration had an effective degrees of freedom (edf) of 9.87 and an F-statistic of 23.56, while the smooth for distance to shore had an edf of 5.70 and an F-statistic of 7.38. The model's intercept was significantly negative (Estimate = -0.857, $t = -28.86$, $p < 0.001$).

The model results support that higher sea ice concentrations are correlated with higher ringed seal densities in Western Hudson Bay. The partial effects plot for sea ice concentration shows a positive, non-linear relationship (edf = 9.87, $p < 0.001$), where seal density is lowest at minimal ice cover (<10%). Density increases steeply between 0-25%, followed by a decline near 30-40%, then increases again from 50-70%. A slight decrease in ringed seal density then occurs at ~75%, followed by a sharp increase toward maximum sea ice concentrations ($\geq 90\%$), where the highest predicted seal densities occurred.

The effect of distance to shore on seal density was also non-linear, and was a significant predictor (edf = 5.70, $p < 0.001$). Densities were higher within 0-25 km of the coastline, then declined, reaching a minimum density around 50 km from shore. From there, density increased gradually to a peak around 225 km from shore, and then declined at distances > 225km. Uncertainty, as indicated by greater confidence intervals increased beyond 225 km.

Table 3-3: Ringed Seal Density Model Selection Summary for GAMs

Predictors Included	AIC	Δ AIC	AICc	Δ AICc	R ² (adj)	Deviance Explained
Sea Ice + Distance to shore	2464.50	0	2465.17	0	0.13	20.3%
Sea Ice + Depth	2484.86	20.36	2485.61	20.44	0.12	19.5%
Sea Ice only	2504.07	39.57	2504.36	39.19	0.11	17.8%
Distance to Shore only	2741.03	276.53	2741.08	275.91	0.05	5.51%
Depth only	2777.90	313.40	2778.13	312.96	0.03	4.29%
Null Model	2840.89	376.39	2840.90	375.73	0	~0%

Generalized additive model (GAM) selection results for ringed seal density, ranked by AICc. All predictors were modeled as smooth terms, including mean sea ice concentration, distance to shore, and depth.

Term	Type	k	EDF	K index	Statistic	P value	Estimate	SE
Mean Sea Ice Conc.	Smooth	20	9.87	0.83	23.56 (F)	< 0.001		
Distance to Shore	Smooth	20	5.70	0.87	7.38 (F)	< 0.001		
(Intercept)	Parametric				t = -28.86	< 0.001	-0.85672	0.02968

WHB Ringed Seal Density

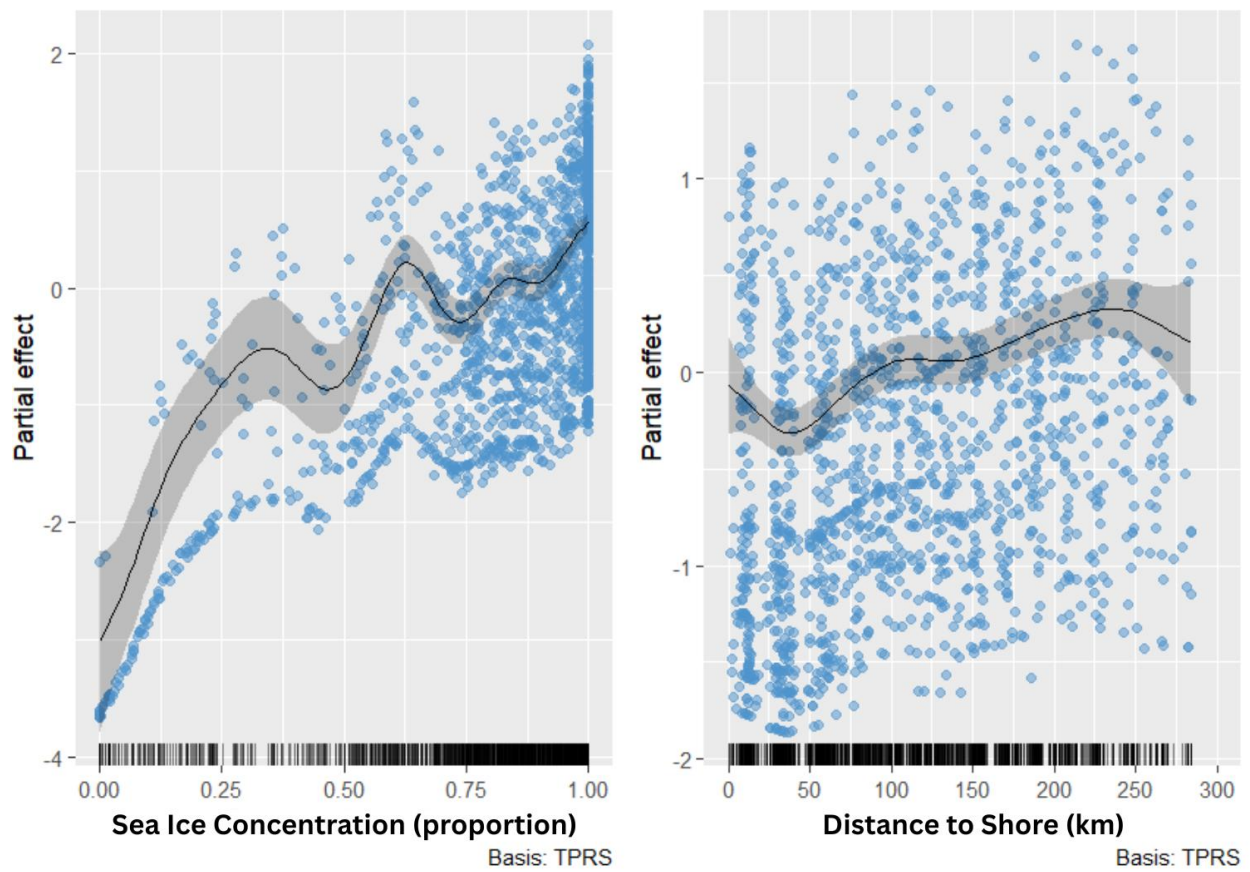


Figure 3-4: Partial effects plots from GAMs showing the response of ringed seal density to key environmental predictors in top-ranked model by AICc: (left) sea ice concentration (%) and (right) distance to shore (km). Shaded areas represent 95% confidence intervals.

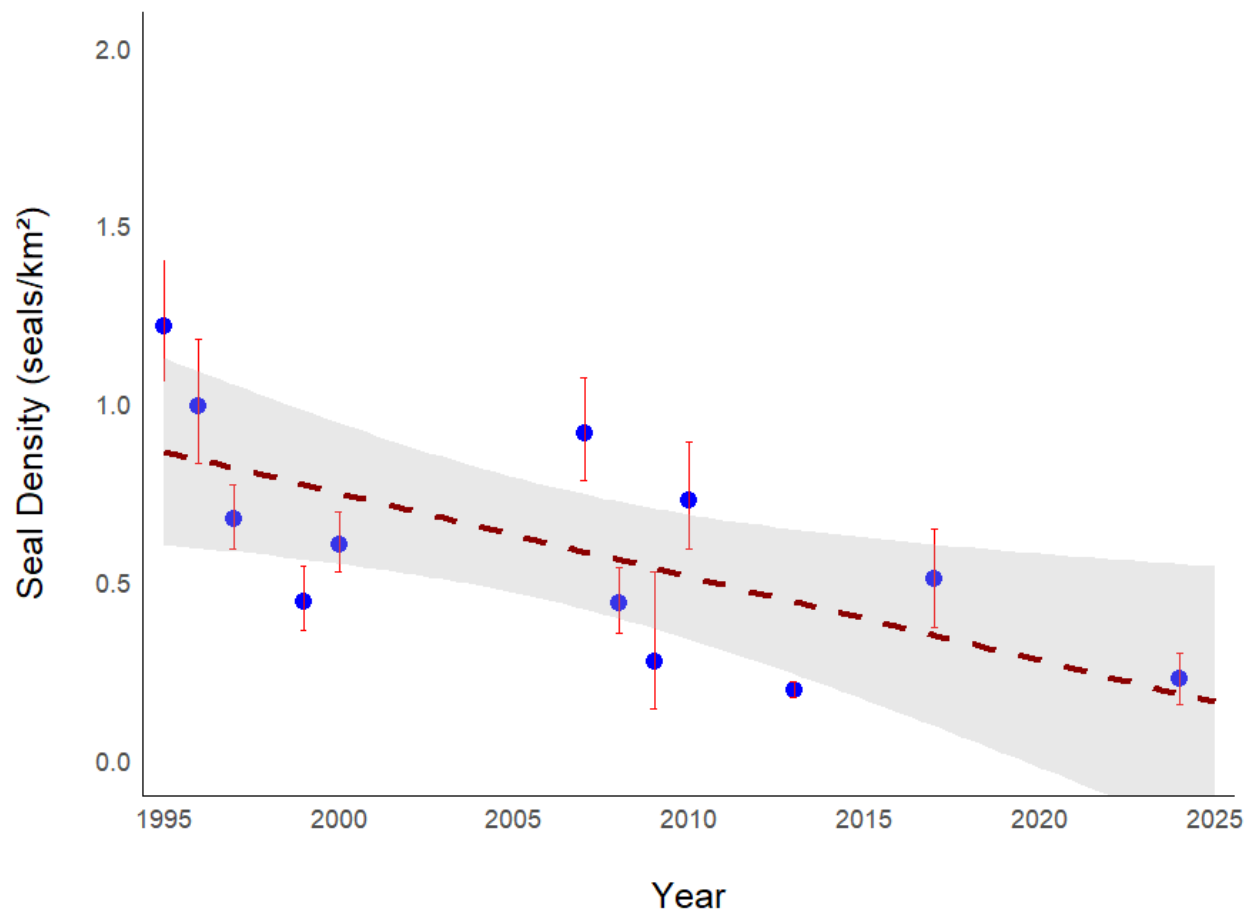


Figure 3-5: Annual ringed seal density (seals/km²) by year. Density estimates for 1995-2014 were compiled from published aerial survey data reported in Lunn et al. (1997), Young et al. (2015), and Young et al. (2019). The 2024 value was added from the most recent aerial survey for direct comparison with past values.

3.4 Discussion

This study provides the first decadal-scale characterization of spatial variation in ringed seal density and habitat use in western Hudson Bay and reveals a continued long-term decline in ringed seal density consistent with previous observations (Lunn et al. 1997; Young et al. 2015, 2019; Carlyle et al. 2022). Across survey years, ringed seal density was consistently higher at intermediate distances from shore (approximately 150-225 km) and at higher sea ice

concentrations of approximately 70-100% (Figure 3-4). Core density hotspots appeared consistently between 58° and 61° latitude, located approximately 150-200 km from shore and primarily in the central survey transects that span the middle of Western Hudson Bay. Hotspots remained roughly consistent, exhibiting robustness to variable transect effort over the course of survey years (Figure 3-3). Overall, ringed seal density was strongly associated with higher sea ice concentrations and greater distance from shore, suggesting that ringed seal distribution reflects a balance between access to suitable ice habitat and prey resources, and avoidance of nearshore predation and human disturbance.

3.4.1. Predictors of spatial variation in ringed seal density

As predicted, ringed seal density was strongly linked to sea ice concentration, which in Western Hudson Bay is exclusively seasonal/first-year ice (Environment and Climate Change Canada, 2025, *Sea Ice in Canada*). Sea ice is essential habitat for ringed seals, functioning as a resting platform and supporting the maintenance of breathing holes and birth lairs. The use of multiple, spatially distributed breathing holes by ringed seals greatly reduces susceptibility to predation by polar bears by decreasing predictability during surfacing (Pilfold et al. 2015). Thereby, habitats with more suitable sea ice coverage would offer more opportunities to maintain breathing holes and reduce predation risk.

When sheets and floes collide and buckle, they create a textured and irregular surface, facilitating the formation of snow drifts that subsequently provide sheltering areas for maintaining breathing holes and subnivean lairs (Smith and Stirling, 1975). During pupping season, stable ice with sufficient snow cover provides critical insulation and protection for

nursing mothers and pups (Ferguson et al. 2005), with landfast ice having the benefit of being over comparatively shallow waters- potentially reducing foraging travel for post-partum females (Smith and Stirling 1975; Smith & Hammill 1981; Hauser et al. 2021). Previous studies have shown that female ringed seals select for more stable fast ice when building and maintaining subnivean lairs where reliable drift-snow accumulation is necessary for insulation and protection (Smith and Stirling 1975; Smith & Hammill 1981; Krafft et al. 2007; Kelly et al. 2010). This suggests that areas nearby textured ice with snow cover may be the most suitable for post-partum females, as there is evidence that individuals display a high degree of interannual site fidelity (Kelly et al. 2010). Newly weaned juveniles may remain in the vicinity of their prior denning areas immediately after lair collapse or move nearby to more open expanses of sea ice, as they have been shown to allow for better surveillance of approaching predators while minimizing ambush sites (Kelly 2022). Altogether, these findings suggest that observed areas with the highest seal densities could have the ideal mix of suitable snow and texture nearby, while also having smoother ice expanses where seals can scan for predators.

Kernel density analysis revealed a persistent offshore hotspot of high ringed seal density across nearly all survey years, located approximately 150-200 km from shore. The Kivalliq polynya is a recurring open-water feature that extends from Cape Churchill to Southampton Island and encompasses much of the survey area (Bruneau et al. 2021). Formed by strong northwesterly winds that drive ice offshore, the polynya generates areas of thin, divergent ice and distinct sea ice drift and circulation patterns. These dynamics can influence both ice structure and prey distribution in adjacent regions. Like other Arctic polynyas, the Kivalliq Polynya plays a key ecological role by enabling nutrient upwelling and enhancing biological productivity. Seals may exploit foraging opportunities in areas located adjacent to or “down-ice” from the polynya,

where physical forcing could be aggregating prey. While this may partly explain the consistent offshore density peak, other overlapping drivers, such as bathymetry, sea ice texture, predation pressure or prey behavior, may also contribute. The consistent emergence of this hotspot highlights the potential role of oceanographic features like polynyas in the formation of potentially rich foraging zones influencing habitat use for ice-dependent predators in a changing Arctic.

Observed ringed seal densities were significantly higher farther offshore, suggesting spatial avoidance of nearshore areas with potentially higher hunting and predation risk. It was observed that density hotspots emerged nearshore south of 60 degrees latitude, but hotspots typically shifted farther offshore when nearing Arviat (Figure 3-3). Additionally, Western Hudson Bay supports a polar bear population of approximately 618 individuals as of 2021, exerting predation pressure on ringed seals (Hamilton and Derocher 2018; Atkinson et al. 2022). The observed presence of ringed seals farther offshore may also reflect avoidance of this nearshore risk (Ferguson et al. 2017). Although landfast ice provides the most stable base for lairs and resting, dense and cohesive pack ice farther offshore can also serve as important haul-out habitat. Seals tend to select for landfast ice in areas where offshore ice is scattered or transient, making offshore ice suboptimal for maintaining lairs and breathing holes (Smith and Stirling 1975; Smith & Hammill 1981). However, when solid, continuous expanses of pack ice form offshore, they may offer greater protection from predation (Wiig et al. 1999; Hauser et al. 2021; U.S. National Marine Fisheries Service [NOAA], 2024). Interpretation of observed spatial patterns should also account for variation in the probability of detection during aerial surveys. In addition to missed observations due to seals being underwater, individuals utilizing landfast ice may also go undetected while inside subnivean lairs, though the timing of the surveys are

organized to occur after the peak denning period. These findings may suggest the potential for ringed seals to shift spatial distribution in response to dynamic predator-prey interactions and changing ice conditions, underscoring the importance of considering both biological and environmental drivers in habitat use assessments in relation to climate change.

The trade-off between predation risk and availability of prey is well documented, with seals potentially choosing the more protective area and traveling farther distances to forage (Ogloff et al. 2021; Florko et al. 2023). This might contribute to more competition for resources, or force seals to travel farther while foraging. This competition for resources is an influence on juvenile ringed seals, that disperse farther offshore once weaned (Lone et al. 2019; Von Duyke et al. 2020). Juveniles and subadults typically are out competed in prime areas by older, larger individuals, meaning that they spread into more marginal zones- contributing to the overall spread in densities. The impacts of sea ice absence in low years may be detrimental to these individuals, which are forced into areas with fewer resources and higher predation pressure.

Distance to shore was a significant predictor of ringed seal density and was strongly correlated with depth and was generally highest in a similar area 150-200 km offshore as illustrated in the KDE maps suggesting a potential preference for intermediate distances aligned with bathymetric features that influence sea ice structure and prey availability. Seals were also shown to prefer shallower areas, likely due to easier access to benthic prey such as invertebrates and crustaceans (Chambellant et al. 2013; Von Duyke et al. 2020; Young et al. 2013). However, shallow bathymetry often coincides with a closer proximity to shore, and great sea ice concentrations in the form of landfast ice, suggesting the ringed seal preference for certain depths may be linked to interrelated environmental predictors (Oksanen et al. 2015). In Svalbard, density peaks have been observed near the 50% sea ice isopleth, which aligns with the

continental shelf break, an area typically associated with high biological productivity due to upwelling (Lone et al. 2019; Freitas et al. 2008). This suggests that bathymetric features may act as ecological hotspots by concentrating prey. While ringed seals feed on a variety of prey types, their offshore distribution may indicate areas of greater prey abundance driven by regional oceanographic processes such as nutrient upwelling or current convergence. While depth and distance were shown to influence seal density and distribution, other unmeasured environmental characteristics, such as prey quality/quantity, sea ice texture, or detectability differences, may also contribute. These findings underscore the importance of considering the benthic and under-ice habitats and the resulting, unseen prey aggregation dynamics when interpreting spatial patterns in ringed seal density.

3.4.2. Temporal variation in ringed seal density

Despite interannual variability in environmental conditions and ringed seal survey counts, ringed seal density aggregations in western Hudson Bay exhibited a relatively predictable spatial configuration over three decades, suggesting that persistent environmental gradients, including sea ice concentration, bathymetry, and distance from shore, continue to structure habitat use with other potential environmental factors such as predation pressure and interspecific competition influencing overall distribution. Previous studies have reported interannual fluctuations in ringed seal density that may be linked to prey cycles and demographic pressures such as pup survival (Young et al. 2015; Ferguson et al. 2017). The persistence of hotspots suggests that stable environmental features or effects consistently impact densities of ringed seals through time. Examining how this interannual variation in sea ice and other physical drivers like

bathymetry influences the expression of this persistent spatial pattern provides insight into temporal dynamics in ringed seal habitat use, especially in the context of a rapidly changing Arctic and declining sea ice conditions.

Overall ringed seal densities in Western Hudson Bay have displayed a marked decline over time, with aerial surveys from 1995 to the most recent 2024 survey indicating a persistent downward trend as opposed to cyclic interannual variability (Figure 3-5). This decline suggests that the ringed seal population is being impacted by ongoing changes in habitat suitability and resource availability, which is altering overall abundance in the region. Several previous studies have identified the Western Hudson Bay ringed seals as a population of concern, with Young et al. (2015; 2019) and Carlyle et al. (2025) highlighting lower seal counts in the last decade, and the 2024 survey continuing with this trend. Additional studies have observed significant reductions in body condition and overall reproductive success, linked to longer open water periods and earlier breakup (Chambellant et al. 2012; Ferguson et al. 2017). Longer open water periods may affect ringed seal foraging success by impacting the lifecycles of higher quality prey items such as Arctic cod, which has implications for ringed seal survival, which may contribute to reduced population density (Ferguson et al. 2017). Another potential contributor to the ringed seal decline could include increasing mortalities of pups associated with collapsed lairs due to early breakup. Reimer et al. predicted between 50% to 99% median population decline in the Amundsen Gulf and Prince Albert Sound by the year 2100 due to ongoing sea ice loss mortalities (Reimer et al. 2019).

3.4.3. Factors impacting seal observations during surveys

Daily weather is shown to influence the number of ringed seals hauled out given the conditions, with subsequent sightability being largely affected (Burns and Harbo 1972; Frost et al. 2004; Carlens et al. 2006). It was noted that higher numbers of ringed seals were observed on sunnier and warmer survey days, as opposed to colder or cloudier days, or days with precipitation. Though this is solely an observation in our survey, this has been shown to markedly influence seal presence in other studies (Burns and Harbo 1972; Frost et al. 2004; Carlens et al. 2006). There are current studies examining ringed seal densities in more northern regions of the Canadian Arctic, with these areas experiencing a potential increase in ringed seal density. These findings support that ringed seals may be moving northward in response to changing sea ice conditions, with areas previously more dominated by multiyear ice now having a higher percentage of more-suitable seasonal sea ice (Lone et al. 2019; Carlyle et al. 2025). It should be noted that the 2024 survey saw highly unusual conditions with a higher coverage of sea ice than what is typical during that time of year. A pressure system over Hudson Bay pushed a large aggregation of broken and rubble ice into the western portion of the bay. The historic conditions potentially may have affected total seal sightings, as the ice was not as uniform and suitable for ringed seals, a community member informed us. The fractured nature of the ice may have been suboptimal for building lairs and maintaining breathing holes for some of the survey area (Lehner & Northrup- Polar Bears International, 2024).

3.5 Conclusion

This study was the first to examine ringed seal densities and distribution for the 30-year span of the Western Hudson Bay aerial surveys. Additionally, this study was the first to use an

extended series of kernel density estimations to compare ringed seal densities. Our findings indicate that ringed seals prefer habitats with higher concentrations of sea ice during the molting period in Western Hudson Bay. Ringed seal density increased overall with the total sea ice, peaking at a 100% concentration, suggesting a strong preference for ice-covered habitat in Western Hudson Bay. These findings may reflect the influence of unmeasured ice features such as stability, snow cover, or predator protection. Distance to shore and depth, though highly interrelated, were strong predictors of habitat use. Ringed seals showed a strong preference for areas approximately 150-225 km from shore and peaked at approximately 130 m depth, suggesting that offshore areas may offer valuable habitat and foraging opportunities. Hotspot analyses supported these patterns, revealing a consistent core area of high seal density approximately 150-200 km offshore in the mid-latitudes. Nearshore landfast ice showed comparatively lower densities, possibly due to higher predation risk, while the farthest offshore areas were also less suitable, possibly due to unstable or scattered ice.

Long-term climate-driven changes and short-term ecological fluctuations both appear to shape ringed seal distribution in Western Hudson Bay. Our findings highlight the importance of accounting for both environmental drivers and seal behavior when interpreting temporal variability, particularly in the context of rapid Arctic change. The results of this study provide valuable insights into tracking ecological changes in the Arctic due to climate change. Through the identification of areas that display consistently high density and their associated environmental characteristics, management decisions are better informed of the needs of an ice-obligate species vulnerable to ongoing shifts in sea ice conditions. Ultimately, this study informs conservation policy of not only ringed seals, but also predators such as polar bears that heavily rely on ringed seals as their primary prey source.

4. Chapter 4: General Conclusion

My thesis combined the analysis of two long-term datasets that provided key insights into marine mammal foraging ecology and distribution in the Arctic in a rapidly changing Arctic. The multi-decadal nature of the data allowed for what might be one of the longest spans of time being evaluated against ongoing environmental shifts. Chapter 2 examined spatiotemporal variability in bowhead whale foraging ecology in relation to sea ice concentration in key portions of their range. My Chapter 2 results revealed that bowhead whale diets have shifted through time in ways consistent with climate-driven restructuring of Arctic food webs. $\delta^{15}\text{N}$ values declined across regions, while fatty-acid markers indicated variable diatom-linked inputs and increasing trophic/carnivory signatures through time. At the same time, $\delta^{13}\text{C}$ patterns differed by region and were nonlinearly associated with sea ice, suggesting that bowheads are integrating changing carbon pathways in different parts of their range. Overall, the biomarker suite supports a narrative of shifting prey-base composition and environmental processes largely influenced by region, rather than a sole increase in trophic position, as sea ice conditions continue to change. Chapter 3 examined spatiotemporal patterns in ringed seal density and distribution using aerial survey data from Western Hudson Bay collected between 1994 and 2024. Results showed that ringed seal densities were consistently associated with higher sea ice concentrations and areas farther offshore, indicating that sea ice remains a key habitat feature for ringed seals during the survey period. Together, these patterns suggest that continued declines in sea ice extent and persistence are likely to constrain suitable habitat for ringed seals in Western Hudson Bay, with potential implications for population distribution and density.

4.1 Limitations

Both chapters of my study encountered some important limitations that likely influenced analysis and subsequent interpretations. The bowhead data encompassed a considerable span of years, with stable isotope data utilized in this study beginning in 1994, going through until 2023. The fatty acid data was sourced from 2001, going through 2022. Given the archival nature of the data, there were some issues with missing or incomplete data, given the age of the datasets. Many individuals from older datasets were missing characteristics such as sex, age class, and length- which ultimately eliminated the possibility of using any as a predictor variable in the models. The stable isotope dataset originally contained many more samples from individuals but was greatly constrained due to incomplete information. For example, all samples with ‘unknown’ for lipid extraction status were excluded from the dataset due to the possibility of confounding the results (it should be noted that all samples explicitly marked as non-lipid extracted had duplicates that were lipid-extracted, thereby eliminating the need for applying a mathematical correction for those that weren’t).

The Western Hudson Bay ringed seal aerial survey data likewise encompassed a 30-year period, making it similarly valuable for assessing long-term density and distribution changes over time. Some important caveats should be acknowledged in the processing of the earlier data, given the age of the dataset and the limitations in recorded information. The ringed seal observations from years 1994-2000, as previously stated, were reconstructed from a combination of recorded transect lengths, average plane speeds, sighting times, and pilot/observer notes. While this was cross-validated with extracted sea ice data to check for overall accuracy and was the only solution in the absence of exact GPS locations or coordinates, there still are likely

inconsistencies between data coarseness in the earlier years when compared to years after 2000 when GPS track lines and exact seal coordinates were available. There were also unavoidable drawbacks as part of the survey methodology itself. There remains the persistent issue of seals going undetected for a variety of reasons during surveys, which have been planned since inception to coincide with the peak ringed seal haul period to maximize the number of observations on ice. Despite this, there is no way to determine the number of seals swimming in the water, either under ice or at depth in open water patches. Though surveys are conducted after the primary whelping period, there is also the possibility that some seals may be resting in subnivean lairs under snow as well (Lindsay et al. 2023). There is also the observed issue of seals fleeing into water before detection can occur. This was noted more in year with digital surveys where observed ringed seals escaped into breathing holes before being recorded in the DSLR camera, though the FLIR camera was sometimes able to pick up thermal imprints from where the seal had been. Similarly, there were likely seals that fled from plane noise well before even visual observation could occur.

4.2 Future Research

Future research on bowhead whale dietary patterns should consider the effects of ongoing changes in sea ice conditions, as well as their implications. A development in the Arctic that exemplifies this would be the increasingly more prominent impact of bowhead habitat selection being influenced by the growing presence of killer whales in the Arctic (Matthews et al. 2020). Whales may be foraging in areas that do not necessarily host the most abundant or high-quality prey aggregations but offer more protection from predation, with the most protective areas

historically being sea ice edge zones (Druckenmiller et al. 2017). While this study was focused on the main environmental predictors of spring sea ice concentration, region, and year- future studies should also consider expanding the focus to include ecological influences such as sea surface temperature in open-water periods, chlorophyll-a concentration as an indicator of phytoplankton bloom magnitude, particulate organic carbon (POC) matter that may impact nutrient cycling and light attenuation that dictates marine primary productivity, and potentially turbidity in areas experiencing increased meltwater/freshwater influx (Granger et al. 2011; Sejr et al. 2022). Though briefly touched on in this study, the North Atlantic Oscillation (NAO) and Arctic Oscillation (AO) likely heavily influences the foraging dynamics of bowhead whales due to combined effects on annual freeze/break up times and impact on total sea ice concentration and coverage, which subsequently affects marine primary productivity and bloom magnitude. In turn, this limits the food available for grazing zooplankton, either through total production or via trophic mismatch from the misalignment between bloom timing and zooplankton phenology, thereby impacting bowhead foraging opportunities (Renaud et al. 2024).

For ringed seals, future research should focus study on fine-scale sea ice characteristics to determine optimal zones with the most suitable seal habitat. Ringed seals' preference for sea ice offshore suggests the potential for consistent pressure ridges, surface texture, and snow accumulation in consolidated pack ice, which offers potentially more protection from predation. The reliable emergence of offshore density hotspots in consistent locations implies a high degree of habitat desirability, potentially linked to environmental characteristics not examined in this study. Identifying which ice texture features determine the most protective habitat from polar bears may better inform management decisions in an area with shifting sea ice dynamics. Recent studies in the high Arctic may suggest that more ringed seals could be shifting northward as

multi-year sea ice declines and more favorable seasonal sea ice becomes more prevalent farther north. However, more research is needed to determine this, and whether redistribution will occur broadly and remains uncertain (Lone et al. 2019; Carlyle et al 2025).

4.3 Significance and Policy Implications

Both bowhead whales and ringed seals are crucial species to Inuit subsistence harvests and their traditional livelihoods. The changes in foraging habits in bowhead whales may signal a shift in feeding habitats due to changing prey dynamics, potentially leading to hunting inaccessibility across their historic range. The marked decrease in ringed seal density in Western Hudson Bay poses a limitation on subsistence harvest availability as numbers decline. The loss of marine resources would have considerable negative impacts on Indigenous communities across the Canadian Arctic, potentially impacting the sustainability of subsistence activities. Marine mammal meat and blubber are central to Inuit diets, and the cost of exporting food and supplies to the Arctic is incredibly costly- meaning that there are few sustainable options outside of traditional subsistence hunting for residents to continue to maintain their livelihoods. While secondary to direct subsistence value, the unavailability of marine mammal products such as seal skins, fur clothing, and artwork such as carvings from bone and ivory would be an additional economic loss to communities with limited means of income opportunities. Additional to this, the most pernicious effect of marine mammal decline for Inuit communities may be the loss of cultural identity closely tied to traditional subsistence hunting. The shared group endeavor of hunting, preparing, and sharing harvested whales and seals is deeply embedded in ancestral

traditions, intergenerational knowledge transmission, and community cohesion (Jensen et al. 2017).

In addition to the loss of food security across Indigenous communities, the loss of ringed seals in Western Hudson Bay would also undoubtedly have deleterious impacts on polar bears as a lost prey source. Ringed seal populations, as the main prey species for polar bears, have a direct effect on polar bear survival. The 2021 polar bear aerial surveys in Western Hudson Bay reported a population of around 618 individuals, which represents a 27% decline in 5 years. Research on the WHB stock began in the 1980s, and the population is now estimated to be roughly half what it was since survey inception (Atkinson et al. 2022), which mirrors observed declining trends in ringed seal populations. In addition to ringed seals as a lost prey source, the loss of beached bowhead whale carcasses as a vital dietary resource for polar bears could be detrimental over the long-term. Bowhead whale carcasses, either from the remains of subsistence hunts or from killer whale predation events, provide a nutritional landfall for scavenging polar bears in the Arctic, which has been suggested to circumvent the deleterious impacts of other prey source losses (Galicía et al. 2016; Laidre et al. 2018). Though currently difficult to predict, there is a possibility that the changing foraging dynamics of bowhead whales could lead to the eventuality of fewer whales supplementing polar bear diets already strained by prey unavailability from sea ice loss and climate change-related impacts (Galicía et al. 2016; Laidre et al. 2018).

In conclusion, the findings of my combined project provide insights on the environmental consequences of environmental change, and may inform management and policy decisions to preserve the populations of these two Arctic endemic marine mammal species in a warmer and rapidly changing North.

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Appendix and Supplementary Materials

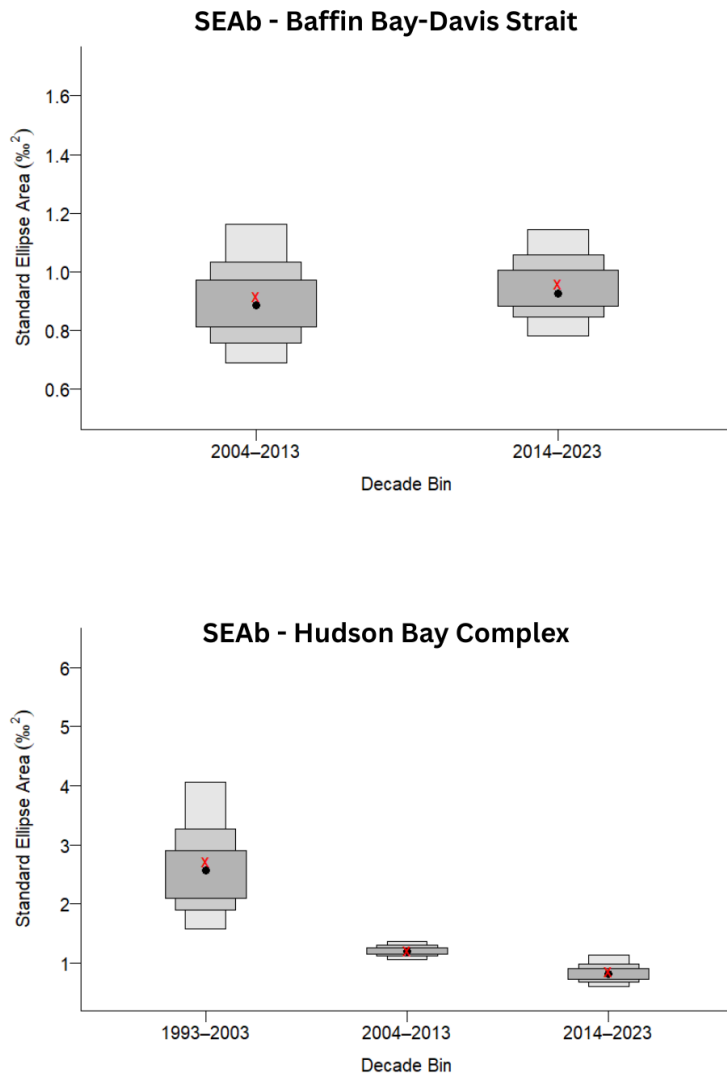


Figure S3-1: Boxplots representing SEAb estimates for isotopic niche breadth of Baffin Bay-Davis Strait and Hudson Bay Complex bowhead whales by region and decade. Boxes indicate Bayesian credible intervals at 50% (dark grey), 75% (medium grey), and 95% (light grey).

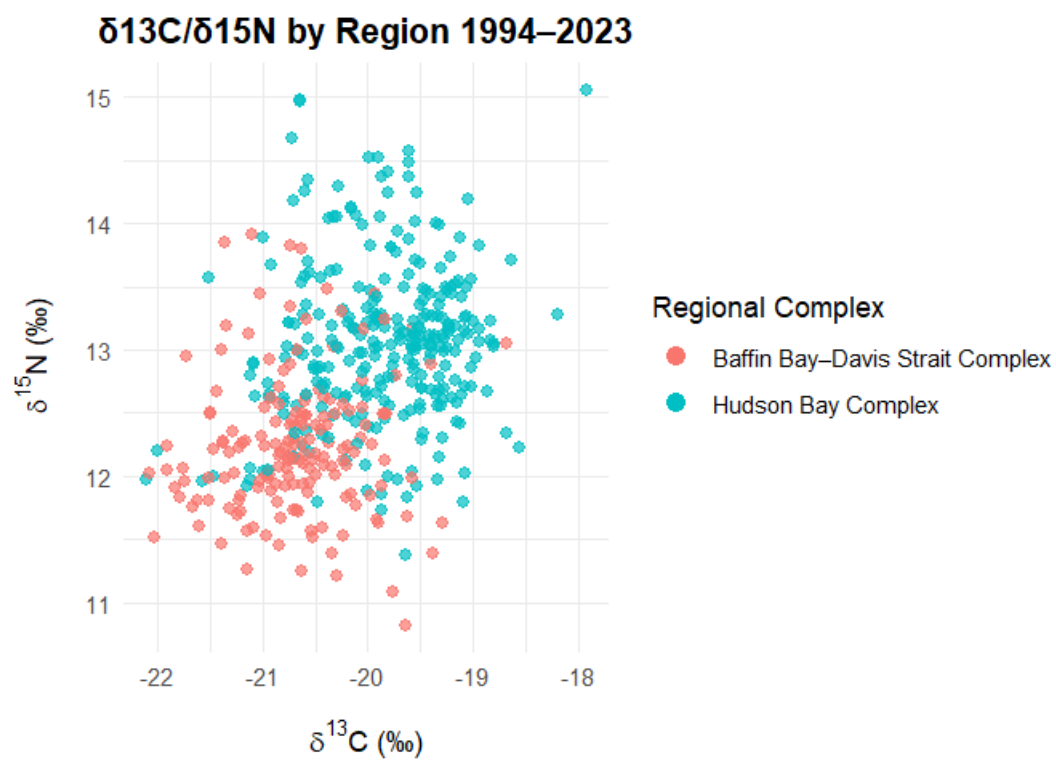


Figure S2-2: Stable isotope biplot of bowhead skin samples from 1994-2023

<i>Metric</i>	Prior-Year Spring Sea Ice	Collection-Year Spring Sea Ice
<i>Adjusted R²</i>	0.548	0.453
<i>Deviance Explained</i>	56.8%	47.6%
<i>REML Score</i>	382.94	429.45
<i>AIC</i>	686.32	773.33
<i>AICc</i>	688.92	775.83
<i>EDF</i>	19.75	19.44
<i>F-stat</i>	25.04	17.29
<i>Smooth p-value</i>	< 0.001	< 0.001

Table S2-1: Model comparison results for generalized additive models (GAMs) predicting $\delta^{13}\text{C}$ values in bowhead whale skin tissue using either prior-year or collection-year average spring sea ice concentration as a single smooth term predictor. Both models used thin plate regression splines with a basis dimension of $k = 30$.

<i>Metric</i>	Prior-Year Spring Sea Ice + Year + Region	Collection-Year Spring Sea Ice + Year + Region	Prior-Year Spring Sea Ice + Region	Collection-Year Spring Sea Ice + Region	Prior-Year Spring Sea Ice + Year	Collection- Year Spring Sea Ice + Year
<i>Adjusted R²</i>	0.58	0.58	0.53	0.48	0.59	0.59
<i>Deviance Explained</i>	60.1%	60.4%	55.10%	50.40%	60.80%	60.90%
<i>REML Score</i>	355.37	361.84	384.55	414.16	358.34	373.36
<i>AIC</i>	652.28	649.78	700.44	747.82	647.99	652.7
<i>AICc</i>	655.18	652.73	702.72	750.28	651.4	656.81
<i>EDF (sea ice)</i>	7.66	14.31	17.65	18.66	8.393	12.04
<i>F-stat (sea ice)</i>	9.57	6.20	11.94	8.02	8.155	6.334
<i>Smooth p-value (sea ice)</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
<i>EDF (year)</i>	11.66	6.10	NA	NA	13.375	12.75
<i>F-stat (year)</i>	9.57	14.19	NA	NA	9.022	12.684
<i>Smooth p-value (year)</i>	<0.001	<0.001	NA	NA	<0.001	<0.001

Table S2-2: Sensitivity analysis comparing the effects of using prior-year versus collection-year spring sea ice concentration in generalized additive models (GAMs) predicting bowhead whale $\delta^{13}\text{C}$ values. Each pair of columns represents the same model structure, with only the sea ice predictor window changed. Models included various combinations of smooth terms for sea ice ($k = 30$) and year ($k = 20$), and region as a parametric factor.

<i>Metric</i>	Prior-Year Spring Sea Ice	Collection-Year Spring Sea Ice
<i>Adjusted R²</i>	0.60	0.61
<i>Deviance Explained</i>	62.00%	62.00%
<i>REML Score</i>	467.56	456.77
<i>AIC</i>	859.84	852.12
<i>AICc</i>	862.25	853.78
<i>EDF</i>	19.19	16.22
<i>F-stat</i>	32.12	38.77
<i>Smooth p-value</i>	<0.001	<0.001

Table S2-3: Model comparison results for generalized additive models (GAMs) predicting $\delta^{15}\text{N}$ values in bowhead whale skin tissue using either prior-year or collection-year average spring sea ice concentration as a single smooth term predictor. Both models used thin plate regression splines with a basis dimension of $k = 30$.

<i>Metric</i>	Prior-Year Spring Sea Ice + Year + Region	Collection-Year Spring Sea Ice + Year + Region	Prior-Year Spring Sea Ice + Region	Collection-Year Spring Sea Ice + Region	Prior-Year Spring Sea Ice + Year	Collection- Year Spring Sea Ice + Year
<i>Adjusted R²</i>	0.61	0.62	0.62	0.60	0.60	0.61
<i>Deviance Explained</i>	61.60%	62.00%	62.30%	60.20%	62.00%	62.90%
<i>REML Score</i>	421.94	421.19	424.46	426.4	468.17	455.42
<i>AIC</i>	835.32	833.35	833.64	847.72	862.59	846.91
<i>AICc</i>	835.62	833.75	834.2	847.88	865.24	849.1
<i>EDF (sea ice)</i>	1.63	2.57	6.58	1.89	17.65	15.87
<i>F-stat (sea ice)</i>	0.193	0.982	2.775	0.713	22.98	29.179
<i>Smooth p-value (sea ice)</i>	0.809	0.338	0.00479	0.506	<0.001	< 0.001
<i>EDF (year)</i>	2.22	2.33	NA	NA	2.46	2.52
<i>F-stat (year)</i>	6.814	6.551	NA	NA	1.872	3.414
<i>Smooth p-value (year)</i>	<0.001	0.62	NA	NA	0.15	0.03

Table S2-4: Sensitivity analysis comparing the effects of using prior-year versus collection-year spring sea ice concentration in generalized additive models (GAMs) predicting bowhead whale $\delta^{15}\text{N}$ values. Each pair of columns represents the same model structure, with only the sea ice predictor window changed. Models included various combinations of smooth terms for sea ice ($k = 30$) and year ($k = 20$), and region as a parametric factor.

<i>FA Ratio</i>	Metric	Prior-Year Spring Sea Ice	Collection-Year Spring Sea Ice
<i>16:1n-7/16:0</i>	Adjusted R²	0.117	0.0647
	Deviance Explained	14.00%	8.42%
	REML Score	149.32	151.93
	AIC	292.73	300.47
	AICc	293.41	301.00
	EDF	3.84	3.06
	F-stat	4.09	2.56
	Smooth p-value	<0.01	0.03

Table S2-5: Model comparison results for generalized additive models (GAMs) predicting the diatom-associated fatty acid ratio (16:1n-7/16:0) in bowhead whale blubber using either prior-year or collection-year average spring sea ice concentration as a single smooth term predictor. Both models used thin plate regression splines with a basis dimension of $k = 6$

	Metric	Prior-Year Sea Ice + Year + Region	Collection-Year Sea Ice + Year + Region	Prior-Year Sea Ice + Region	Collection-Year Sea Ice + Region	Prior-Year Sea Ice + Year	Collection- Year Sea Ice + Year
16:1n-7/16:0	Adjusted R²	0.236	0.231	0.172	0.117	0.215	0.219
	Deviance Explained	27.40%	26.70%	19.90%	13.50%	24.20%	24.50%
	REML Score	140.90	141.21	142.59	145.86	142.95	142.35
	AIC	275.65	274.96	284.10	291.13	276.24	275.43
	AICc	277.4	276.36	284.99	291.59	277.15	276.33
	EDF (sea ice)	1.82	1.0	2.73	1.12	1.0	1.0
	F-stat (sea ice)	0.653	0.214	3.279	1.485	3.783	4.95
	Smooth p- value (sea ice)	0.441	0.645	0.0126	0.153	0.0538	0.0277
	EDF (year)	3.63	3.84	NA	NA	4.03	3.98
	F-stat (year)	3.736	4.672	NA	NA	8.624	8.307
	Smooth p- value (year)	0.0053	0.0007	NA	NA	<0.001	<0.001

Table S2-6: Sensitivity analysis comparing the effects of using prior-year versus collection-year spring sea ice concentration in generalized additive models (GAMs) predicting bowhead whale **16:1n-7/16:0** values. Each pair of columns represents the same model structure, with only the sea ice predictor window changed. Models included various combinations of smooth terms for sea ice ($k = 6$) and year ($k = 6$), and region as a parametric factor.

<i>FA Ratio</i>	Metric	Prior-Year Spring Sea Ice	Collection-Year Spring Sea Ice
<i>18:1n-9/18:1n-7</i>	Adjusted R²	0.17	0.19
	Deviance Explained	18.90%	21.20%
	REML Score	-30.30	-30.36
	AIC	-70.16	-73.31
	AICc	-69.54	-72.58
	EDF	3.48	4.18
	F-stat	7.00	7.93
	Smooth p-value	<0.001	<0.001

Table S2-7: Model comparison results for generalized additive models (GAMs) predicting the trophic-associated fatty acid ratio (**18:1n-9/18:1n-7**) in bowhead whale blubber using either prior-year or collection-year average spring sea ice concentration as a single smooth term predictor. Both models used thin plate regression splines with a basis dimension of $k = 6$

	Metric	Prior-Year Sea Ice + Year + Region	Collection-Year Sea Ice + Year + Region	Prior-Year Sea Ice + Region	Collection-Year Sea Ice + Region	Prior-Year Sea Ice + Year	Collection- Year Sea Ice + Year
<i>18:1n-9/18:1n-7</i>	Adjusted R ²	0.26	0.31	0.20	0.21	0.26	0.32
	Deviance Explained	31.3%	36.2%	23.2%	23.9%	29.3%	35.6%
	REML Score	-29.29	-31.62	-30.47	-30.13	-31.34	-33.95
	AIC	-81.16	-91.968	-73.66	-75.19	-82.43	-93.67
	AICc	-78.51	-89.271	-72.51	-74.08	-80.79	-91.59
	EDF (sea ice)	3.85	3.644	3.71	3.83	2.88	3.91
	F-stat (sea ice)	1.35	2.346	2.91	1.81	3.89	5.20
	Smooth p- value (sea ice)	0.25	0.17	0.02	0.07	<0.01	<0.01
	EDF (year)	3.84	4.511	NA	NA	4.26	4.57
	F-stat (year)	2.46	4.48	NA	NA	3.68	5.09
	Smooth p- value (year)	0.03	<0.01	NA	NA	<0.01	<0.01

Table S2-8: Sensitivity analysis comparing the effects of using prior-year versus collection-year spring sea ice concentration in generalized additive models (GAMs) predicting bowhead whale *18:1n-9/18:1n-7* values. Each pair of columns represents the same model structure, with only the sea ice predictor window changed. Models included various combinations of smooth terms for sea ice ($k = 6$) and year ($k = 6$), and region as a parametric factor.

<i>FA Ratio</i>	Metric	Prior-Year Spring Sea Ice	Collection-Year Spring Sea Ice
<i>20:5n-3/22:6n-3</i>	Adjusted R²	0.05	0.03
	Deviance Explained	7.07%	4.16%
	REML Score	-16.86	-15.31
	AIC	-40.75	-36.95
	AICc	-40.32	-36.58
	EDF	2.50	2.13
	F-stat	3.11	2.03
	Smooth p-value	0.03	0.13

Table S2-9: Model comparison results for generalized additive models (GAMs) predicting the EPA/DHA-associated fatty acid ratio (20:5n-3/22:6n-3) in bowhead whale blubber using either prior-year or collection-year average spring sea ice concentration as a single smooth term predictor. Both models used thin plate regression splines with a basis dimension of $k = 6$

	Metric	Prior-Year Sea Ice + Year + Region	Collection-Year Sea Ice + Year + Region	Prior-Year Sea Ice + Region	Collection-Year Sea Ice + Region	Prior-Year Sea Ice + Year	Collection- Year Sea Ice + Year
20:5n-3/22:6n-3	Adjusted R²	0.06	0.05	0.04	0.03	0.07	0.05
	Deviance Explained	8.93%	8.58%	5.83%	5.45%	9.82%	7.01%
	REML Score	-12.60	-11.82	-14.49	-12.87	-14.90	-13.55
	AIC	-38.72	-36.22	-38.75	-34.76	-40.56	-37.25
	AICc	-37.80	-35.06	-38.33	-34.04	-39.69	-36.51
	EDF (sea ice)	1	1.72	1	2.13	2.39	1.81
	F-stat (sea ice)	2.92	0.90	4.88	0.79	2.15	1.23
	Smooth p- value (sea ice)	0.09	0.41	0.03	0.41	0.07	0.26
	EDF (year)	1.99	1.84	NA	NA	1.93	2.01
	F-stat (year)	1.41	2.10	NA	NA	1.49	1.58
	Smooth p- value (year)	0.22	0.11	NA	NA	0.21	0.19

Table S2-10: Sensitivity analysis comparing the effects of using prior-year versus collection-year spring sea ice concentration in generalized additive models (GAMs) predicting bowhead whale **20:5n-3/22:6n-3** values. Each pair of columns represents the same model structure, with only the sea ice predictor window changed. Models included various combinations of smooth terms for sea ice ($k = 6$) and year ($k = 6$), and region as a parametric factor.

<i>FA Ratio</i>	Metric	Prior-Year Spring Sea Ice	Collection-Year Spring Sea Ice
22:1n-11/20:1n-9	Adjusted R²	0.06	0.08
	Deviance Explained	8.52%	10.20%
	REML Score	36.0	33.07
	AIC	63.71	59.63
	AICc	64.36	60.15
	EDF	3.65	3.00
	F-stat	2.58	3.71
	Smooth p-value	0.04	<0.01

Table S2-11: Model comparison results for generalized additive models (GAMs) predicting the copepod-associated fatty acid ratio (22:1n-11/20:1n-9) in bowhead whale blubber using either prior-year or collection-year average spring sea ice concentration as a single smooth term predictor. Both models used thin plate regression splines with a basis dimension of $k = 6$

	Metric	Prior-Year Sea Ice + Year + Region	Collection-Year Sea Ice + Year + Region	Prior-Year Sea Ice + Region	Collection-Year Sea Ice + Region	Prior-Year Sea Ice + Year	Collection- Year Sea Ice + Year
22:1n-11/20:1n-9	Adjusted R²	0.18	0.19	0.16	0.14	0.08	0.15
	Deviance Explained	22.1%	23.4%	19.4%	17.2%	11.3%	19.0%
	REML Score	30.56	31.02	29.57	29.94	36.71	34.10
	AIC	46.68	47.71	49.37	51.59	61.13	53.68
	AICc	48.18	49.81	50.52	52.53	61.98	55.35
	EDF (sea ice)	4.05	3.17	3.81	3.04	1	3.51
	F-stat (sea ice)	4.57	3.36	3.87	3.94	0.42	2.50
	Smooth p-value (sea ice)	<0.001	0.01	<0.01	<0.01	0.52	0.05
	EDF (year)	1	3.32	NA	NA	3.70	3.51
	F-stat (year)	3.71	2.32	NA	NA	2.96	2.15
	Smooth p-value (year)	0.06	0.14	NA	NA	0.03	0.10

Table S2-12: Sensitivity analysis comparing the effects of using prior-year versus collection-year spring sea ice concentration in generalized additive models (GAMs) predicting bowhead whale **22:1n-11/20:1n-9** values. Each pair of columns represents the same model structure, with only the sea ice predictor window changed. Models included various combinations of smooth terms for sea ice ($k = 6$) and year ($k = 6$), and region as a parametric factor.

Chapter 3 Materials

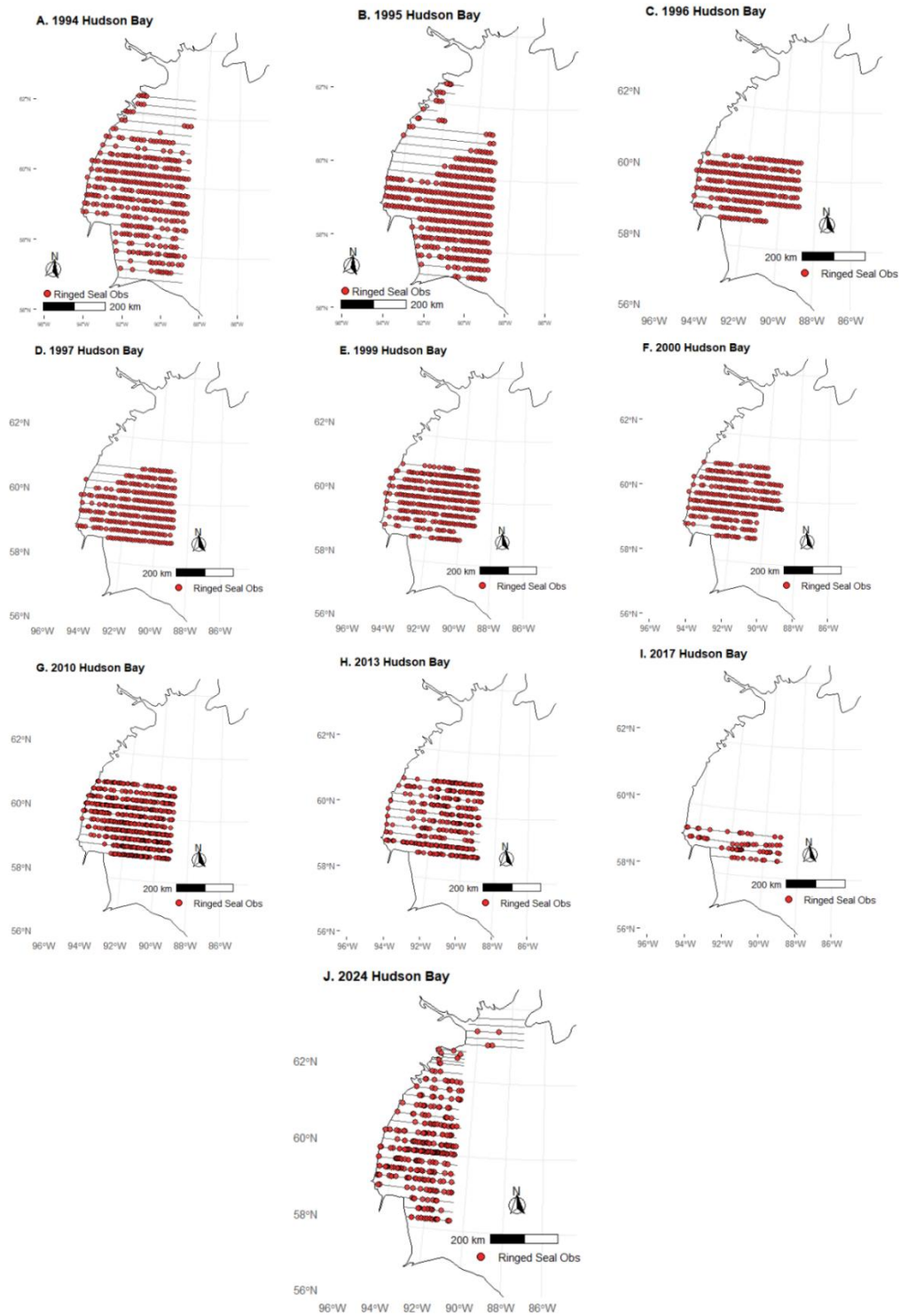


Figure S3-1: Ringed seal sighting locations recorded during aerial surveys in Western Hudson Bay across years 1994-2024. Red points indicate individual seal observations plotted along survey transects.

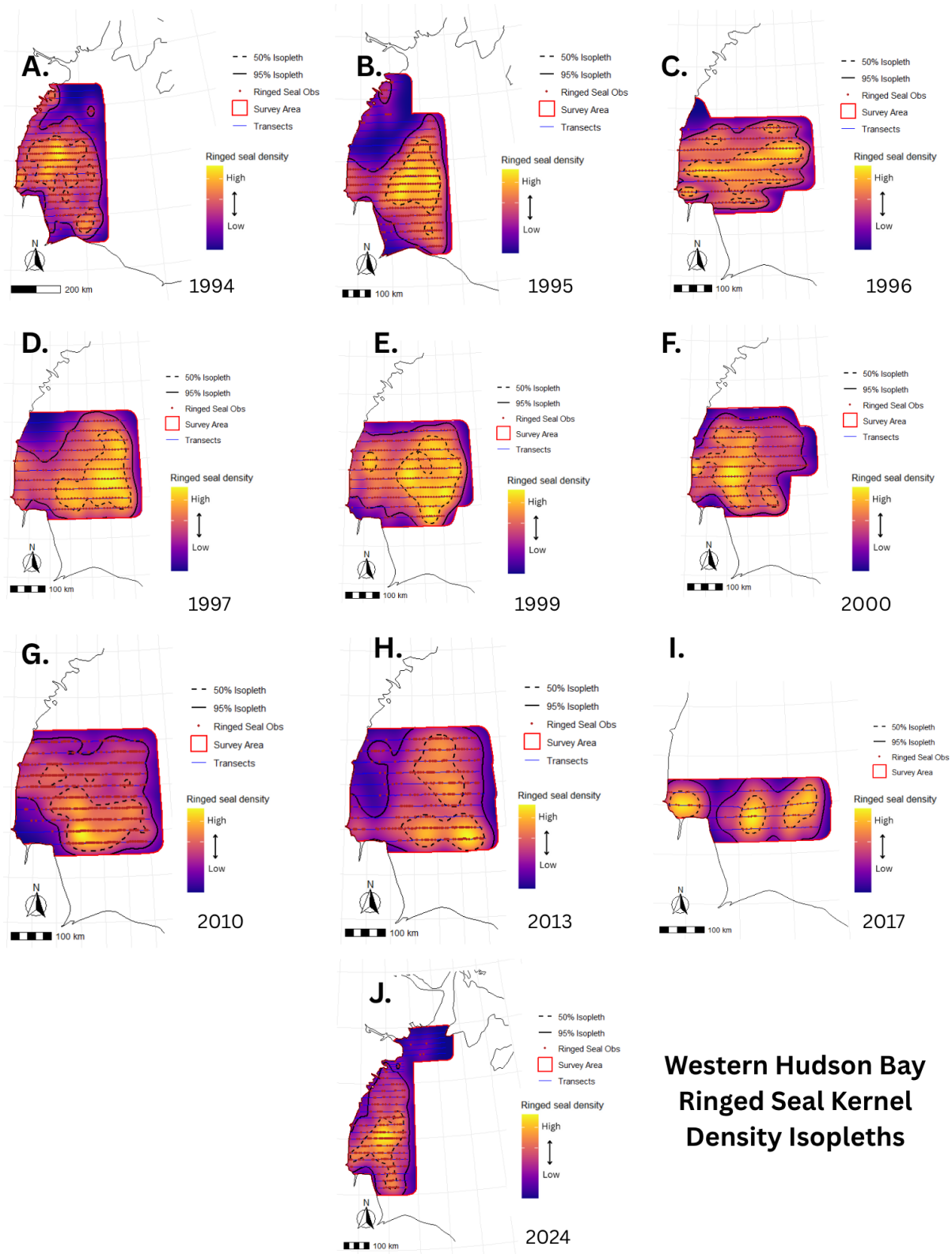


Figure S3-2: Kernel density estimation (KDE) maps of ringed seal sightings in Western Hudson Bay across survey years 1994-2024. Panels show 50% (core use) and 95% (range use) isopleths overlaid on density surfaces, with transects shown in red.

Ringed Seal Density vs Sea Ice Concentration by Transect 1994-2024

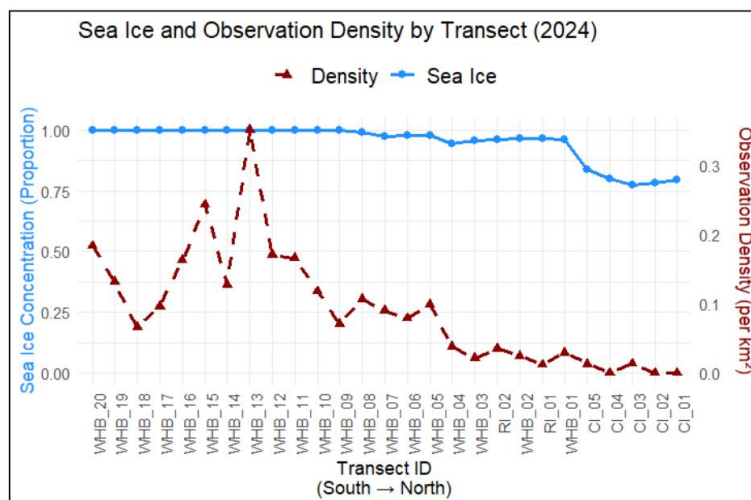
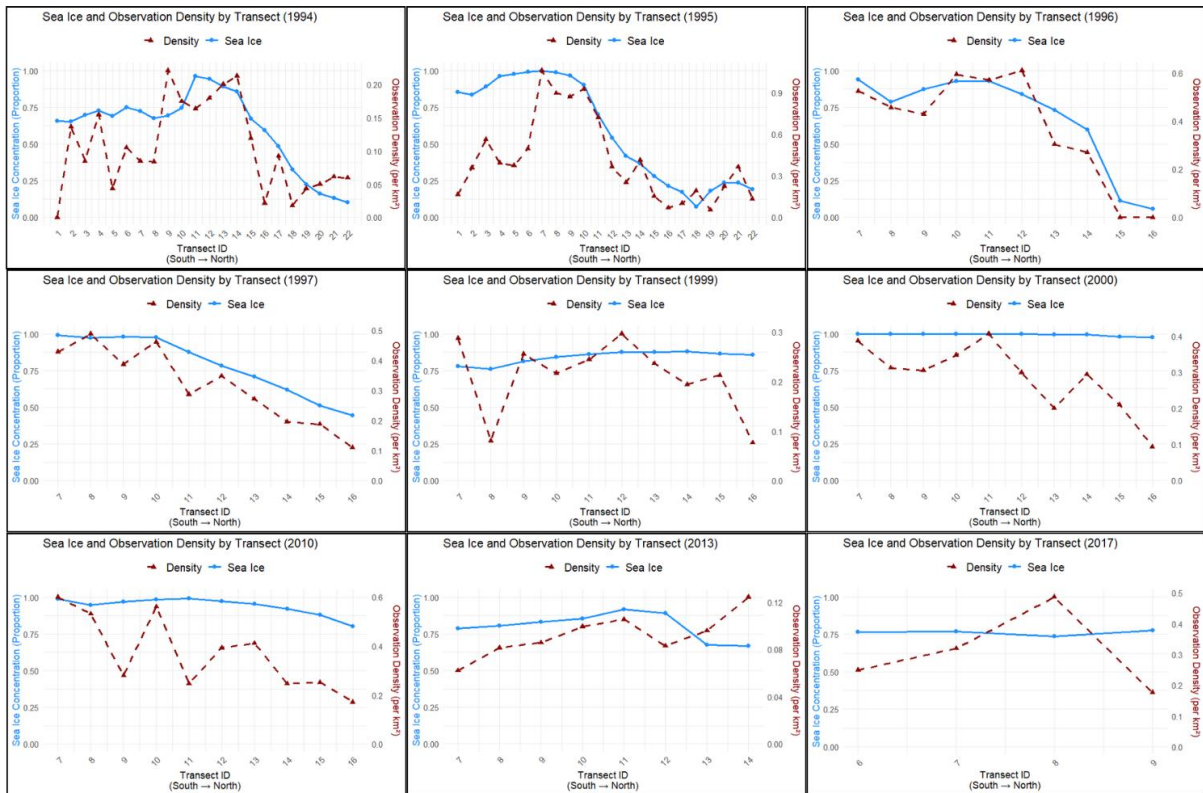


Figure S3-3: Ringed seal density by transect vs sea ice proportion for all survey years 1994-2024