EVALUATING THE EXTENT AND DRIVERS OF DIETARY SPECIALIZATION IN POLAR BEARS (*URSUS MARITIMUS*) ACROSS WESTERN HUDSON BAY

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Abstract

Climate warming has caused significant reductions in the extent of annual sea ice. As an ice-dependent species, the polar bear (*Ursus maritimus*) relies on the ice to hunt, making it susceptible to large-scale changes in sea ice and prey availability. My thesis sought to investigate individual-level foraging habits of polar bears in Western Hudson Bay from 2004-2021. I used fatty acid analyses and the proportional similarity index to investigate the extent and drivers of individual dietary specialization and interindividual differences in foraging habits. My results indicated a significant proportion of specialization, with the degree of specialization differing across age and sex classes. Annual snow depth and the North Atlantic Oscillation (NAO) were strong predictors of specialization, resulting in increased specialization with increasing snow depth and NAO. Continued monitoring efforts are necessary to ensure interindividual variation in foraging is considered when modelling the responses of polar bears to future climatic warming.

Dedicated to my sweet boy, Rufus.

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Chapter I – General Introduction

Polar Bear Foraging Ecology

The polar bear (*Ursus maritimus*) is a large apex predator inhabiting the circumpolar north. Its range spans the Arctic nations of Canada, the United States of America (Alaska), Greenland, Norway, and Russia (Prestrud and Sterling 1994) and is composed of 19 distinct subpopulations (PBSG 2010). Polar bears are reliant on the sea ice for hunting, mating, travelling, and maternal denning (Stirling and Archibald 1977; Smith 1980), and as a result, are classified as marine mammals in some countries (Marine Mammal Commission and NOAA's National Marine Fisheries Service 2019). However, their reliance on the sea ice can leave them particularly vulnerable to climate-induced sea ice loss (Stirling and Derocher 1993, 2012; Stirling et al. 1999).

Polar bears are a vital component of the Arctic marine food web, serving as a top predator across the Arctic. Polar bears feed primarily on ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) across most of their range (Stirling and Archibald 1977; Thiemann et al. 2008). Their diets are often supplemented with a number of alternative prey species, such as harbour seals (*Phoca vitulina*), harp seals (*Pagophilus groenlandicus*), and hooded seals (*Cystophora cristata*; Thiemann et al. 2008). Despite their preference for primary prey types such as the ringed seal, polar bears are also opportunistic feeders and have been documented consuming prey items such as walruses (*Odobenus rosmarus*; Calvert and Stirling 1990), narwhals (*Monodon monoceros*; Smith and Sjare 1990), beluga whales (*Delphinapterus leucas*; Freeman 1973; Smith and Sjare 1990), and conspecifics (Taylor et al. 1985; Amstrup et al. 2006; Stirling and Ross 2011). Although many of these large pinnipeds and cetaceans are killed infrequently, the energetic gain from killing or scavenging on a single individual could justify the time and effort required to kill such a large prey type (Calvert and Stirling 1990).

As a marine predator that consumes blubber-rich prey items like seals, polar bears have colloquially been referred to as “lipivores” (Derocher 2012). The consumption and subsequent deposition of fat allow the bear to survive increasingly long fasting periods as a result of climate warming (Stirling and Derocher 1993, 2012; Derocher 2004). Thus, it is essential that polar bears can hunt on the sea ice and consume a blubber-rich diet. Without adequate access to sea ice, it will not be possible to maintain viable polar bear subpopulations in the long term (Stirling and Derocher 2012).

Quantitative Fatty Acid Signature Analysis

The use of fatty acids for dietary analysis is a widely used method for studying the foraging habits of large, free-ranging animals (Budge et al. 2006; Thiemann et al. 2008, 2022; Sciullo et al. 2017; Goetsch et al. 2018). In mammalian predators, many dietary fatty acids are incorporated predictably into the animal's adipose tissue due to biochemical limitations to fatty acid synthesis (Ackman and Eaton 1966; Iverson et al. 1995). Along with the predictable nature of fatty acid deposition in predator adipose tissue, the sheer abundance and diversity of fatty acids in marine systems have allowed fatty acids to be used in determining trophic relationships in several marine food webs (Budge et al. 2006).

Over the years, many techniques have been used to analyze the diet composition of free-ranging animals. These methods include direct observation (Stirling 1974), the use of biochemical tracers such as stable isotope analysis (Hobson and Wassenaar 1999; Boecklen 2011), as well as stomach and fecal content analysis (Petta et al. 2020; Ross et al. 2022).

Although these methods have been widely used, an approach to diet estimation known as quantitative fatty acid signature analysis (QFASA) is especially effective at providing diet estimates for a suite of marine-based species over a period of 30 to 90 days prior to sampling (Iverson et al. 2004; Thiemann et al. 2008, 2022).

QFASA is a statistical model developed by Iverson et al. (2004) that analyzes the fatty acid composition of a predator and its prey items to provide an estimate of the proportions of individual prey species that make up the diet of the predator. The model analyzes the fatty acid composition, or the fatty acid "signature," of the predator and compares it to the average fatty acid signature of each potential prey species to determine the most likely combination of prey signatures that best matches that of the predator signature (Iverson et al. 2004). Since mammalian predators metabolize or deposit the individual fatty acids they consume, it is important to determine the extent of this metabolism to ensure that diet can be adequately estimated. Calibration coefficients account for the metabolism of specific fatty acids by comparing the percentage of a particular fatty acid in the predator with the percentage of the same fatty acid in the diet (Iverson et al. 2004). The results of this method provide an overview of a predator's diet composition over the weeks or months before tissue samples were collected (Iverson et al. 2004; Thiemann et al. 2022).

QFASA has been used to estimate the diet composition of several marine and Arctic predators (see Beck et al. 2007; Budge et al. 2012). In marine ecosystems, the diversity of fatty acids is high, which is one of the factors that allows QFASA to estimate predator diets accurately (Iverson et al. 2004). Other studies investigating the foraging ecology of an Arctic predator such as the polar bear have utilized QFASA to determine the diet composition of individual bears (see Thiemann et al. 2008, 2011; Galicia et al. 2015, 2016; Sciullo et al. 2017). QFASA is especially useful for studying polar bear foraging ecology due to the lipid-rich prey items consumed (Iverson et al. 2004; Thiemann et al. 2022).

Dietary Specialization

General Overview

It has long been known that not all individuals within a population demonstrate similar patterns of foraging or resource use (e.g., Van Valen 1965). In many cases, generalist populations contain a combination of dietary generalists with a number of specialized individuals that utilize a subset of the available resources (Bolnick et al. 2003; Araújo et al. 2011). These specialized individuals differ from their generalist conspecifics due to among-individual niche variation or resource use heterogeneity (Knudsen et al. 2010; Dall et al. 2012). The phenomenon of specializing on a subset of available resources, known as individual dietary specialization or intrapopulation niche variation (Van Valen 1965), refers to individuals occupying a distinctly narrow dietary niche within the population niche or individuals that demonstrate a limited overlap with the population niche (Roughgarden 1974; Bolnick et al. 2002, 2003; Sargeant 2007). According to optimal foraging theory, individuals should select a foraging strategy that would maximize their net rate of energy intake (MacArthur and Pianka 1966; Stephens and Krebs 1986). This optimal, energetically efficient foraging strategy should, therefore, in theory, be characteristic of the population. However, previous studies have demonstrated that differences between individuals, such as movement patterns, body size, growth rate, and reproductive status, result in differences in the foraging opportunities of individuals within the population (e.g., Clutton-Brock et al. 1987; Houston and Shine 1993). Thus, differences in foraging habits and resource usage can encourage the development of dietary specialization within the population.

There are two predominant metrics for quantifying the extent of dietary specialization within a population: The proportional similarity index (PS_i; Feinsinger et al. 1981; Schoener 1986) and the total niche width (TNW; Roughgarden 1974; Bolnick et al. 2002). The PS_i metric is used to determine the similarity of an individual's diet to that of the population. If individuals consume a diet directly proportional to the population diet, they receive a PS_i value of 1. In contrast, individuals whose diets do not closely resemble the population diet would receive values nearing 0, as they overlap less with the rest of the population. The second metric used for quantifying dietary specialization is based on the optimal foraging theory framework that the total niche width (TNW) of a population is determined by a combination of within- and between-individual components (WIC and BIC) (Roughgarden 1974). Therefore, TNW = WIC + BIC and the metric, WIC/TNW, can measure the proportion of the total niche width an individual would consume (Bolnick et al. 2002; Araújo et al. 2011). This metric is similar to the PS_i metric, as the resulting value would be a proportion between 0 and 1, with 1 indicating a dietary generalist and 0 indicating a dietary specialist. In most cases, individuals will not demonstrate a dietary niche width as wide as their population but rather a gradient of narrower widths, indicating varying degrees of specialization (Araújo et al. 2011).

Causes of Dietary Specialization

Previous studies have demonstrated that differences in foraging patterns can emerge because of necessity or the need to learn prey-specific foraging behaviours (Partridge 1976; Estes et al. 2003), as a response to intraspecific competition (Schindler et al. 1997; Tinker et al. 2008), or because of spatiotemporal variability in resource distribution (Woo et al. 2008). However, identifying the specific drivers of dietary specialization for individual species requires further research. Bolnick et al. (2003) confirmed that dietary specialization is maintained within a given population due to disruptive selection, where specialists in specific environments can outcompete their generalist conspecifics with respect to reproductive success. Although this is true in some environments, other studies have demonstrated that in ecosystems prone to environmental stochasticity, such as the Arctic, specialization may be detrimental to the individual, with ecological flexibility being advantageous in said environments (Thiemann et al. 2011; Galicia et al. 2021). Bolnick et al. (2003) also noted the importance of understanding individual resource acquisition to comprehend what drives specialization within a population.

Optimal foraging theory provides the fundamental knowledge base for understanding how an individual selects its resources by accounting for factors that would maximize the net benefit to the individual. Such factors include the rate of prey encounters, handling time, and predation risk, along with factors related to the individual's physiology (Afik and Karasov 1995), morphology (Price 1987), foraging experience (Werner et al. 1981), and search and handling behaviours (Goss-Custard and Durell 1983). The result of these factors interacting with one another and many environmental factors (e.g., social interactions, prey availability) can reasonably predict or explain an individual's resource usage.

It is also important to consider how phenotypic variations between individuals result in their selection of resources based on preference and resource-use efficiency. When phenotypic variation exists within a population, it results in functional variation, leading to differences in resource-use efficiency and preference. This functional variation is only possible if an individual's resource-use efficiency is constrained. The most plausible explanation for this constraint is ecological trade-offs (Bolnick et al. 2003). Trade-offs are situations in which a change in a given trait (such as a foraging strategy) results in increased fitness, while a simultaneous change to another trait results in a reduction in fitness. These trade-offs help to explain how specialists and generalists can coexist within the same population. Functional trade-offs can exist in many facets of foraging, including resource recognition, search efficiency (Bernays 1998), and resource handling (Robinson 2000). It is these functional trade-offs that allow for specialist individuals to specialize on one prey type, while a generalist might be adequate at the capture and handling of more than one (Bolnick et al. 2003).

Examples of Dietary Specialization

Over the years, there have been an increasing number of studies identifying specialization across many taxa. A study by Aguiar-Santos et al. (2022) investigated the impacts of river fragmentation on dietary specialization in two subpopulations of the Amazonian predatory fish, *Cichla temensis*. Using stable isotope analysis, they determined the extent of dietary specialization in fish inhabiting fragmented and undammed rivers in the Uatumã River basin of the Amazon. The study's results demonstrated that undammed rivers seemed to promote dietary specialization compared to fragmented rivers (Aguiar-Santos et al. 2022). This study illustrates how various life history traits or extrinsic factors can drive specialization. Hall et al. (2021) investigated dietary specialization as it related to age and sex and their impact on seasonal resource partitioning in the migratory shorebird, the western sandpiper (*Calidris mauri*). The study demonstrated that specialization differed between demographic groups and seasons, with interindividual diet composition being similar in the winter but vastly different in the spring. Differences in diet composition in the spring were correlated with bill length and body mass explaining 31% of the variation in diet. This finding indicated that there might be reduced intraspecific competition for resources at the onset of the western sandpiper breeding migration in the spring (Hall et al. 2021). Mammalian dietary specialization was investigated in a study by Jory et al. (2021) that examined individual- and population-level dietary specialization in the St. Lawrence Estuary fin whale (*Balaenoptera physalus)* population. Jory et al. (2021) discovered that as the primary prey of the fin whale, Arctic krill (*Thysanoessa* spp.), decreased in biomass, nearly 60% of individuals demonstrated a widening of their dietary niche width to adopt generalist foraging strategies. The abrupt declines in Arctic krill resulted in a population once composed of both Arctic krill and lipid-rich pelagic fish specialists to become a population composed of either Arctic krill specialists or dietary generalists who fed on zooplankton and fish. Although the fin whale population in the St. Lawrence Estuary was once composed almost entirely of specialists, adopting generalist foraging strategies likely coincided with declines in intraspecific competition (Jory et al. 2021).

Dietary Specialization in Polar Bears

To date, Thiemann et al. (2011) is the only study to investigate individual dietary specialization in an Arctic marine carnivore such as the polar bear, *Ursus maritimus*. Using quantitative fatty acid signature analysis (QFASA; Iverson et al. 2004; Bromaghin 2017), as well as an index of longitudinal dietary change, Thiemann et al. (2011) were able to determine the extent of dietary specialization in 64 individual polar bears sampled in Western and Southern Hudson Bay between 1994 and 2003. The study focused on four primary hypotheses: (1) Adult male bears would be most likely to demonstrate temporally variable diets; (2) Subadult bears would have limited variability and diversity in their diets; (3) Females with dependent cubs would be most likely to have the least variable diets; and (4) The variability of the diet of solitary females would likely fall between the highly variable diets of adult males and the low variable diets of females with dependent cubs.

The proportional similarity index (PS_i) was used to quantify individual specialization by determining the extent of overlap of an individual's diet with that of the population (Feinsinger et al. 1981; Bolnick et al. 2002). To gain a measure of how diets varied through time, Thiemann et al. (2011) developed the dietary change index (*DCI*), where an individual bear was scored on a scale from 0 (unchanged diet) to 2 (complete replacement of the prey items previously present). Using these metrics, Thiemann et al. (2011) determined that adult males had the most temporally variable diets, as predicted. They also found that all adult female bears seemed to demonstrate similar dietary metrics, regardless of the presence or absence of cubs. As was expected, subadult bears did not exhibit the same levels of dietary diversity as adult males, with adult male bears having the most diverse and variable diets over time. Adult males were also shown to be the most likely to be bearded seal (*Erignathus barbatus*) specialists, with bearded seal consumption correlating with dietary specialization (Thiemann et al. 2011).

Climate Change

Sea ice is the foundation of the Arctic marine ecosystem, playing a vital role in primary productivity (Laidre et al. 2008). Beyond establishing the Arctic marine food web, the sea ice is also a vital component to the survival of higher trophic level species such as marine mammals and polar bears. Many ice-dependent species of seals utilize the sea ice for reproduction and overwintering (Lowry et al. 1980; Tynan and Demaster 1997), while polar bears depend on the sea ice for hunting, movement, reproduction, and even maternal denning (Stirling and Archibald 1977; Smith 1980). Given that the Arctic is predicted to undergo accelerated climate warming, ice-dependent species are faced with increasing interannual variability in climate and sea ice concentration (Hughes 2000), which may drastically alter prey availability and distribution, leading to declines in predator survival (Tynan and Demaster 1997). Higher trophic-level species, such as the polar bear, will likely have to adopt a more flexible foraging strategy in response to increasing interannual changes in prey availability or risk food stress and starvation as sea ice diminishes (Stirling and Derocher 1993).

As studies continue to predict rapid declines in the population sizes of the southernmost polar bear subpopulations (Molnár et al. 2010, 2011, 2020), conservation efforts must be directed at investigating and quantifying how climate change will impact individuals within these regions. With non-linear declines in population size predicted to occur with increasing sea ice loss (Stirling and Parkinson 2006; Regehr et al. 2007), it is important to develop a mechanistic understanding of the impacts on polar bears. By investigating the foraging patterns and strategies used by individual polar bears, researchers will be better able to determine the influence these strategies may have on polar bear demographics and population size. Understanding how the effects of climate warming may vary between dietary specialists and dietary generalists will allow researchers to more accurately predict how these effects will influence bears at the individual level and assess the implications for population-level demographics.

Thesis Objectives and Organization

The objective of this research was to determine the extent to which dietary specialization exists and identify the intrinsic (age, sex, reproductive status) and extrinsic drivers (habitat conditions, sea ice loss) that influence individual dietary specialization in polar bears in the Western Hudson Bay subpopulation. The thesis is organized into three chapters, with Chapter I and Chapter III serving as introductory and conclusion chapters, respectively. *Chapter II, Dietary Specialization in a Marine Top Predator: An Evaluation of the Extent and Drivers of Specialization in Western Hudson Bay*, was a re-evaluation of the extent of individual dietary specialization as well as an examination of the intrinsic and extrinsic drivers of specialization in polar bears in Western Hudson Bay. The first and only previous study to examine dietary specialization in polar bears was conducted by Thiemann et al. (2011). The study examined the extent of dietary specialization in polar bears in the Western and Southern Hudson Bay subpopulations from 1994 – 2003. This thesis utilized similar methodology to examine individual specialization in Western Hudson Bay between 2004 and 2021, while exploring additional intrinsic and extrinsic drivers. The extent of dietary specialization was determined by investigating long-term trends in individual diet composition. Drivers of individual dietary specialization were examined in relation to an individual's proportional similarity index (PS_i) to determine their relative influence on specialization.

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Chapter II – Dietary Specialization in a Marine Top Predator: An Evaluation of the Extent and Drivers of Specialization in Western Hudson Bay

Introduction

Individual dietary specialization, or intrapopulation niche variation, refers to individuals occupying a distinctly narrow dietary niche within the population niche or individuals that demonstrate a limited overlap with the population niche (Roughgarden 1974; reviewed by Bolnick et al. 2003; Sargeant 2007). According to optimal foraging theory and the dietary niche concept, feeding strategies, such as dietary specialization, are continuously influenced by the abundance or the quality of available resources (Hutchinson 1957; noted in Jory et al. 2021). A population's ability to adapt to changing resource availability is dependent on the extent of dietary specialization within the population (Bolnick et al. 2003). Several studies have noted the implications of dietary specialization on an individual's ability to adapt to variations in resource availability (see Galicia et al. 2021), demonstrating that dietary specialists are generally less capable of adapting to changes in resource abundance or distribution compared to generalist foragers (Kassen 2002).

Foraging opportunities have been shown to vary based on an individual's size, movement patterns, or reproductive status, resulting in intraspecific differences in foraging habits and strategies. Patterns of individual specialization within a population likely arise in response to prey-specific foraging requirements (Estes et al. 2003), intraspecific competition (Schindler et al. 1997; Tinker et al. 2008), or due to variability in resource distribution and abundance (Woo et al. 2008). In some cases, individual foraging strategies have been shown to endure over time, with some individuals passing these strategies to their offspring (Estes et al. 2003; Lillie et al. 2018).

Within populations, the degree of individual dietary specialization can be influenced by both intrinsic (phenotypic constraints) and extrinsic drivers (environmental conditions) (Stephens and Krebs 1986). Intrinsic drivers are phenotypic characteristics that impact an individual's ability to access prey items. These characteristics could include an individual's sex, age, and body size and the effects these traits would have on their foraging experience or dominance (Thiemann et al. 2011). Extrinsic drivers are environmental conditions related to ecological factors that impact the abundance and richness of the available prey items. Both the richness and species evenness of food sources available to an individual significantly influence their foraging decisions (Stephens and Krebs 1986). This is best seen in studies in which individuals begin to access alternative sources of food in times of resource instability or declines in primary prey abundance (see Galicia et al. 2021).

Factors such as intraspecific competition, interspecific competition, ecological opportunity, and predation determine the extent of interindividual diet variation. Empirical evidence demonstrates that intraspecific competition positively correlates with the degree of specialization within a population, with high population density resulting in higher levels of individual specialization (Svanbäck and Persson 2004). In an experimental population of stickleback (*Gasterosteus aculeatus*), competition was found to drive increased specialization and an increased population niche width via interindividual variation over a two-week experimental period (Svanbäck and Bolnick 2007). This result suggests that behavioural plasticity plays a vital role in resource use as population density increases. Interspecific competition typically reduces individual specialization, but this is not always the case. (see Bolnick et al. 2010). Interspecific competition is often more substantial in species-rich environments, reducing individual specialization. For example, individual Arctic charr

(*Salvelinus alpinus*) demonstrated greater resource use variation in a lake with primarily Arctic charr compared to a nearby lake with greater species richness (Knudsen et al. 2007).

Ecological opportunity involves expanding foraging opportunities available to an individual and is dependent on habitat diversity, environmental stochasticity, and resource diversity (Araújo et al. 2011). Individual specialization should increase as ecological opportunity increases within a population (Roughgarden 1974). An example of this can be seen in grey wolves (*Canis lupus*), in which resource diversity was positively correlated with individual specialization (Darimont et al. 2009). As prey abundance in an environment changes or prey types undergo behavioural modification in response to predation, the degree of specialization can be affected. Eurasian perch (*Perca fluviatilis*) young of the year were exposed to two habitats (pelagic or littoral). When an adult predatory perch was present in one of the habitats, individual specialization was reduced as the young perch would take refuge in the habitat devoid of predatory fish and begin to specialize on habitat-specific prey. The result was a trade-off between predator avoidance and resource acquisition, which could lead to morphological changes in developing perch (Eklöv and Svanbäck 2006).

Individual dietary specialization has been observed in species of fish (Schindler et al. 1997), birds (Partridge 1976; Woo et al. 2008), herbivores (Herath et al. 2021), and mammalian predators (Estes et al. 2003; Tinker et al. 2008; Thiemann et al. 2011; Balme et al. 2020). Several studies have investigated the extent and drivers of individual specialization in populations of mammalian predators. In a study conducted by Jory et al. (2021), individual- and population-level dietary specialization was examined in a marine predator, the fin whale (*Balaenoptera physalus*). The study demonstrated a significant change in the dietary niche width of the whale when individuals were exposed to declines in their primary prey, Arctic krill (*Thysanoessa* spp.).

Nearly 60% of individuals exhibited a widening of their dietary niche to adopt generalist foraging strategies (Jory et al. 2021). In another study by Balme et al. (2020), dietary specialization was quantified in a solitary mammalian predator, the leopard (*Panthera pardus*). Dietary specialization was identified most in male leopards, likely due to their large size, and individuals with greater access to prey tended to be more specialized. This result indicated that ecological opportunity was a significant determinant in the extent of individual specialization in solitary predators. Balme et al. (2020) also demonstrated a disadvantage of dietary specialization during periods of environmental stochasticity, with specialist males interacting with fewer resident females, resulting in fewer cubs born in their home ranges compared to generalist males.

The Arctic is a particularly variable environment in which resource distribution occurs seasonally, resulting in strong trophic interactions (Post et al. 2009). Large, Arctic mammals are susceptible to the rapidly changing environment and associated variability in resource distribution (Laidre et al. 2008). The polar bear (*Ursus maritimus*) is a top Arctic predator that feeds primarily on ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) (Stirling and Archibald 1977; Thiemann et al. 2008). As their primary food source, polar bears are reliant on ringed and bearded seal populations, with previous studies demonstrating a correlation between polar bear and ringed seal abundance (Stirling and Oritsland 1995). This dependency on ringed seals could prove to be problematic, as significant variation in the survival and reproductive success of ringed seals occur interannually (Smith and Stirling 1975; Stirling 2002). Studies have shown that climate warming has caused substantial losses to annual sea ice availability, reducing access to ringed seals, and leading to food stress in polar bears (Stirling and Derocher 1993; Derocher 2004). However, in times of food stress, polar bears that exhibit a generalist feeding strategy may also turn to alternative prey sources to supplement losses experienced by reduced access to primary prey (Thiemann et al. 2008; Galicia et al. 2021b).

Only one previous study has investigated individual dietary specialization in polar bears. Thiemann et al. (2011a) assessed the extent of individual dietary specialization within the Western and Southern Hudson Bay subpopulations of polar bears and investigated potential intrinsic drivers (e.g., age and sex) that may influence dietary specialization. The results of this study revealed that adult male bears were most likely to be dietary specialists, with many male bears being defined as bearded seal specialists, specifically. Adult male bears were also shown to have the greatest dietary diversity and flexibility (Thiemann et al. 2011). Alternatively, subadults and adult female polar bears were shown to have much narrower diets with less dietary flexibility, relying more heavily on ringed seal availability. The heavy reliance on a single prey species could result in increased vulnerability of females and subadults to climate-induced changes in prey availability (Ferguson et al. 2005; Stirling 2005).

As global temperatures rise, the Arctic is experiencing annual sea ice loss at an accelerated rate of -10.2 ± 0.8% per decade (1979 – 2018; Kumar et al. (2020). The loss of sea ice in the Arctic is detrimental on a global scale but directly impacts the dynamics of Arctic food webs (Peacock et al. 2010; Post 2017). As an apex predator, the polar bear relies on the sea ice for hunting, mating, and travel, all of which are vital to their survival in the Arctic. In years when global temperatures are higher, we see an extended open-water period, in which many polar bears across the circumpolar north are forced to fast onshore (Derocher 2004). Warmer temperatures are driving an early spring sea ice break-up and a delayed winter freeze-up (Lam et al. 2022). Warming temperatures can also affect precipitation, with monthly snow depth declining as temperatures increase (Ferguson et al. 2005). Annual changes in temperature and snow depth can negatively impact seal recruitment and survival during pupping season in the spring (Ferguson et al. 2005). Like temperature, the North Atlantic Oscillation (NAO) and Arctic Oscillation (AO) can significantly affect annual sea ice conditions in the Arctic (Hurrell J.W. 1995). The NAO describes the variability in two recurring atmospheric pressure patterns centred over the North Atlantic Ocean (Visbeck et al. 2001), while the AO describes variability in pressure between the mid-latitudes of the North Atlantic and Pacific oceans and the Arctic. $NAO_{(t-1)}$, the previous year's NAO index, is highly correlated with the subsequent year's sea ice conditions (Stern and Heide-Jørgensen 2003). Given its correlation with sea ice conditions, $NAO_{(t-1)}$ was also a strong predictor of ringed seal recruitment (Ferguson et al. 2005). Given the effects these environmental variables have on sea ice and seal survival, these variables may also have a powerful effect on the foraging ecology of polar bears.

Polar bear foraging habits and diet composition have been studied extensively via the trophic transfer of fatty acids (e.g., Thiemann et al. 2011a; Galicia et al. 2016). Dietary fatty acids are directly incorporated into the adipose tissue of a predator as a result of biochemical restrictions on fatty acid synthesis (Iverson et al. 2004). Using quantitative fatty acid signature analysis (QFASA), the fatty acid profile of the predator can be compared with fatty acid profiles of potential prey species to estimate the relative proportion of each species in the diet of the predator (Iverson et al. 2004; Budge et al. 2006). By comparing fatty acid profiles, QFASA can provide estimates of individual diet composition over weeks or months (Iverson et al. 2004; Thiemann et al. 2022).

In this study, I aimed to use QFASA to identify the extent and drivers of dietary specialization in polar bears in the Western Hudson Bay. My research sought to address the following hypotheses: (1) I hypothesize that individual specialization will be present in the population because polar bears exhibit characteristics that encourage specialization, such as intraspecific competition, low interspecific competition, and behavioural plasticity (Araújo et al. 2011). (2) I hypothesize that adult male bears will show the highest degree of individual specialization because their large body size allows them to exploit prey unavailable to other age and sex classes. (3) I predict solitary females will exhibit a greater degree of dietary specialization than females with dependent cubs because mothers will avoid areas with infanticidal males, limiting their access to a range of prey types. (4) In years where sea ice break-up occurs later, I predict that higher levels of dietary specialization will be observed, as bears can remain on the ice and hunt, allowing for selective feeding. (5) The previous winter's NAO strongly correlates with the sea ice break-up date (Stern and Heide-Jørgensen 2003), with earlier break-up resulting in lower ringed seal pup survival, increasing intraspecific competition among polar bears. Therefore, when the previous year's NAO is high, I predict that the degree of specialization will be higher due to increased competition. (6) Dietary specialization is predicted to be greater when snow depth is lower, as seal reproduction has been shown to correlate with snow depth (Hezel et al. 2012). If snow depth is lower, seal recruitment and survival will decrease, resulting in greater intraspecific competition among bears.

Methods

Capture and Sample Collection

Adipose tissue samples were collected from individual polar bears in the Western Hudson Bay (WH) subpopulation in Northeastern Manitoba from 2004 to 2021 (Figure 2.1.). Capture of the bears and the subsequent adipose tissue sampling was conducted by Environment and Climate Change Canada during the fall open-water period (August – September). During annual sampling in the fall, the same individual bears were often sampled in multiple years. Polar bears were located from a helicopter and immobilized via remote injection of 8-9 mg of Telazol® (Fort Dodge Laboratories, Fort Dodge, Iowa, USA or Zoletil®, Virbac S.A., Carros, France) per kg of body weight (Stirling et al. 1989). Once immobilized, bears that had not been previously captured were fixed with an identification tag in each ear and tattooed with the associated identification number on the inside of the upper lip. A vestigial premolar tooth was extracted and sectioned to determine age of independent bears which had not been captured previously (Calvert and Ramsay 1998). Bears were categorized by age as either cubs of the year (COY, < 1 year), yearlings (dependent cubs, 1 year), two-year-olds (dependent or independent, 2 years) subadults (independent bears, 2.5-4 years), or adults (≥ 5 years) (Sciullo et al. 2016). Adult female bears were additionally classified based on their reproductive class: solitary adult females, adult females with COY, adult females with yearling cubs, and adult females with two-year-old cubs (Sciullo et al. 2017). A subcutaneous adipose tissue sample was collected from each bear using an 8 mm disposable biopsy punch (Miltex Inc., York, Pennsylvania), approximately 15 cm lateral to the base of the tail (Ramsay et al. 1992; Thiemann et al. 2006). Samples were stored at -20°C until analysis. Handling procedures were reviewed and approved on an annual basis by the Animal Care and Use Committees at York University and Environment Canada (Prairie and Northern Region). Table 2.1. and Table 2.2. summarize sample collection across age and sex classes.

Laboratory Analyses

Subcutaneous adipose tissue samples were prepared for analysis by removing epithelial tissue and fur from the tissue biopsies. To determine the fatty acid composition of each sample, the Folch extraction method (Folch et al. 1957), modified by Iverson et al. (2001) was used to extract and isolate lipid. Fatty acid methyl esters (FAME) were derived from the extracted lipid using sulfuric acid as a catalyst (Thiemann et al. 2004; Budge et al. 2006). Samples were analyzed in duplicate via temperature-programmed gas-liquid chromatography, utilizing the Perkin Elmer Autosystem II capillary gas chromatograph and flame ionization detector (Agilent Technologies, Palo Alto, California, USA; Budge et al. 2006). Fatty acids were classified according to the nomenclature, $A{:}Bn - X$, where A represents the length of the carbon chain, B refers to the number of double bonds, and – X indicates the position of the first double bond, relative to the terminal methyl group. Individual fatty acids were quantified as the mass percent of all fatty acids ± standard error of the mean (SEM) contained within the lipid sample (Table 2.3.; Budge et al. 2006). Fatty acid analysis was limited to those fatty acids that occurred in a proportion of $> 0.1\%$ of the total fatty acid composition (Budge et al. 2012). I used Compass CDS software (Version 3.0, Bruker Daltonics Inc., Germany) to verify all fatty acid identifications based on retention time (Budge et al. 2006).

Diet Estimation

Polar bear diet composition was estimated using the quantitative fatty acid signature analysis (QFASA) method of Iverson et al. (2004). This approach has been widely used to estimate the diets of marine and Arctic predators, including polar bears (e.g., Thiemann et al. 2008; Galicia et al. 2016; McKinney et al. 2017). During QFASA, a predator's fatty acid profile or "signature," is modelled as a linear combination of mean prey signatures. Diet is estimated by identifying the combination of prey signatures that minimizes the distance between the observed and modelled predator while accounting for patterns of fatty acid metabolism using calibration coefficients (Thiemann et al. 2008). The original QFASA methodology developed by Iverson et al. (2004) was modified to utilize the Aitchison distance between the observed and modelled predator signatures, as outlined by Bromaghin et al. (2015, 2016a). The diet estimates of the bears reflect individual diet composition in the weeks or months before samples were collected, thought to span approximately 30 to 90 days (Iverson et al. 2004; Thiemann et al. 2022).

A prey library is a collection of prey fatty acid signatures used in the QFASA model to estimate predator diets. For QFASA to accurately quantify predator diets, the prey library must include fatty acid profiles for all known prey types consumed by the predator. The fatty acid profiles of prey types can also affect estimation precision, as prey types with similar fatty acid profiles can result in prey confounding and, thus, inaccurate diet estimates (Bromaghin et al. 2017a). I used diagnostic functions within the R package qfasar (version 3.2.3) (Bromaghin 2017), leave-one-prey-out (LOPO), and divisive magnetic clustering (DIMAC) to investigate the prey library for confounding between prey types and variability within prey types (Bromaghin et al. 2016b). A LOPO analysis in qfasar examines the distinctiveness of prey types by temporarily removing a single signature from the prey library and estimating it as if it were a predator (i.e., determining the combination of remaining signatures that best matches the removed sample), and returning the signature before repeating the process for every signature. The mean “diet” estimate is then computed for each prey type. If a prey type is correctly identified each time, then the fatty acid signatures for that prey type are highly distinctive from other prey types in the library. However, prey types are not always perfectly estimated, and thus, the degree of confounding is a result of the extent of prey signatures attributed to incorrect prey types (Bromaghin 2017).

Structure within prey types can form when some individuals are more similar to each other (i.e., forming a cluster) than other members of the same prey type. Clusters can form due to spatial or temporal variability in fatty acid composition within a species. The DIMAC function investigates structure within a prey type by clustering individuals more similar to one another than the rest of their prey type. When all signatures were clustered, a partitioned prey library was created, and diet estimates were run with the original and partitioned prey library to assess the library's performance (Bromaghin et al. 2017a).

An established marine mammal prey library for Western Hudson Bay, developed by Sciullo et al. (2017), was used for diet estimation. The marine mammal prey database was composed of fatty acid signatures derived from the blubber samples of bearded seal (n = 33), beluga whale (*Delphinapterus leucas*; n = 37), harbour seal (*Phoca vitulina*; n = 17), harp seal (*Pagophilus groenlandicus*; n = 42), ringed seal (n = 98), and walrus (*Odobenus rosmarus*; n = 21). Predator fatty acid data was compiled for polar bears sampled in Western Hudson Bay during August and September from 2004 – 2021, excluding 2020. A total of 1,373 samples were used as predator samples for diet estimation.

Fatty acid sets (or suites) are supplied to QFASA models to indicate which fatty acids should be used to estimate diet. Analyzing marine lipids can return over 70 fatty acids, which are not all relevant to diet estimation due to predator metabolism. I generated diet estimates using 29 fatty acids outlined by Florko et al. (2021). A calibration coefficient must be provided for each fatty acid to account for fatty acid-specific metabolism in the predator (Budge et al. 2012). Calibration coefficients are typically derived from a ratio of the quantity of the fatty acid present in the adipose tissue of the predator relative to the quantity present in a known, controlled diet (Iverson et al. 2004). This study used published calibration coefficients derived from captive feeding studies of mink (*Mustela vison*; Thiemann et al. 2008) and grizzly bears (*Ursus arctos*; Thiemann et al. 2022). Calibration coefficients can also be estimated computationally using only prey and predator fatty acid data (i.e., simultaneous diet and calibration estimation; Bromaghin et al. 2017b). I compared diet estimates produced using empirically derived calibration coefficients in the qfasar package with estimates from simultaneously estimated calibration coefficients produced using the R package QFASA. All QFASA estimates were run in R (version 4.2.3) (R Foundation for Statistical Computing, Vienna, Austria) using the package qfasar (Bromaghin et al. 2016b; Bromaghin 2017) or the package QFASA (Stewart et al. 2022).

A total of six iterations of the QFASA model were run to estimate diet, summarized in Table 2.4. A set of calibration coefficients and a fatty acid suite were defined for each iteration. Calibration coefficient sets were either empirically derived from mink (Thiemann et al. 2008) or grizzly bear (Thiemann et al. 2022) feeding trials or simultaneously estimated along with the diet estimates (Bromaghin et al. 2017b). Fatty acid suites were based on either Florko et al. (2021) (29 fatty acids) or the Thiemann et al. (2022) set of fatty acids (22). The resulting iterations were coined as Mink All, Mink Marine, Dog Food + Salmon, Dog Food + Anchovy, Sim-29FA, and Sim-22FA. Diagnostic testing was performed for each iteration to evaluate the estimation performance of each calibration coeffcient set. Signature and calibration coefficient consistency was assessed using the function pred_beyond_prey() of the qfasar package. Pred_beyond_prey() was used to determine the predator signature proportions that fell beyond the scope of the mean prey signature proportions. When a model demonstrates a high proportion of predator signatures outside the range of prey signatures, it is assumed that the prey library is missing prey species or the calibration coefficients are imprecise. The results of the predator beyond prey analysis were evaluated for each fatty acid to identify the effects of individual fatty acids on signature consistency. The top five scoring fatty acids based on the sum of predator-beyond-prey values for a given fatty acid were compared for each calibration coefficient set and fatty acid suite combination to determine if there were any consistently problematic fatty acids. These fatty acids would need to be removed from the analysis to ensure proper identification of prey items in the diet. All diagnostics were performed in the qfasar package in R (Bromaghin 2017).

Habitat and Sea Ice Metrics

Extrinsic drivers of specialization included in this study were Arctic Oscillation (AO), North Atlantic Oscillation (NAO), annual sea ice break-up, and snow depth. AO and NAO values were obtained from the National Oceanic and Atmospheric Administration of the National Centers for Environmental Information (https://www.ncei.noaa.gov/). NAO values were collected and averaged for the months of December to February betweeen 2004 and 2021 (Ferguson et al. 2017). Previous research indicated that the previous year's NAO index ($NAO_{(t-1)}$) is strongly correlated with the current year's sea ice conditions (Stern and Heide-Jørgensen 2003), and so, both NAO and $NAO_{(t-1)}$ were included along with AO and $AO_{(t-1)}$.

Annual spring break-up dates, as well as the duration of the ice free season for the period of 2004 – 2021 were generously provided by Dr. Nick Lunn and Environment and Climate Change Canada. The sea ice break-up date was defined as the day in which the sea ice concentration fell and remained below 50% (Stirling et al. 1999). As a result of collinearity between the break-up dates and the length of the open water period, the latter was removed from analysis. Snow depth data was obtained from the Government of Canada's historical weather database (https://climate.weather.gc.ca/historical_data/search_historic_data_e.html). Snow depth data was collected and averaged across eight research stations along the Southern and Western coasts of Hudson Bay. The weather stations included in the study were located in Churchill, Arviat, Rankin Inlet, and Whale Cove. Daily snow depth data was collected for the months of April and May from each station with available data and averaged per day. Daily averages were then averaged to obtain an annual value.

Statistical Analysis

I used generalized linear mixed effects models (GLMMs) to determine if differences existed in polar bear diet composition across age and sex classes. A series of GLMMs with a beta regression and logit link function were structured using individual prey types as the response variable, while the interaction between age, sex, and ‘dependent,’ a binomial factor created to account for a potential correlation between mothers and their cubs, were used as fixed effects. Individual bears and the sampling year were included as random effects. In subsequent models, year was treated as a fixed effect to investigate temporal trends in diet. A Bonferroni correction was used to evade the risk of a type I error by adjusting the level of significance ($\alpha = 0.008$) for multiple comparison testing between prey items that make up the diet composition of the bears (Curtin and Schulz 1998).

Dietary niche breadth was calculated using the Shannon-Wiener index (*H’*) for each sample, to provide an estimate of the dietary diversity for each individual:

$$H' = -\sum_{j=1}^{S} p_j \ln p_j$$

where p_j represents the proportion of a given prey species, j, and S represents the number of prey species consumed by all bears. Dietary diversity was evaluated using a series of linear mixed effects models (LMM) where the Shannon-Wiener Index was used as the response variable. Age, sex, and 'dependent' were used as fixed effects, while sampling year and bear ID were included as random effects. Dietary niche breadth was first analyzed across the entire population, before investigating age and the effect of dependency on each sex separately.

The dietary change index (*DCI*) developed by Thiemann et al. (2011) was used to determine the degree to which individual diets of bears changed through time:

$$DCI = \sum_j \left(\frac{\sum_{y-1} \left| p_{jt} - p_{jt-1} \right|}{y-1} \right)$$

where y is the number of years in which the bear was captured, p_{jt} is the proportion of a given prey item, j, sampled in year t. The *DCI* is a summative value that indicates the average annual change in the proportion of each prey item consumed. The *DCI* values range from 0, indicating a consistent diet, to 2, indicating a total replacement of prey items. Only bears sampled two or more times within the same age class (n = 221) were used to investigate *DCI* to account for potential ontogenetic shifts in the diet. Kruskal-Wallis rank sum tests were used to evaluate significance between age classes, sex, and reproductive status in the *DCI* values. To simplify the analysis, females with COY, two-year-old cubs, and yearling cubs were amalgamated to investigate any female with dependent cubs. Significant values were further explored using a post-hoc Dunn's Test with a Bonferroni correction.

The extent and drivers of dietary specialization within the subpopulation were assessed using the proportional similarity index (PS_i). PS_i was used to demonstrate dietary specialization by comparing the overlap between an individual's diet and that of the population (Feinsinger et al. 1981). The population diet was considered the average diet composition for all bears sampled throughout the study period. If an individual is specialized, their diet should minimally overlap with the population, returning a low PS_i value. PS_i was determined for each individual using

IndSpec1 (Bolnick et al. 2002). To evaluate the extent of specialization within the Western Hudson Bay subpopulation, any bear with a PS_i value of ≤ 0.50 was deemed to be a specialist. Given that low PS_i values are characteristic of specialists while high PS_i values are characteristic of generalists (Feinsinger et al. 1981; Bolnick et al. 2002), a PS_i value of ≤ 0.50 was selected as the threshold to categorize an individual as a specialist. Trends in age class and sex were investigated with respect to an individual's degree of specialization (PS_i). I investigated the relationships between the dietary niche breadth, the dietary change index, and the proportional similarity index by running a series of Kendall Rank Correlation tests to determine the correlation strength between each dietary metric.

A series of GLMMs, with PS_i as the response variable, were used to determine the effects of intrinsic and extrinsic drivers on an individual's degree of dietary specialization. A GLMM was run for the total population, followed by a series of GLMMs used to analyze the sexes independently since sex was shown to be a strong predictor of specialization (see Results). For the population model, sex, age, dependent, snow depth, AO, $AO_{(t-1)}$, NAO, $NAO_{(t-1)}$ and the annual break-up date were modelled as fixed effects, while bear ID and the sampling year were used as random effects. The male bear model closely resembled the population model, apart from the inclusion of sex. In contrast, the female model included reproductive stage as an additional fixed effect. Bear ID and the sampling year were used as random effects. Model outputs were then run through the function glmmTMB:::Anova.glmmTMB() to obtain the chi-squared value, degrees of freedom and the p-value. All models were evaluated for multicollinearity, singularity, and overdispersion using the performance package in R (Lüdecke et al. 2021). The level of significance is $\alpha = 0.05$ unless otherwise stated.

Results

Diet Estimate Method Evaluation

The prey library diagnostic testing involved a leave-one-prey-out (LOPO) analysis and divisive magnetic clustering (DIMAC). The LOPO diagnostic returned a value of 78.3% for the mean proportion of prey correctly estimated across all prey types, unweighted by the sample size of each prey type. The proportion of correctly estimated signatures for all individuals, regardless of the type of prey, resulted in 75.5% of signatures correctly estimated. The DIMAC function found no evidence of substructure within prey species, indicating minimal spatial or temporal variability in fatty acid composition within a prey type. Thus, the partitioned and original prey libraries performed comparatively, and the original prey library was used for diet estimation. The top five fatty acids resulting in predator signatures going beyond the range of prey signatures were investigated by utilizing the results of the pred_beyond_prey diagnostic. No single fatty acid seemed to score high across all models consistently; therefore, no fatty acids were eliminated prior to analysis.

Considering previous studies of polar bear diets (e.g., Thiemann et al. 2008), the diet estimates produced by estimating diets and calibration coefficients simultaneously (i.e., the simultaneous method) were not deemed to be ecologically plausible. The simultaneous estimates generated using the set of 29 fatty acids (Sim-29FA) identified harp seal as the dominant prey item. Estimates based on the set of 22 fatty acids (Sim-22FA) were more plausible but overestimated harp seal consumption relative to known evidence from Western Hudson Bay. For this reason, the simultaneous diet estimation method was not used to estimate diet in this study.

The remaining feeding trial calibration coefficient sets were assessed using diagnostic testing in the package qfasar. The pred_beyond_prey diagnostic test determined the percentage of predator signatures that fell outside the range of prey signatures. The Dog Food + Salmon method produced the lowest proportion of samples beyond the ranged of prey signatures at 0.267. The Mink All method had the second lowest score of 0.327, followed by Mink Marine (0.352) and Dog Food + Anchovy (0.403). Given that the pred_beyond_prey diagnostic testing results showed comparable results between the calibration coefficient sets, the final diet estimates were produced by averaging the Mink Marine and Mink All diet estimates as per Thiemann et al. (2008). Given their extensive use in the literature, utilizing the mink diet estimates offers the greatest consistency and comparability with the existing literature. Mean diet estimates for each estimation method are summarized in Table 2.5 and Figure 2.2.

Dietary Habits

Ringed seal was a prominent prey item in the diets of both male and female polar bears in Western Hudson Bay, comprising an average of 40.2 ± 0.01% (Figure 2.3.). Many adult male polar bears demonstrated a significant proportion of bearded seal in their diets (36.3 ± 0.01%) compared to proportions observed in adult females (24.9 ± 0.01%), subadults (21.6 ± 0.02%), and dependent cubs (21.9 ± 0.01%). However, one adult female (X32037) demonstrated the greatest proportion of bearded seal observed, with a proportion of 95% in her diet. Harbour seal (15.9 ± 0.004%), beluga (7.6 ± 0.003%), and harp seal (4.3 ± 0.002%) contributed to smaller proportions in the diets, with walrus contributing trace amounts (3.9 ± 0.0015%; Figure 2.3.). The largest proportion of each prey type in a given individual's diet was bearded seal (95%), beluga (92%), harbour seal (85%), harp seal (88%), ringed seal (100%), and walrus (30%).

Across the study period, the mean percentage of bearded seal in the diet increased from 5.7 ± 1.2% in 2004 to 41.6 ± 2.1% in 2021, maintaining a steady increase throughout ($\chi2$ = 1133, df = 17, $p < 0.008$). The proportion of beluga whale in the diet was sporadic between 2004 and 2007 but remained relatively low from 2007 onwards, with only minor fluctuations ($\chi 2 = 646$, df = 17, $p < 0.008$). Harbour seal proportions declined throughout the study ($\chi 2 = 379$, df = 17, $p < 0.008$), beginning with a proportion of 18.9 ± 1.06% in 2004 and falling to only 8.7 ± 1.30% of the diet in 2021. In 2004, harp seals comprised 15.8 ± 1.60% of the diets but immediately fell to less than 1% in 2005. For the remainder of the study, harp seal proportions ranged from 1.2 ± 0.21% to 10.0 ± 1.52%. Ringed seal proportions were cyclical, with significant declines occurring in 2009, between 2015 and 2018, and 2021 ($\chi 2 = 243$, df = 17, $p < 0.008$; Figure 2.4.). Throughout the study, walrus proportions were reasonably consistent, slightly increasing from 2.1 ± 0.25% in 2004 to 5.8 ± 0.40% in 2021 ($\chi 2 = 475$, df = 17, $p < 0.008$). Temporal changes in diet composition are summarized in Figure 2.3. and Figure 2.4.

Sex was a strong predictor of diet composition for select prey items. Male polar bears derived a larger percentage (32.9 ± 0.009%) of their diet from bearded seal than did female bears (23.2 ± 0.008%; $R^2 = 0.794$, $\chi^2 = 57.70$, df = 1, $p < 0.008$). Female bears tended to consume more harbour seal than males ($R^2 = 0.558$, $\chi^2 = 7.72$, df = 1, $p = 0.005$), with females consuming an average of 16.7 ± 0.59% and males consuming 15.1 ± 0.56%. Harp seal was consumed in greater proportions by male bears (5.5 ± 0.39%) compared to female bears (3.1 ± 0.27%; $R^2 = 0.071$, $\chi^2 = 24.37$, df = 1, $p < 0.008$). The proportion of ringed seal in the diet seemed to be influenced by the interaction between age and sex ($R^2 = 0.873$, $\chi^2 = 8.03$, df = 1, $p = 0.005$), with younger female bears consuming greater proportions of ringed seal than both older and male bears (Figure 2.3.). The proportion of walrus in the diets of female bears was slightly higher on average (4.0 ± 0.14%) than in male bears (3.7 ± 0.16%; $R^2 = 0.526$, $\chi^2 = 21.61$, df = 1, $p < 0.008$). Age was another strong predictor of diet composition with the proportion of bearded seal

($\chi 2 = 29.69$, df = 1, $p < 0.008$, R = 0.11) and walrus ($\chi^2 = 10.66$, df = 1, p = 0.001, R = 0.026) increasing with age and the proportion of ringed seal decreasing with age ($\chi^2 = 34.42$, df = 1, $p < 0.008$, R = -0.11). None of age, sex, or the presence of an accompanying bear seemed to influence the proportion of beluga whale (Figure 2.3.). Examples of individual diet composition over time are represented in Figure 2.5.

At the population level, adult male bears showed the greatest dietary diversity (*H'* = 0.689 ± 0.015) compared to other sex and age classes (*H'* = 0.322 – 0.672; Table 2.6.). Overall, male bears demonstrated a broader dietary niche breadth than female bears ($R^2 = 0.424$, df = 1, F = 15.345, $p < 0.05$) across all age classes. Sex was also a strong predictor of dietary diversity, with male bears (0.653 ± 0.013) demonstrating higher average *H'* values compared to female bears (0.461 ± 0.010; $R^2 = 0.424$, df = 1, F = 15.345, $p < 0.05$). When analyzed separately, the age of female bears was not a strong predictor of dietary niche breadth, and thus, was not a strong predictor of dietary diversity ($R^2 = 0.408$, df = 1, F = 0.582, p = 0.446). However, in male bears, age was a strong predictor of dietary diversity ($R^2 = 0.390$, df = 1, F = 13.36, $p < 0.05$).

Between 2004 and 2021, 221 bears were sampled two to ten times each in Western Hudson Bay, for a total of 582 sampling events (Table 2.2.). The majority of bears sampled two or more times were adults (n = 218) with the remaining bears classified as subadults (n = 3). While age class showed no effect on an individual's *DCI* value (Kruskal-Wallis; p = 0.30), the sex of an individual showed significant differences between mean *DCI* values (Kruskal-Wallis; p = 0.015), with adult males (n = 118) demonstrating greater temporal variability in their diets compared to adult females (n = 100; Kruskal-Wallis; p = 0.031). Solitary adult females (*DCI* = 0.694; Bonferroni p = 0.006) and females with young cubs (*DCI* = 0.737; Bonferroni p = 0.004) showed greater temporal variation in their diets compared to subadult females (*DCI* = 0.193;

Kruskal-Wallis p = 0.006; Figure 2.6.). Results involving subadult bears should be interpreted cautiously due to the small sample size.

Extent of specialization

Out of the 1,373 samples collected from 2004 – 2021, 179 samples demonstrated a *PSi* value ≤ 0.50, indicating that 13.0% of the total samples collected emulated a more specialist style rather than a generalist feeding style (Figure 2.7.). PS_i values in the study ranged from 0.15 to 0.94, with the smallest (i.e., most specialized) value of 0.15 produced by a 15-year-old adult male bear sampled in 2011 and the largest value of 0.94 produced by a 13-year-old adult female bear sampled in 2016. Of the 179 samples demonstrating specialist tendencies, 58 samples were derived from female bears, with the remaining 121 samples from male bears. Although PS_i was not significantly different between age classes ($R^2 = 0.772$, $\chi^2 = 5.26$, df = 4, p = 0.26), the 179 samples were derived from 127 adult bears, 20 subadults, five two-year-olds, six yearlings, and 21 cubs of the year. The percentage of samples demonstrating individual specialization each year are outlined in Figure 2.8.

Throughout the study, 913 individual bears were sampled. Of the 913 individuals, 158 bears demonstrated a PS_i value of ≤ 0.50, indicating that 17.3% of the individual bears sampled emulated a more specialist rather than generalist feeding style. Of the 158 individual bears demonstrating specialist tendencies, 55 were female, and the remaining 103 were male. Although PS_i was not proven to be significantly different between age classes ($R^2 = 0.772$, $\chi^2 = 5.26$, df = 4, p = 0.26), the 158 bears were split between all five age classes. A number of the bears sampled multiple times throughout the study period were sampled across two or more age classes, making it difficult to summarize the number of individuals per age class that demonstrated specialization.

Examples of individual specialist and generalist diets across age and sex classes throughout the study period can be found in Figure 2.9.

A comparison of the dietary metrics revealed significant correlations between an individual's PSi, *DCI,* and *H'* values. Dietary niche breadth (*H'*) increased as the DCI increased (R = 0.09, $p < 0.05$). PS_i was negatively correlated with *H'*, with PS_i decreasing as *H'* increases (R = - 0.27, $p < 0.05$). PS_i was also negatively correlated with DCI, with PS_i values decreasing as DCI values increased (R = - 0.18, $p < 0.05$; Figure 2.10.).

Intrinsic Drivers

Sex, age, and the reproductive status of female bears were investigated as potential intrinsic drivers of individual specialization. A generalized linear mixed effects model (GLMM) investigating the relevant drivers of dietary specialization found that sex was a significant driver of specialization ($R^2 = 0.790$, $\chi2 = 13.68$, df = 1, $p < 0.05$), with males (n = 694; $PS_i = 0.643 \pm 0.006$) averaging a lower PS_i, and therefore greater degree of specialization compared to female bears (n = 679; $PS_i = 0.682 \pm 0.005$; Table 2.8.). Unlike sex, age across all samples was not a significant driver of specialization ($R^2 = 0.790$, $\chi2 = 3.27$, df = 1, p = 0.07). When sexes were analyzed separately, age strongly predicted specialization in male bears with older male bears demonstrating a greater degree of specialization compared to younger, dependent bears ($R^2 = 0.713$, $\chi2 = 0.04$, df = 1, p = 0.0026). Female bears, however, did not seem to demonstrate any significant trends in their degree of specialization with age ($R^2 = 0.834$, $\chi2 = 0.014$, df = 1, p = 0.90). The reproductive stage of females did not seem to affect specialization significantly. However, solitary female bears ($PS_i = 0.654 \pm 0.005$) tended to have lower PS_i values than females with dependent cubs ($PS_i = 0.678 \pm 0.006$), indicating a more generalist feeding style among family groups ($R^2 = 0.834$, $\chi2 = 9.49$, df = 7, p = 0.22). Differences in average PS_i between sex and age class are outlined in Table 2.7. and Figure 2.9.

Extrinsic Drivers

The generalized linear mixed effects model (GLMM) investigating the relevant drivers of dietary specialization also found that a combination of ecological factors helped to explain the variation in dietary specialization within the subpopulation over time. Snow depth was the strongest predictor of specialization, with PS_i decreasing as snow depth increased ($R^2 = 0.790$, $\chi2 = 8.34$, df = 1, $p < 0.05$). With a strong correlation between declining annual snow depth (April – May) and year (R = - 0.08, $p < 0.05$), it is unclear if the trend toward specialization will continue. North Atlantic Oscillation (NAO) also seemed to be a strong predictor of specialization, with PS_i values declining with higher NAO indices ($R^2 = 0.790$, $\chi2 = 6.12$, df = 1, p = 0.01).

When analyzed separately, individual specialization in male bears was best explained by annual snow depth and the NAO index. Like the total population, snow depth was the strongest predictor of male individual specialization ($R^2 = 0.713$, $\chi2 = 5.51$, df = 1, p = 0.02), with specialization increasing with increased snow depth. NAO was also a significant driver of specialization ($R^2 = 0.713$, $\chi2 = 4.45$, df = 1, p = 0.03) and increased as the NAO index increased. Individual specialization in female bears was also best explained by snow depth ($R^2 = 0.834$, $\chi2 =8.60$, df = 1, p = 0.003) and the NAO ($R^2 = 0.834$, $\chi2 = 4.94$, df = 1, p = 0.03). As snow depth increased, the degree of specialization would also increase, as seen at both the population level and in male bears. In years when the NAO index was more positive, female bears demonstrated a greater degree of specialization. Both the current and previous year's AO, the previous year's NAO, and the date of sea ice break-up did not strongly affect individual specialization. A summary of the model outputs can be found in Table 2.8. The models showed no evidence of multicollinearity, with all fixed effects returning low correlation. No evidence of singularity or overdispersion was found.

Discussion

Understanding the dietary habits of a species is necessary to assess the impacts of future climatic stress on a population. Although many studies consider the resource use of conspecifics equivalently, there have been numerous examples of populations in which a proportion of individuals demonstrate individual-level niche variation or specialization within their otherwise generalist populations (Bolnick et al. 2003). Individual dietary specialists are individuals within a population that exhibit a dietary niche that minimally overlaps with the population niche or individuals that use a small subset of available resources, resulting in a narrow dietary niche compared to the population. Within a generalist population, dietary specialists have been shown to coexist, suggesting a combination of spatiotemporal variation in prey availability on a decadal scale that may provide periods of advantageous foraging for both specialists and generalists (Woo et al. 2008).

In Western Hudson Bay, polar bears have primarily adopted a generalist foraging style, with a ranging degree of specialization occurring within the population. The results of this study add to the growing body of literature regarding generalist populations interspersed with specialist individuals and how understanding foraging dynamics at the population and individual levels is essential for the conservation and management of a species. This study identified both intrinsic (age, sex, reproductive stage) and extrinsic (snow depth, sea ice conditions) drivers of dietary specialization within the Western Hudson Bay subpopulation. The results demonstrated a significant degree of specialization with the subpopulation, with adult male bears showing a high degree of individual specialization compared to other age and sex classes. The reproductive stage of a female did not significantly impact her degree of specialization, but family groups were typically less specialized than solitary females. Additionally, the NAO and snow depth were strong predictors of specialization, while the date of sea ice break-up did not significantly impact individual specialization. These results are consistent with the original hypotheses, apart from the date of sea ice break-up which returned an insignificant result.

Diet Estimate Method Evaluation

Diet estimates were obtained by running a series of quantitative fatty acid signature analyses (QFASA) in the qfasar and QFASA packages in R. Individual model iterations differed in the calibration coefficients used, the R package, and the fatty acid suite. The most ecologically plausible estimates were derived from averaging the Mink Marine and Mink All diet estimates. The mink method estimated the population diet at 43.22 ± 0.24% ringed seal, 28.13 ± 0.62% bearded seal, 15.91 ± 0.41% harbour seal, 7.57 ± 0.30% beluga whale, 4.33 ± 0.24% harp seal, and 3.86 ± 0.11% walrus. My estimates for female bears align well with previously published estimates for polar bears in Western Hudson Bay between 2004 and 2014 (Sciullo et al. 2017), with the only notable difference in methodology being the R package used to produce the estimates (qfasar vs QFASA); despite this difference in methodology, the mean estimates for female bears were similar, which speaks to the accuracy of the diet estimate outputs across packages.

The QFASA iteration utilizing the calibration coefficients derived from captive grizzly bears fed either Dog Food + Salmon oil or Dog Food + Anchovy oil (Thiemann et al. 2022) produced dissimilar results that differed considerably from the mink-derived estimates. The mink-derived estimates were consistent with previously published results, thus providing confidence to the estimates. The diet estimates produced using the Dog Food + Salmon calibration coefficients resulted in questionable proportions of mean prey items in the diet. Most notably, mean bearded seal consumption was only 1.71 ± 0.15% of the diet. Given that bearded seal is a primary prey item for polar bears across the Arctic, we would expect to see a larger average proportion in the diets of the bears (Stirling 1974; Stirling and McEwan 1975; Stirling and Archibald 1977; Derocher et al. 2002). Comparatively, the mean value of bearded seal in this study was 28.13 ± 0.62%. Alternative prey sources for bears in the Western Hudson Bay are most commonly, beluga whale, harp seal, harbour seal, and walrus. The Dog Food + Salmon diet estimates seemed to largely overestimate the proportion of ringed seal (78.59 ± 0.50%) while underestimating the contributions of bearded seal, beluga whale, and harbour seal. Proportions of walrus and harp seal demonstrated comparative estimates.

Using stable isotope analysis of polar bear hair in Western Hudson Bay, Johnson et al. (2019) investigated the diet composition and isotopic niche size of bears from 1993 – 1994 and 2004 – 2016. They found that ringed seal was the dominant prey item for most age and sex classes (49% of the population diet), with adult females with young demonstrating the largest proportion (67%) compared to solitary females (51%), adult males (28%), and subadults (F: 59%, M: 53%). Bearded seal was found to be highest in the diets of adult male bears (29%), while harbour seal and harp seal proportions comprised 20% and 12% of the population diet, respectively. It should be noted that beluga and walrus were not included in this study, and therefore, the proportional diet comparisons should be interpreted with caution. However, given that the estimates in the Johnson et al. (2019) study, for example, still reflect and emulate previous and current dietary trends, it suggests that the estimates produced using the Dog Food + Salmon method were lacking. Although from a diagnostic perspective, the Dog Food + Salmon QFASA iteration was the strongest, from an ecological perspective, the estimates produced using this method were largely unsupported.

Similarly, the Dog Food + Anchovy QFASA iteration produced ecologically implausible diet estimates, with harbour seal diet estimates amassing 48.08 ± 0.69% of the population diet, while ringed seal made up only 43.91 ± 0.66%. Once again, bearded seal only contributed a small proportion (2.93 ± 0.24%) to the population diet, with beluga (0.40 ± 0.13%), harp seal (0.02 ± 0.02%), and walrus (4.66 ± 0.08%) contributing very little to the population diet. Although the ringed seal, harp seal, beluga, and walrus values were comparable to the average mink estimates, the overestimation of harbour seal and the underestimation of bearded seal in the diet was problematic. Although decreasing sea ice conditions may have positively impacted the abundance of harbour seals in Hudson Bay (Florko et al. 2018), it is unlikely that harbour seal proportions would be greater than the remaining alternative prey items combined. QFASA diagnostics demonstrated that this iteration did not perform the estimations well, with over 40% of the bear samples beyond the range of prey signatures, indicating an incomplete prey library or imprecise calibration coefficients. The latter is more likely, as these calibration coefficients have not been used in polar bear diet estimation. Also, given the smaller number of fatty acids used (22) compared to the 29 fatty acids in the mink analysis, it is possible that an estimation analysis using the Dog Food + Anchovy calibration coefficients with a larger fatty acid set could result in plausible diet estimates and should be investigated further.

To improve the quality and efficiency of the quantitative fatty acid signature analysis (QFASA) method of diet estimation, Bromaghin et al. (2017b) developed a new model to simultaneously estimate both the calibration coefficients for individual fatty acids and the diet estimates themselves. The model circumvents the existing criticisms of QFASA by eliminating any bias or uncertainty surrounding the inability to verify the accuracy of feeding trial-derived calibration coefficients (Bromaghin et al. 2017b). Utilizing this model, polar bear samples from Western Hudson Bay were run using either the mink fatty acid set or the grizzly bear fatty acid set. The resulting diet estimates for the 22 fatty acid simultaneous method (Sim-22FA) showed comparable estimates to the mink-derived estimates. However, the 29 fatty acid simultaneous method (Sim-29FA) demonstrated a stark contrast in harp seal proportions, with the Sim-29FA method estimating harp seal at over 40% of the diets.

In the Bromaghin et al. (2017b) study, the simultaneous estimation method was tested using data from Chukchi Sea polar bears. The resulting diet estimates showed greater dietary diversity and evenness than feeding trial-derived calibration coefficient diet estimates (Rode et al. 2014; Bromaghin et al. 2017b), a pattern consistent with the results of this study. The calibration coefficients derived using the simultaneous method and those derived from mink feeding trials (Thiemann et al. 2008) were comparable, providing confidence that the mink-derived calibrations provide reliable diet estimates (Bromaghin et al. 2017b).

Foraging Habits

The results of this study demonstrated the changing dietary habits of polar bears in Western Hudson Bay between 2004 and 2021. Ringed seal and bearded seal had the greatest contributions to the diets at the population level, followed by contributions from harbour seal, beluga whale, harp seal, and walrus. Ringed seal and bearded seal are the most commonly consumed prey types across much of the polar bear's range (Smith 1980; Derocher et al. 2002;

Thiemann et al. 2008; Sciullo et al. 2017). As the smallest seal in the Arctic, ringed seals are accessible to bears across all age and sex classes, most notably during the spring pupping season, during which ringed seals are especially vulnerable to predation (Stirling and McEwan 1975; Stirling and Archibald 1977). Adult male polar bears consumed the largest proportion of bearded seal compared to females and younger bears, which is consistent with previous diet estimates of adult males in Western Hudson Bay (Thiemann et al. 2011). Adult male polar bears are approximately double the size of adult female polar bears, enabling them to hunt and kill larger prey, such as the bearded seal which can weigh over 350 kg (Smith 1981). Hunting various age or sex classes of bearded seals or scavenging of bearded seal remains could explain the moderate proportions of the species in the diets of young or female bears (Thiemann et al. 2008, 2011).

Secondary prey species including harbour seal, beluga whale, harp seal, and walrus were also found in the diets of bears across age and sex classes. As the duration of the open water period continues to lengthen as a result of climatic warming, the availability of open-water species may increase (Stirling and Derocher 1993). High proportions of alternative prey species in the diets are likely a result of opportunistic foraging or variation in locally abundant prey (Galicia et al. 2021b). In Western Hudson Bay, harbour seal and harp seal abundance has likely increased due to greater open water periods (McKinney et al. 2009). For example, in 2016 a maximum of 142 harbour seals were observed hauled out in the Churchill River, compared to a maximum of only 32 observed during annual observations between 1996 and 2005 (Florko et al. 2018). This strongly suggests that a continued increase in harbour seal abundance is probable if the annual open water period continues to elongate. Additionally, there have been many instances of bears hunting or scavenging on beluga whale (Freeman 1973; Smith and Sjare 1990; Florko et al. 2020), and walrus carcasses (Calvert and Stirling 1990; Thiemann et al. 2008; Stirling et al.

2021). Actively hunting walrus, like bearded seal, is challenging due to their size, and thus, large adult male bears are the most likely to prey upon them (Thiemann et al. 2007). The results of this study reflect this trend, with the highest proportions of walrus in the diets of adult male bears.

Longitudinal trends in the data showed a consistent increase in the proportion of bearded seal in the diet throughout the study. This increase in bearded seal consumption is consistent with previously published temporal changes in polar bear diets in Hudson Bay from 1994 to 2004 (Sciullo et al. 2017) as well as temporal changes in Foxe Basin from 1999 – 2003 and 2010 – 2018 (Galicia et al. 2021b). The decadal sinusoidal trends in bearded and ringed seal density align with a reduction in bearded and ringed seal consumption, most notably in 2008, when both density and consumption were low (Chambellant et al. 2012). In Western Hudson Bay, ringed seal density and abundance seem to follow a cyclical pattern, with declines in density and abundance occurring in 2009 and highs in 2007 and 2010 (Young et al. 2015). The cyclical nature of ringed seal abundance can be seen in the proportion of ringed seal in the diet, with major lows occurring in 2009 and 2015 and highs occurring in 2007, 2010 – 2014, and 2019. These decadal trends in ringed seal abundance seem to translate in the diet estimates of the bears, likely reflecting the long-standing relationship between polar bear and ringed seal productivity (Stirling and Oritsland 1995).

Mean consumption of harbour seal and harp seal trended downwards throughout the study period, with minor fluctuations in diet contribution aligning inversely with ringed seal proportions. This finding was first reported by Sciullo et al. (2017), in which they discussed the proportion of ringed seal in the diets of female bears, declining in 2005 and 2009, with a corresponding increase in the proportion of harbour seal. These findings are consistent with the results of the current study, with the observed inverse relationship extending to harp seal, walrus, beluga, and bearded seal increasing as ringed seal consumption declined sharply in 2015 and 2016. Sea ice break-up in 2015 occurred on May 17th, resulting in a 191-day open water period. As an ice-adapted species, ringed seal abundance and recruitment largely depend on sea ice conditions and annual snowfall (Ferguson et al. 2005). In 2010, extreme NAO, AO, and El Niño-Southern Oscillation atmospheric patterns resulted in an early sea ice break-up and a late sea ice freeze-up. This extreme warming event negatively impacted ringed seal fitness with a higher incidence of elevated physiological stress, low natality, and increased illness in Hudson Bay (Ferguson et al. 2017). The result of this extreme climatic stress was a decrease in ovulation rates the following year, decreasing seal recruitment and survival (Stirling 2005; Ferguson et al. 2017). Thus, because of an extreme increase in the open water period in 2015, it is likely that once again, ringed seals experienced immense physiological stress and reduced natality, thereby explaining the seemingly sudden reduction in ringed seal consumption and the subsequent increase in the proportions of harbour seal, harp seal, beluga, and walrus. In general, walrus proportions remained the most consistent throughout the study, while beluga whale proportions seemed to decline and remain consistent thereafter. As previously mentioned, secondary prey items are most commonly acquired as a result of ecological opportunity, scavenging, or variation in locally abundant prey types (Galicia et al. 2021b).

Trends in dietary niche breadth were investigated across age and sex classes, with adult male bears demonstrating the greatest dietary diversity. Adult male polar bears have frequently demonstrated greater dietary diversity than other sex and age classes, likely due to their large size, enabling them to prey on larger species such as the bearded seal (see Thiemann et al. 2011). As a size-dimorphic species, the range in foraging habits and dietary diversity across age and sex classes is broad. Larger-bodied individuals often exhibit a greater degree of dietary flexibility as a result of increased energetic demands and, thus, engage in opportunistic foraging to meet said demands (Clutton-Brock et al. 1987). This implies that large male polar bears are more likely to be flexible in their diets due to their comparatively large energy requirements. The overall dietary breadth of adult males as a group also allows some individuals to specialize on subsets of available resources (i.e., adopt dietary specialization; see below).

In addition to having the greatest dietary diversity, adult male polar bears also had the most temporally variable diets (*DCI*). These results are consistent with Thiemann et al. (2011), who found that the diets of adult male polar bears were both the most temporally variable and the most specialized compared to other age and sex classes. Adult males likely exhibit such temporal variation in their diets because of their large size, enabling them to hunt prey of varying sizes. This foraging flexibility would allow adult males to be more adaptable to fluctuations in prey availability. Thus, their diets would be more variable over time because they can exploit a broader range of prey types. Solitary females and females accompanied by dependent cubs showed no significant difference in their temporal patterns of prey selection, while prey selection in subadults was relatively less variable. The level of temporal consistency in the foraging habits of subadults suggests that they are actively hunting rather than scavenging. If the bears were scavenging, we would expect to see a broader, more temporally variable diet, given the ability to forage on any available carrion. Their lack of hunting experience and smaller size may limit these bears to hunting and consuming ringed seals, as these seals are smaller and have a ubiquitous distribution (Stirling and McEwan 1975).

Adult female bears, with or without cubs, demonstrated a more consistent diet over time relative to adult males. Given their smaller size, females have fewer choices when actively hunting various prey types, which could result in a more consistent diet and a narrow dietary niche. However, many females may supplement their diets by scavenging on available carrion, which would lead to an increased dietary niche breadth and a temporally variable diet. Given the greater consistency in the diets, the results suggest that females, like subadults are likely hunting ringed seals and supplementing with small proportions of available carrion. Females with dependent cubs must also take into account the risk of infanticidal males and avoid hunting on the pack ice, where males in Hudson Bay are known to frequent (Taylor et al. 1985; Stirling and Derocher 1993). Thus, female bears are demonstrating less temporally variable diets than males likely because of size dimorphism affecting hunting opportunities, and a limitation in space-use strategies to protect their cubs from infanticidal males.

Dietary niche breadth (H'), the dietary change index (DCI), and the proportional similarity index (PS_i) demonstrated significant relationships between metrics. An individual's measure of dietary diversity was positively correlated with their dietary change index. This trend suggests that individuals with broader dietary niches or greater dietary diversity exhibit higher turnover in their dietary preferences over time. Thus, individuals with broader niches are likely subject to greater ecological opportunity, encouraging specialization (Roughgarden 1974). Further, as an individual's dietary diversity increased, their degree of specialization also increased. This suggests that increasing dietary niche breadth and temporal variation in diet encourage individual dietary specialization due to increased ecological opportunity (Roughgarden 1974; Araújo et al. 2011).

Dietary Specialization

In an environment in which resource availability is predictable along spatial and temporal scales, individuals exhibiting specialist foraging strategies are supported. Specialist foraging strategies are often energetically favourable, reducing the energetic costs of decision-making and prey switching (Forister et al. 2012). In less predictable environments, generalist foraging strategies are typically favoured, as the ability to exhibit ecological flexibility encourages adaptability when prey availability and abundance are highly variable (Gilmour et al. 2018; Galicia et al. 2021b). However, a growing body of literature demonstrates that populations are not always well-defined as either a specialist or generalist population, but rather, a heterogeneous population in which specialists and generalists coexist (Bolnick et al. 2003; Estes et al. 2003; Svanbäck and Bolnick 2007; Thiemann et al. 2011; Balme et al. 2020). The results of the present study revealed the prevalence of individual dietary specialization within the seemingly generalist Western Hudson Bay subpopulation of polar bears between 2004 and 2021. Similarly to previously published work on dietary specialization within a large solitary mammal, the degree of specialization within the population was driven by phenotypic constraints and environmental conditions (Thiemann et al. 2011; Balme et al. 2020).

In this study, specialists were defined as any individual or sample that returned a PS_i value of ≤ 0.50. Within this study, 13.0% of all samples collected were derived from dietary specialists, while 17.3% of all individuals sampled showed evidence of specialist foraging habits. These results are consistent with the hypothesis that evidence of individual specialization would likely be found in polar bears in the Western Hudson Bay as a result of intraspecific competition, low interspecific competition, and behavioural plasticity (Araújo et al. 2011). Across the study, a range of individual dietary specialization was observed, with many individuals modifying their degree of specialization and foraging habits between years. For example, an adult male bear (X12697) was sampled ten times throughout the study (Figure 2.5A.), reflecting interannual variation in his foraging habits, dietary diversity, and degree of specialization. This bear demonstrated a range in his degree of specialization (*PS_i*) from 0.43 – 0.80, indicating that his foraging behaviours differed significantly between years. Figure 2.5A. shows a marked increase in the consumption of bearded seal in 2008, comprising 85% of his diet and resulting in his highest degree of specialization throughout the study. Comparatively, 2016 exhibited a diet that more closely resembled the population, indicating he was foraging more flexibly than in 2008.

In contrast, another adult male (X12224) sampled five times during the study exhibited a much more temporally variable diet (greater *DCI*) than X12697 but remained above a PS_i value of 0.64 (more generalized) for the duration of the study. Given that temporally variable diets can encourage specialization, it is interesting that X12697 had a more consistent diet but exhibited greater specialization. Thus, although individual specialization is often correlated with increased temporal variation and dietary diversity, it is important to consider that the Western Hudson Bay subpopulation is a collection of individuals who each exhibit unique variations in their foraging habits and behaviours. Additional examples of individual diet composition across age and sex classes over time can be found in Figure 2.5.

There are many feasible explanations for why an individual may specialize that could begin to explain the extent of specialization within the population. Factors such as the development of hunting abilities (Coleman and Wilson 1998; Araújo et al. 2011), sexual size dimorphism (Clutton-Brock et al. 1987), behavioural plasticity (Kobler et al. 2009; Gilmour et al. 2018), the abundance or distribution of prey (Araújo et al. 2011), or inter- and intra-specific competition (Bolnick et al. 2003, 2010; Svanbäck and Bolnick 2007) could all encourage the development of dietary specialization within the population.

Polar bears undergo a matrilineal transmission of foraging skills, with mothers teaching their cubs how to hunt specific prey types (Estes et al. 2003). Studies of on-shore hunting behaviour in the Southern Beaufort Sea indicated that mother-offspring social learning contributed to increased on-shore behaviours of polar bears during the late summer and fall (Lillie et al. 2018). Throughout their lives, polar bears, through lived experience and observing their mothers, learn how to hunt and become more efficient with age (Stirling and Latour 1978). In the present study, age was not a strong predictor of dietary specialization, with PS_i values remaining consistent across age classes. This result suggests that hunting experience likely does not play a significant role in an individual polar bear's degree of specialization.

As a sexually size dimorphic species, male bears are roughly twice the size of female bears (Ramsay and Stirling 1986). The significant size dimorphism between male and female bears was thought to develop as a result of sexual selection and intrasexual competition for females. However, it could very well have been selected for as larger bears gained access to larger, energetically-rich prey items (Stirling and Derocher 1990). Males in the present study demonstrated a higher degree of specialization than females, consistent with previous studies (Thiemann et al. 2011; Balme et al. 2020). As a result of their large size, males have a greater selection of available prey. Thus, the results support the hypothesis that larger male bears are more likely to specialize because they can exploit prey unavailable to other age and sex classes.

Behavioural plasticity is a phenomenon in which an individual will modify their behaviour in response to their environment and encompasses both innate and learned behavioural responses (Mery and Burns 2010). Polar bears, like all ursids, exhibit behavioural plasticity (Derocher 2004), often taking the form of variation in home range size (McCall et al. 2015) or distinctive space-use strategies. One example of this in polar bears would be female bears with dependent cubs choosing to avoid offshore pack ice, where the chances of running into an adult male are greater (Taylor et al. 1985; Derocher and Stirling 1990). The spatial segregation occurring due to behavioural plasticity in female bears can affect foraging opportunities as prey availability differs across spatial scales and, thus, the degree of specialization between solitary females and females with dependent cubs, as observed in this study. The results demonstrated that females with dependent cubs exhibited a lower degree of specialization compared to solitary females, supporting the hypothesis that spatial segregation and prey availability may play a role in explaining specialization across reproductive stages.

As sea ice conditions worsen in response to warming temperatures in the Arctic, many marine prey species could end up undergoing mass redistribution as they attempt to remain within their preferred environments (Learmonth et al. 2006; Galicia et al. 2021a) Further, variation in prey availability and distribution occurs on an annual basis, with minor variations occurring over periods as short as days or weeks (Stirling et al. 1982). This unpredictable variation in prey abundance and distribution could drive certain individuals to occupy a distinctive dietary niche to supplement a loss of foraging on primary prey species such as the ringed seal. Additionally, the diversity of prey in an area could also impact the degree of specialization, with specialization increasing as ecological opportunity increases (Roughgarden 1974). For example, the degree of specialization in the fruit bat, *Rousettus aegyptiacus*, varied seasonally, with higher specialization occurring in the spring when there was a greater diversity of fruit-bearing plants available (Herrera M et al. 2008). Since the abundance and distribution of prey are highly variable, some individual bears could find themselves in an area with higher prey diversity, which may lead to an increase in their degree of specialization, provided they are capable of foraging on the prey types available.

As an apex predator, the polar bear experiences little to no interspecific competition for prey (Miller et al. 2015). Intraspecific competition, however, may be common and has been shown to correlate with the degree of specialization within a population (Estes et al. 2003; Svanbäck and Persson 2004). In years where ringed seal abundance is diminished (e.g., 2015), bears may be forced to compete over a limited amount of their primary prey. Such intraspecific competition may result in resource partitioning, leading to increases in the consumption and subsequent specialization on secondary prey species. In 2015, beluga whale, harbour seal, harp seal, walrus, and bearded seal increased in the diets as ringed seal declined. As these secondary prey species become more critical to the diets of polar bears, we may begin to see the increased utilization of secondary prey types serving as available dietary niches for specialist individuals when ringed seal abundance is low.

Across all samples, snow depth was the strongest predictor of individual specialization, with specialization increasing as snow depth increased. This finding contradicts the prediction that specialization would be greater when snow depth was lower due to increased intraspecific competition resulting from a decline in ringed seal recruitment and survival (Hezel et al. 2012). Instead, increased snow depth might result in a greater degree of specialization because of the increased protection of seals from polar bear predation. A study conducted by Iacozza and Ferguson (2014) investigated variability in snow depth across spatial and temporal scales in relation to ringed seal pup survival in Western Hudson Bay. Their results showed that snow on the sea ice varies interannually and inter-seasonally, relating to variation in seal pup survival. Areas with uniform, consistent snow coverage were more likely to be selected for birthing lairs due to the extended period of protection during the spring polar bear feeding period (Smith 1980; Iacozza and Ferguson 2014). However, in areas with high variability, snow depth was often lower, resulting in an earlier melt, thereby exposing seal pups to the elements earlier than if snow depth were thicker and consistent. Thus, areas in which snow depth is less variable typically result in increasing seal pup survival (Iacozza and Ferguson 2014). Similarly, in areas in which snow depth was 20 cm, a value considered to be a minimum threshold for subnivean birth lairs, seals sought out deeper snow drifts along pressure ridges for their birth lairs (Smith and Stirling 1975). This reliance on deeper snow may lead to an increase in seal survival, perhaps across species, increasing the diversity of prey in the area, favouring ecological opportunity and, thus, dietary specialization (Araújo et al. 2011).

The North Atlantic Oscillation index demonstrated a significant effect on the degree of specialization, with positive NAO values resulting in greater specialization. The current year's NAO index was correlated with the date of sea ice break-up, with early break-up occurring during years with more positive NAO values, resulting in increased specialization. Given that seal body condition has been shown to decline after years with positive NAO indices (Ferguson et al. 2020), the results suggest that due to declining body condition and survival, intraspecific competition for seals would increase, leading to a rise in individual specialization. As discussed previously, 2015 showed a substantial decline in the proportion of ringed seals in the diets of polar bears. It boasted the earliest date of sea ice break-up and the largest positive NAO index, resulting in the greatest percentage of specialist samples over the study period. Although the previous year's NAO index ($NAO_{(t-1)}$) did not support the initial hypothesis, the proposed mechanism was upheld, with intraspecific competition helping to explain the significance of the NAO and sea ice break-up date on individual specialization.

Though the date of sea ice break-up was not shown to be a significant driver of specialization, when discussed with respect to NAO and snow depth conditions, these effects seem to work in tandem to produce conditions suitable for the development and maintenance of individual specialization. The initial prediction stated that in years when sea ice break-up occurs later, higher levels of specialization would be observed due to a greater amount of time to hunt, encouraging selective feeding. A minor relationship between the date of sea ice break-up and PS_i values reflected a trend towards increased specialization with a later date of sea ice break-up. However, the results were not significant, and therefore, the hypothesis was not supported.

Conclusion

This study aimed to examine the foraging habits of polar bears in Western Hudson Bay, emphasizing the investigation of the extent and drivers of individual dietary specialization. The findings show that foraging habits are changing across spatial and temporal scales, with polar bears occupying distinctive dietary niches, as increasing variation and subsequent declines in the abundance of ringed seal drives intraspecific competition. The underlying drivers of specialization were a combination of sexual size dimorphism, intraspecific competition, and ecological opportunity manifesting as a result of changing environmental conditions. The results of this study aid in our understanding of the foraging behaviours of a large Arctic carnivore forced to adapt to relentless environmental pressures. It is increasingly important to quantify foraging patterns at both the individual and population levels to understand better how changing environmental conditions will affect bears with narrower dietary niches as well as those that are better equipped to forage flexibly. If all bears within the subpopulation are treated equivalently when modelling the effects of climate warming, we risk misrepresenting how a given subpopulation will react to projected climate-induced population declines (Molnár et al. 2010, 2011, 2020). Future research should continue to model climate-induced population declines while accounting for variation in interindividual niche variation.

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Table 2.1. The total number of polar bears sampled arranged according to year, sex, and age class. Sampling occurred between 2004 and 2021, with no sampling in 2020. Bears were categorized by one of five age classes, including adult (≥ 5 years old), subadult (2.5 – 4 years old; independent), 2-year-old (2 – 2.5-year-olds; may still be with mother), yearling (1 – 2 years old), and cub of the year (0 – 1-year-old; COY).

Year	Adult		Subadult		2 Year		Yearling		COY		Total		Sum
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	
2004	59	23	10	13	8	7	2	2	0	0	79	45	124
2005	31	31	4	7	0	2	9	8	0	0	44	48	92
2006	32	29	5	6	2	1	1	0	0	0	40	36	76
2007	28	17	3	0	2	4	1	2	0	0	34	23	57
2008	20	27	5	5	2	5	1	0	0	1	28	38	66
2009	31	30	5	11	0	4	1	2	2	1	39	48	87
2010	37	26	3	2	5	0	4	1	0	0	49	29	78
2011	33	32	5	8	1	0	0	2	0	0	39	42	81
2012	24	15	4	5	1	1	0	0	5	4	34	25	59
2013	26	21	4	2	1	2	1	0	5	8	37	33	70
2014	27	33	1	5	0	0	0	0	0	0	28	38	66
2015	20	23	2	2	1	4	2	1	6	7	31	37	68
2016	22	24	1	1	2	1	5	6	7	5	37	37	74
2017	37	27	0	1	1	3	2	5	9	10	49	46	95
2018	29	42	3	3	3	1	10	6	8	7	53	59	112
2019	20	23	4	4	5	5	1	1	5	10	35	43	78
2020	-	-	-	-	-	-	-	-	-	-	0	0	0
2021	25	27	7	5	1	1	3	12	2	7	38	52	90
Totals	501	450	66	80	35	41	43	48	49	60	694	679	1373

Table 2.2. The number of polar bear samples collected from individual polar bears sampled two or more times over the course of the study (n = 582 samples). Samples were not collected in 2020. The samples were arranged according to year, sex, and age class. Only bears sampled multiple times within the same age class were included to account for ontogenetic shifts.

Year	Adult		Subadult		Total		Sum
	Male	Female	Male	Female	Male	Female	
2004	28	11	0	0	28	11	39
2005	21	18	0	1	21	19	40
2006	23	10	0	1	23	11	34
2007	19	9	0	0	19	9	28
2008	15	13	0	0	15	13	28
2009	21	16	0	0	21	16	37
2010	20	16	0	0	20	16	36
2011	24	20	0	0	24	20	44
2012	21	8	0	1	21	9	30
2013	24	15	1	1	25	16	41
2014	22	19	1	0	23	19	42
2015	18	13	0	0	18	13	31
2016	15	15	0	0	15	15	30
2017	25	21	0	0	25	21	46
2018	22	17	0	0	22	17	39
2019	8	10	0	0	8	10	18
2020	-	-	-	-	0	0	0
2021	9	10	0	0	9	10	19
Totals	**335**	**241**	**2**	**4**	**337**	**245**	**582**

Table 2.3. Mean fatty acid composition (mean mass % of total fatty acid ± SEM) of adipose tissue samples collected in Western Hudson Bay between 2004 – 2021. Bolded FAs were used for final diet estimations (Average Mink Marine and Mink All).

Fatty Acid	Adult	Subadult	2 Year	Yearling	Cub of the Year
	n = 951	n = 146	n = 76	n = 91	n = 109
12:0	0.034 ± 0.001	0.042 ± 0.004	0.045 ± 0.006	0.029 ± 0.002	0.029 ± 0.001
13:0	0.030 ± 0.002	0.043 ± 0.006	0.042 ± 0.007	0.025 ± 0.004	0.018 ± 0.001
i-14:0	0.032 ± 0.001	0.038 ± 0.003	0.042 ± 0.007	0.028 ± 0.002	0.024 ± 0.001
14:0	3.526 ± 0.016	3.656 ± 0.041	3.803 ± 0.062	3.797 ± 0.042	3.851 ± 0.037
14:1n-9	0.060 ± 0.001	0.080 ± 0.008	0.067 ± 0.003	0.064 ± 0.002	0.056 ± 0.001
14:1n-7	0.044 ± 0.001	0.047 ± 0.002	0.052 ± 0.002	0.045 ± 0.001	0.052 ± 0.001
14:1n-5	1.083 ± 0.007	1.128 ± 0.014	1.135 ± 0.022	1.118 ± 0.018	1.006 ± 0.016
i-15:0	0.261 ± 0.004	0.277 ± 0.011	0.275 ± 0.018	0.219 ± 0.007	0.185 ± 0.003
ai-15:0	0.105 ± 0.001	0.114 ± 0.002	0.119 ± 0.004	0.104 ± 0.003	0.100 ± 0.003
15:0	0.290 ± 0.002	0.272 ± 0.004	0.266 ± 0.005	0.277 ± 0.003	0.267 ± 0.003
15:1n-8	0.021 ± 0.003	0.049 ± 0.013	0.031 ± 0.015	0.011 ± 0.006	0.006 ± 0.002
15:1n-6	0.001 ± 0.000	0.001 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
i-16:0	0.135 ± 0.001	0.133 ± 0.005	0.135 ± 0.012	0.116 ± 0.005	0.105 ± 0.003
16:0	7.813 ± 0.038	7.411 ± 0.092	7.260 ± 0.113	7.725 ± 0.091	8.801 ± 0.135
16:1n-11	0.318 ± 0.003	0.331 ± 0.012	0.326 ± 0.021	0.301 ± 0.009	0.252 ± 0.006
16:1n-9	0.521 ± 0.002	0.524 ± 0.005	0.525 ± 0.006	0.494 ± 0.006	0.498 ± 0.005
16:1n-7	16.749 ± 0.067	15.770 ± 0.173	15.480 ± 0.238	16.753 ± 0.221	15.718 ± 0.279
16:1n-5	0.317 ± 0.002	0.308 ± 0.004	0.300 ± 0.005	0.321 ± 0.005	0.291 ± 0.005
17:1a	0.110 ± 0.002	0.088 ± 0.003	0.105 ± 0.007	0.118 ± 0.005	0.118 ± 0.005
i-17:0	0.188 ± 0.004	0.188 ± 0.007	0.156 ± 0.010	0.111 ± 0.009	0.091 ± 0.007
16:2n-6	0.033 ± 0.000	0.040 ± 0.002	0.042 ± 0.004	0.031 ± 0.002	0.025 ± 0.001
ai-17:0	0.157 ± 0.002	0.147 ± 0.004	0.142 ± 0.005	0.129 ± 0.004	0.112 ± 0.005
17:1b	0.222 ± 0.002	0.203 ± 0.004	0.192 ± 0.004	0.184 ± 0.004	0.177 ± 0.003
16:2n-4	0.322 ± 0.002	0.327 ± 0.004	0.320 ± 0.005	0.322 ± 0.005	0.285 ± 0.005
17:0	0.201 ± 0.002	0.181 ± 0.004	0.172 ± 0.004	0.170 ± 0.004	0.181 ± 0.004
16:3n-4	0.040 ± 0.001	0.055 ± 0.005	0.060 ± 0.009	0.041 ± 0.004	0.025 ± 0.001
17:1	0.306 ± 0.002	0.276 ± 0.004	0.261 ± 0.004	0.255 ± 0.004	0.256 ± 0.003
16:4n-3	0.056 ± 0.002	0.064 ± 0.005	0.059 ± 0.008	0.052 ± 0.006	0.026 ± 0.002
16:4n-1	0.021 ± 0.001	0.027 ± 0.003	0.028 ± 0.005	0.020 ± 0.002	0.015 ± 0.001
18:0	2.110 ± 0.013	2.043 ± 0.034	2.048 ± 0.047	2.040 ± 0.034	2.601 ± 0.080
18:1n-13	0.058 ± 0.001	0.043 ± 0.002	0.034 ± 0.003	0.033 ± 0.003	0.022 ± 0.002
18:1n-11	1.583 ± 0.018	1.749 ± 0.046	1.966 ± 0.071	2.025 ± 0.053	2.078 ± 0.043
18:1n-9	22.704 ± 0.058	23.327 ± 0.147	23.423 ± 0.180	22.556 ± 0.167	23.476 ± 0.189
18:1n-7	5.987 ± 0.022	5.623 ± 0.038	5.463 ± 0.043	5.565 ± 0.044	5.626 ± 0.042
18:1n-5	0.690 ± 0.002	0.695 ± 0.005	0.692 ± 0.009	0.683 ± 0.007	0.633 ± 0.006
18:2d5,11	0.074 ± 0.001	0.078 ± 0.003	0.071 ± 0.004	0.070 ± 0.004	0.058 ± 0.003
18:2n-7	0.096 ± 0.001	0.097 ± 0.002	0.093 ± 0.004	0.087 ± 0.003	0.085 ± 0.003
18:2n-6	2.817 ± 0.014	2.833 ± 0.035	2.972 ± 0.062	3.019 ± 0.050	3.515 ± 0.049

Fatty Acid	Adult	Subadult	2-Year	Yearling	Cub of the Year
	n = 951	n = 146	n = 76	n =91	n = 109
18:2n-4	0.099 ± 0.001	0.094 ± 0.001	0.091 ± 0.002	0.087 ± 0.001	0.080 ± 0.001
18:3n-6	0.108 ± 0.001	0.111 ± 0.002	0.115 ± 0.003	0.101 ± 0.003	0.091 ± 0.002
18:3n-4	0.204 ± 0.001	0.206 ± 0.002	0.195 ± 0.004	0.189 ± 0.003	0.166 ± 0.002
18:3n-3	0.556 ± 0.003	0.547 ± 0.008	0.564 ± 0.018	0.552 ± 0.010	0.589 ± 0.010
18:3n-1	0.086 ± 0.001	0.082 ± 0.002	0.075 ± 0.003	0.072 ± 0.002	0.063 ± 0.001
18:4n-3	0.316 ± 0.002	0.295 ± 0.004	0.311 ± 0.006	0.311 ± 0.005	0.287 ± 0.006
18:4n-1	0.106 ± 0.001	0.095 ± 0.002	0.088 ± 0.003	0.103 ± 0.003	0.084 ± 0.003
20:0	0.055 ± 0.001	0.055 ± 0.002	0.058 ± 0.003	0.044 ± 0.002	0.037 ± 0.002
20:1n-11	1.293 ± 0.011	1.439 ± 0.028	1.440 ± 0.036	1.254 ± 0.025	1.128 ± 0.038
20:1n-9	5.225 ± 0.038	5.932 ± 0.097	6.066 ± 0.117	5.536 ± 0.098	4.757 ± 0.124
20:1n-7	0.751 ± 0.007	0.691 ± 0.011	0.674 ± 0.015	0.637 ± 0.011	0.589 ± 0.012
20:2n-9	0.029 ± 0.001	0.016 ± 0.002	0.021 ± 0.004	0.022 ± 0.004	0.031 ± 0.004
20:2n-6	0.303 ± 0.001	0.295 ± 0.002	0.293 ± 0.003	0.272 ± 0.003	0.278 ± 0.004
20:3n-6	0.124 ± 0.001	0.125 ± 0.001	0.123 ± 0.002	0.121 ± 0.001	0.145 ± 0.002
20:4n-6	0.318 ± 0.003	0.270 ± 0.005	0.258 ± 0.007	0.271 ± 0.004	0.310 ± 0.006
20:3n-3	0.064 ± 0.001	0.067 ± 0.002	0.056 ± 0.003	0.047 ± 0.003	0.042 ± 0.002
20:4n-3	0.503 ± 0.003	0.469 ± 0.007	0.434 ± 0.008	0.455 ± 0.006	0.441 ± 0.007
20:5n-3	2.473 ± 0.020	2.254 ± 0.049	2.134 ± 0.062	2.324 ± 0.052	2.007 ± 0.062
22:0	0.010 ± 0.000	0.012 ± 0.001	0.010 ± 0.001	0.007 ± 0.001	0.004 ± 0.001
22:1n-11	0.658 ± 0.011	0.737 ± 0.026	0.735 ± 0.028	0.673 ± 0.026	0.500 ± 0.028
22:1n-9	0.317 ± 0.003	0.349 ± 0.007	0.348 ± 0.009	0.308 ± 0.007	0.263 ± 0.009
22:1n-7	0.068 ± 0.001	0.070 ± 0.002	0.071 ± 0.004	0.059 ± 0.003	0.051 ± 0.004
22:2n-6	0.007 ± 0.000	0.010 ± 0.001	0.011 ± 0.002	0.007 ± 0.001	0.003 ± 0.001
21:5n-3	0.319 ± 0.001	0.316 ± 0.003	0.316 ± 0.005	0.308 ± 0.003	0.301 ± 0.003
22:4n-6	0.145 ± 0.002	0.128 ± 0.003	0.115 ± 0.003	0.106 ± 0.002	0.114 ± 0.003
22:5n-6	0.194 ± 0.002	0.187 ± 0.003	0.183 ± 0.004	0.169 ± 0.003	0.166 ± 0.003
22:4n-3	0.081 ± 0.001	0.089 ± 0.003	0.085 ± 0.004	0.074 ± 0.002	0.065 ± 0.001
22:5n-3	6.092 ± 0.030	6.472 ± 0.079	6.570 ± 0.110	6.237 ± 0.079	6.219 ± 0.073
22:6n-3	10.306 ± 0.056	10.205 ± 0.146	10.286 ± 0.204	10.661 ± 0.159	10.465 ± 0.118
24:1n-9	0.071 ± 0.001	0.071 ± 0.003	0.073 ± 0.003	0.055 ± 0.002	0.059 ± 0.003

Table 2.4. An overview of the six QFASA diet estimation iterations run to compare effectiveness and similarity between methods. Each iteration is categorized by its fatty acid set, calibration coefficient set, the R package used, and the associated reference.

QFASA Iteration	FA Set	Calibration Coefficients	R Package	Reference
Mink Marine	29	Mink	qfasar	Thiemann et al. 2008
Mink All	29	Mink	qfasar	Thiemann et al. 2008
Dog Food + Salmon	22	Grizzly	qfasar	Thiemann et al. 2022
Dog Food + Anchovy	22	Grizzly	qfasar	Thiemann et al. 2022
Sim-29FA	29	Simultaneous Estimation	QFASA	Bromaghin et al. 2017
Sim-22FA	22	Simultaneous Estimation	QFASA	Bromaghin et al. 2017

Table 2.5. Mean percentage ± SEM of prey items in the diets of polar bears in the Western Hudson Bay subpopulation, estimated using each of the six QFASA diet estimation iterations. Estimates were based on samples collected during the study period between 2004 and 2021, with no sampling conducted during 2020.

	Mink Marine	Mink All	Dog Food + Salmon	Dog Food + Anchovy	Sim-29FA	Sim-22FA
Bearded Seal	23.845 ± 0.608	32.419 ± 0.685	1.714 ± 0.154	2.927 ± 0.243	12.340 ± 0.423	13.863 ± 0.456
Beluga Whale	9.454 ± 0.357	5.690 ± 0.258	2.963 ± 0.238	0.400 ± 0.132	13.722 ± 0.427	12.541 ± 0.301
Harbour Seal	5.968 ± 0.316	25.846 ± 0.540	1.527 ± 0.158	48.084 ± 0.687	9.723 ± 0.388	12.480 ± 0.439
Harp Seal	7.039 ± 0.343	1.625 ± 0.159	10.454 ± 0.346	0.022 ± 0.017	41.531 ± 0.564	14.529 ± 0.403
Ringed Seal	48.083 ± 0.730	32.317 ± 0.625	78.585 ± 0.498	43.906 ± 0.664	18.028 ± 0.513	39.554 ± 0.709
Walrus	5.610 ± 0.131	2.103 ± 0.095	4.758 ± 0.084	4.661 ± 0.076	4.656 ± 0.113	7.033 ± 0.097

Table 2.6. Mean dietary niche breadth ± SEM for male and female polar bears across age classes in the Western Hudson Bay subpopulation between 2004 and 2021. The mean dietary niche breadth is represented by the Shannon-Wiener Index (*H’*).

	Adult	Subadult	2 Year	Yearling	Cub of the Year
	n = 951	n = 146	n = 76	n = 91	n = 109
Female	0.471 ± 0.013	0.493 ± 0.029	0.471 ± 0.044	0.468 ± 0.033	0.322 ± 0.032
Male	0.689 ± 0.015	0.672 ± 0.039	0.568 ± 0.053	0.492 ± 0.043	0.466 ± 0.038

Table 2.7. Extent of dietary specialization across all samples (n = 1,373). Mean PS_i ± SEM is listed by age class and sex. Samples were collected from Western Hudson Bay between 2004 and 2021, with no sampling during 2020.

	Adult n = 951	Subadult n = 146	2 Year n = 76	Yearling n = 91	Cub of the Year n = 109
Female	0.684 ± 0.006	0.668 ± 0.014	0.686 ± 0.017	0.687 ± 0.017	0.680 ± 0.017
Male	0.640 ± 0.007	0.667 ± 0.019	0.673 ± 0.022	0.656 ± 0.016	0.614 ± 0.025

Table 2.8. The GLMM output summarizing the fixed and random effects of the male and female driver models. Significant p-values are in bold. See supplement for abbreviations.

Model	Response	Effects	Estimate	SE	z-value	p-value	2.5% CI	97.5% CI
Female	PS_i	**Fixed**						
		Intercept	0.365	0.779	0.469	0.639	-1.161	1.891
		Age	0.001	0.004	0.120	0.905	-0.008	0.009
		ReproAF 2YR	0.001	0.321	0.003	0.998	-0.628	0.630
		ReproAF COY	-0.032	0.106	-0.302	0.762	-0.240	0.176
		ReproAF Solitary	-0.112	0.103	-1.091	0.275	-0.314	0.089
		ReproAF YRLG	0.035	0.113	0.307	0.759	-0.187	0.257
		ReproCOY	0.033	0.108	0.307	0.759	-0.179	0.245
		ReproSUBAD	-0.111	0.102	-1.091	0.275	-0.311	0.089
		ReproYRLG	0.074	0.115	0.640	0.521	-0.152	0.299
		Snow	-0.010	0.004	-2.932	**0.003**	-0.017	-0.003
		AO	0.041	0.050	0.828	0.408	-0.057	0.140
		AOt	0.057	0.064	0.895	0.371	-0.068	0.182
		NAO	-0.165	0.074	-2.222	**0.026**	-0.311	-0.019
		NAOt	-0.180	0.095	-1.887	0.059	-0.366	0.007
		Break	0.006	0.005	1.148	0.251	-0.004	0.015
		Random						
		Effect	*Variance*	*SD*				
		Bear	0.0035	0.059				
		Year	0.026	0.16				
Male	PS_i	**Fixed**						
		Intercept	0.900	0.727	1.238	0.216	-0.526	2.326
		Dependent1	-0.140	0.086	-1.627	0.104	-0.309	0.029
		Age	-0.014	0.005	-3.006	**0.003**	-0.023	-0.005
		Snow	-0.007	0.003	-2.348	0.019	-0.014	-0.001
		AO	0.025	0.047	0.520	0.603	-0.068	0.117
		AOt	0.076	0.060	1.266	0.206	-0.041	0.192
		NAO	-0.146	0.070	-2.110	**0.035**	-0.287	-0.011
		NAOt	-0.087	0.088	-0.991	0.322	-0.259	0.085
		Break	0.001	0.005	0.250	0.802	-0.008	0.010
		Random						
		Effect	*Variance*	*SD*				
		Bear	0.050	0.224				
		Year	0.020	0.141				

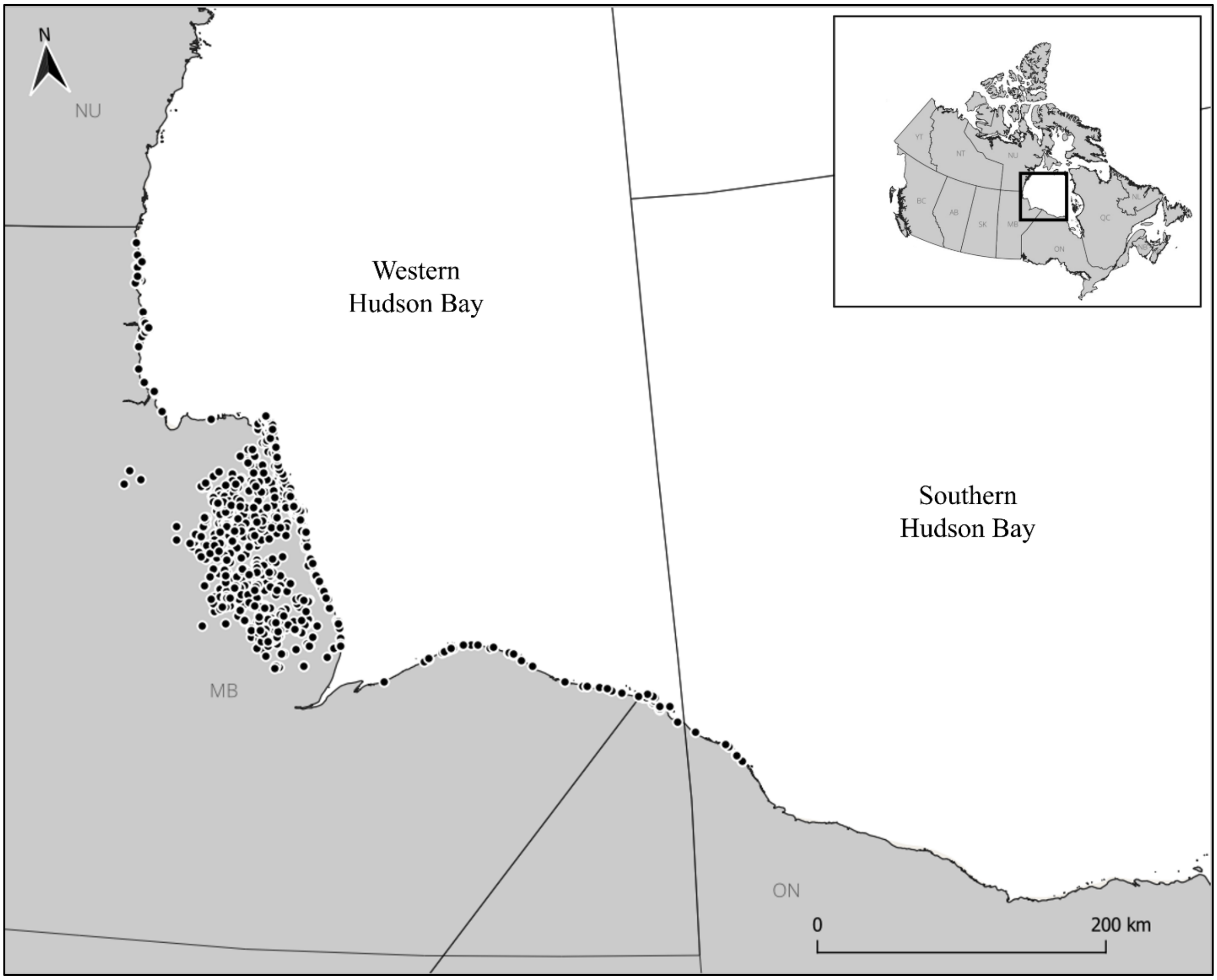

Figure 2.1. Location of 1,373 polar bear captures from 2004 – 2021 in the Western Hudson Bay and Southern Hudson Bay subpopulations. Most samples were collected in the study population of Western Hudson Bay. The inset shows the location within Canada.

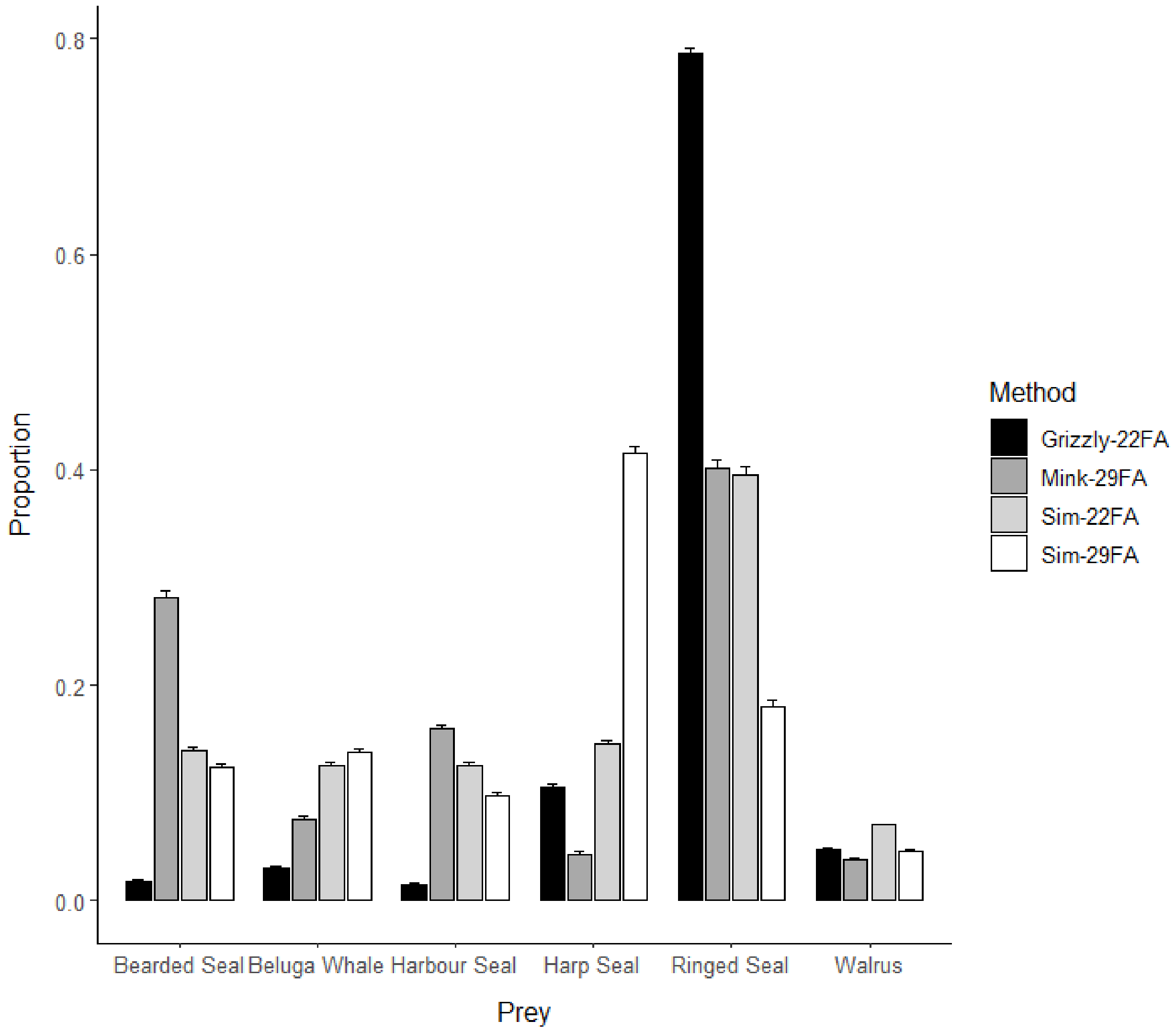

Figure 2.2. Contribution of each prey type to the diets of Western Hudson Bay polar bears (n = 1,373) between 2004 – 2021, estimated using the Dog Food + Salmon method (Grizzly-22FA), the average of Mink Marine and Mink All method (Mink-29FA), as well as the simultaneous estimates derived using the set of 22 fatty acids (Sim-22FA) and the set of 29 fatty acids (Sim-29FA).

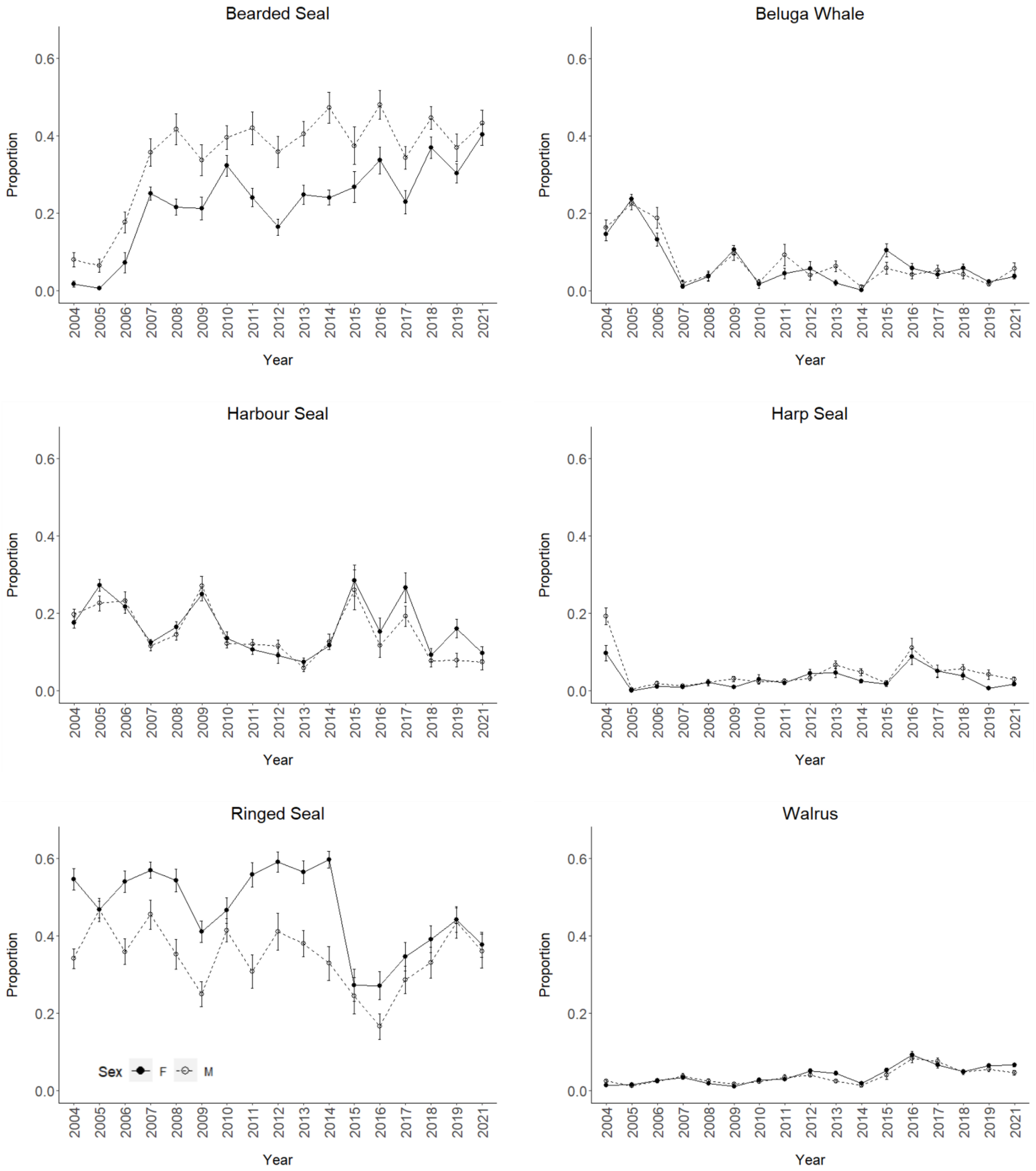

Figure 2.3. The mean proportion of (A) Bearded Seal, (B) Beluga Whale, (C) Harbour Seal, (D) Harp Seal, (E) Ringed Seal, and (F) Walrus in the diets of polar bears in the Western Hudson Bay subpopulation, sampled from 2004 – 2021 (n = 1,373). No sampling was conducted during 2020. Each point represents the mean proportion of each prey item in the diets of male and female bears each year, with error bars representing ± SEM.

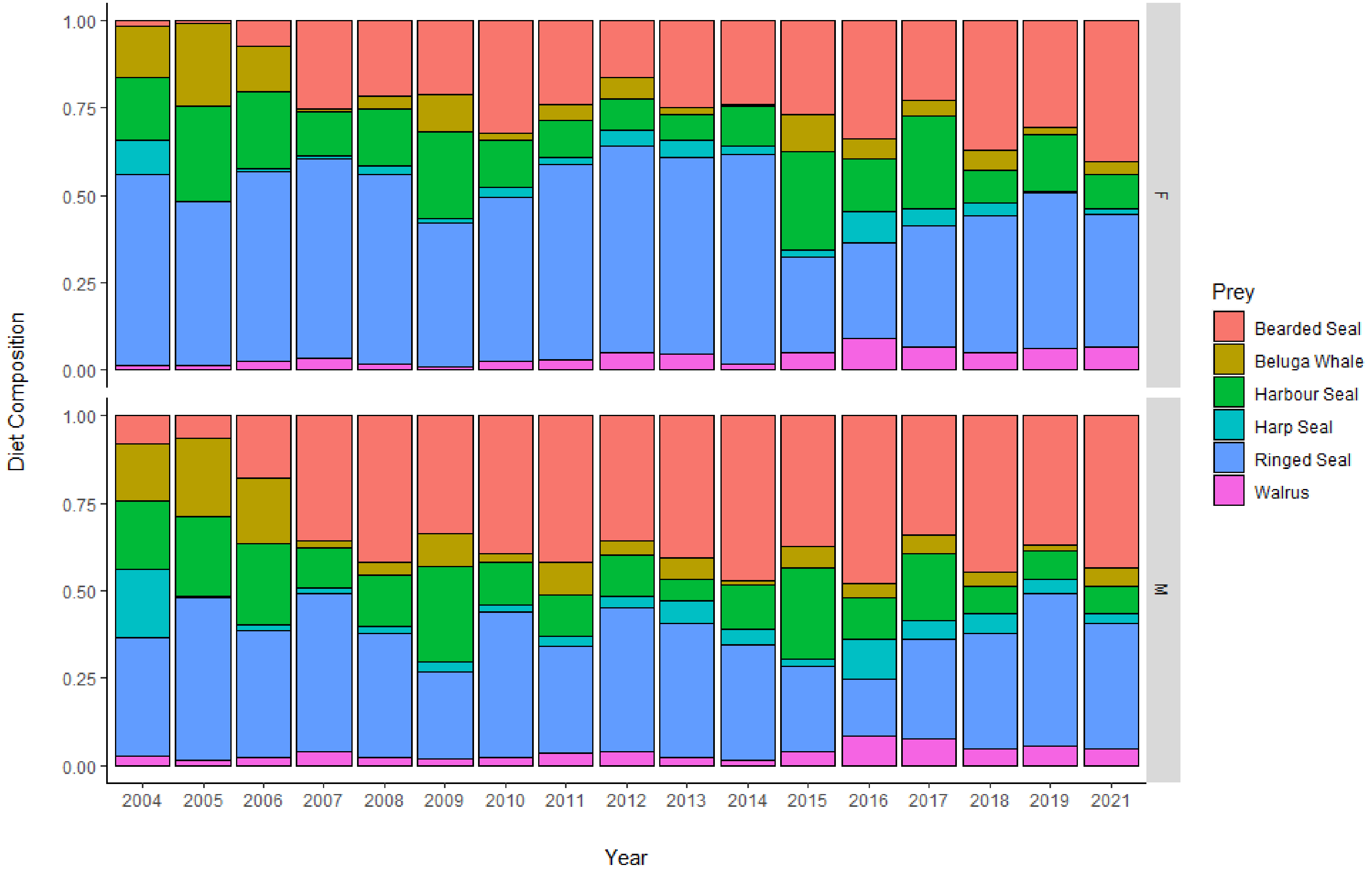

Figure 2.4. The mean proportion of bearded seal, beluga whale, harbour seal, harp seal, ringed seal, and walrus in the diets of polar bears in the Western Hudson Bay subpopulation, sampled from 2004 – 2021 (n = 1,373). No sampling was conducted during 2020. Each bar represents the mean diet composition of male and female bears each year.

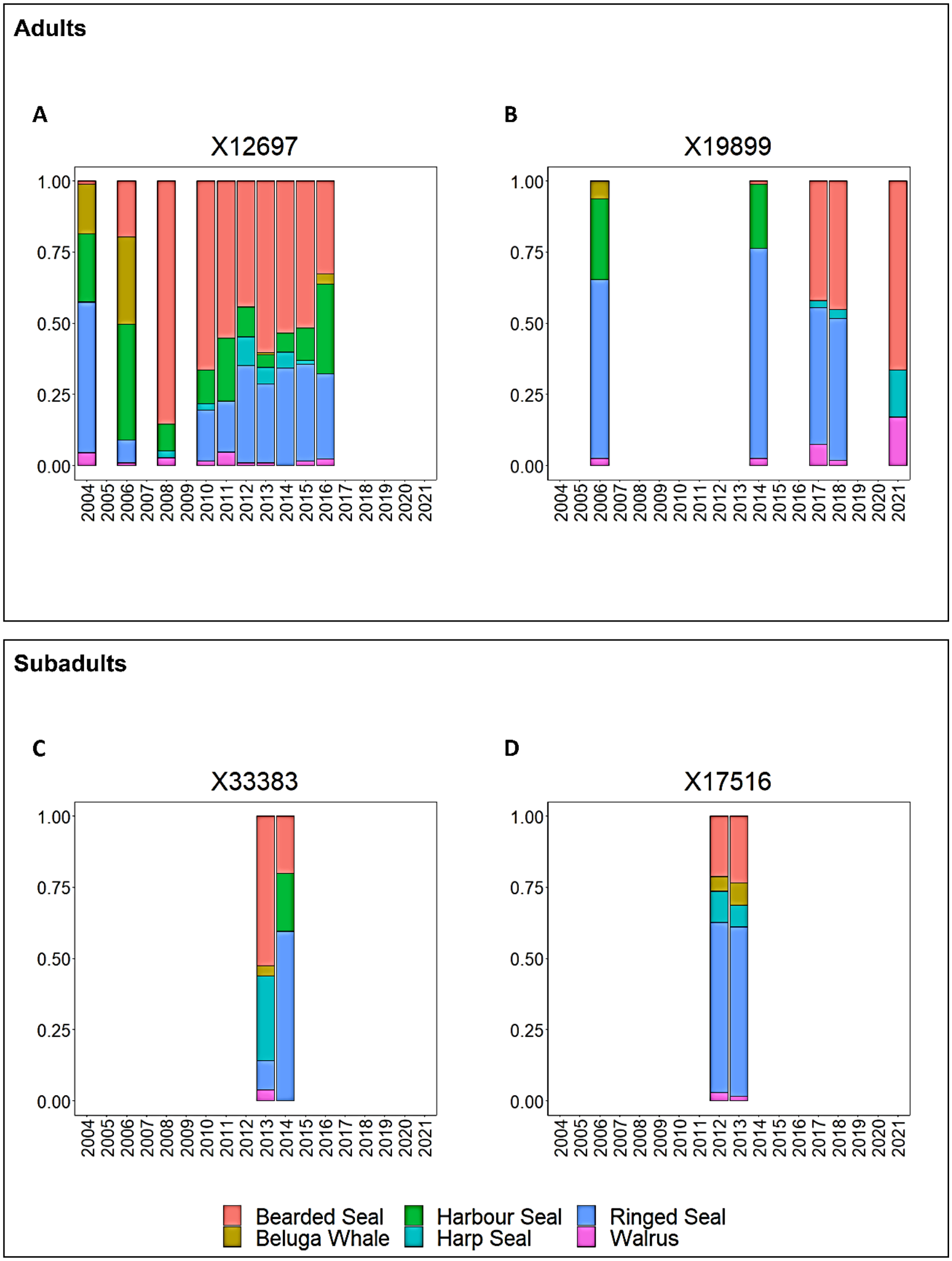

Figure 2.5. Diet composition of individual generalist and specialist bears across age and sex classes sampled multiple times in Western Hudson Bay between 2004 and 2021. The coloured bars indicate the proportion of each prey item in the diet for a given sampling year. Each bear is identified with a unique identification number (e.g., X12697). (A) An adult male bear, (B) An adult female bear, (C) A subadult male bear, and (D) A subadult female bear.

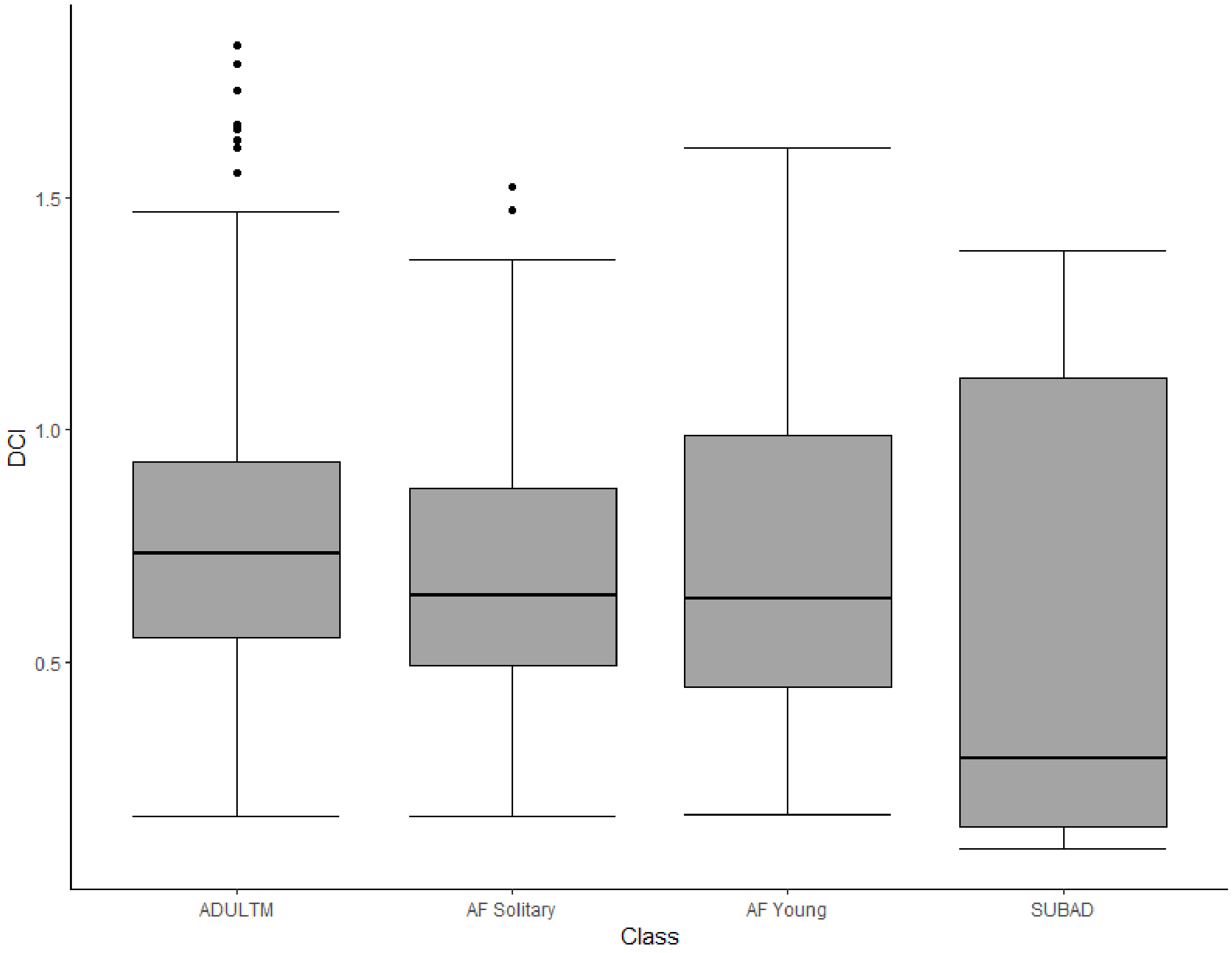

Figure 2.6. The dietary change index (*DCI*) for adult polar bears of both sexes across reproductive stages in the Western Hudson Bay subpopulation between 2004 – 2021. The lines on the plot represent the median along with the upper and lower limits of the interquartile range. The whiskers represent minimum and maximum values, with points representing outliers in the data. Adult male bears tended to have greater mean *DCI* values compared to females (Kruskal-Wallis; p = 0.031).

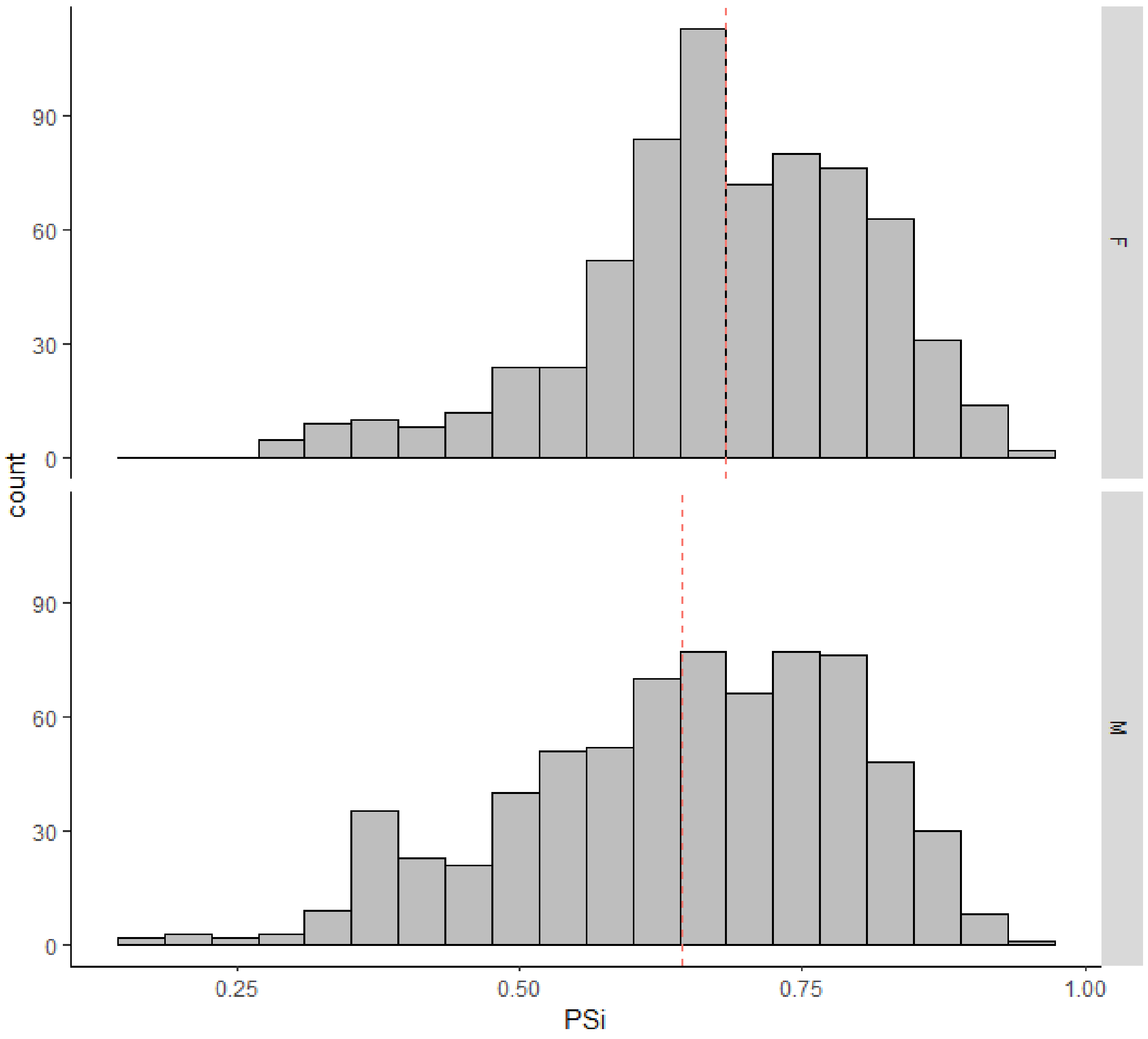

Figure 2.7. Histogram detailing the extent of dietary specialization ($PS_i \leq 0.50$) and dietary generalization ($PS_i > 0.50$) within the Western Hudson Bay polar bear subpopulation. Data is separated by sex, with female samples represented in the top panel and male samples on the bottom panel, as sex was shown to be a significant driver of mean differences in PS_i ($R^2 = 0.790$, $\chi2 = 13.68$, df = 1, $p < 0.05$). The dotted line denotes the location of the mean for both female (0.682 ± 0.005) and male bears (0.643 ± 0.006).

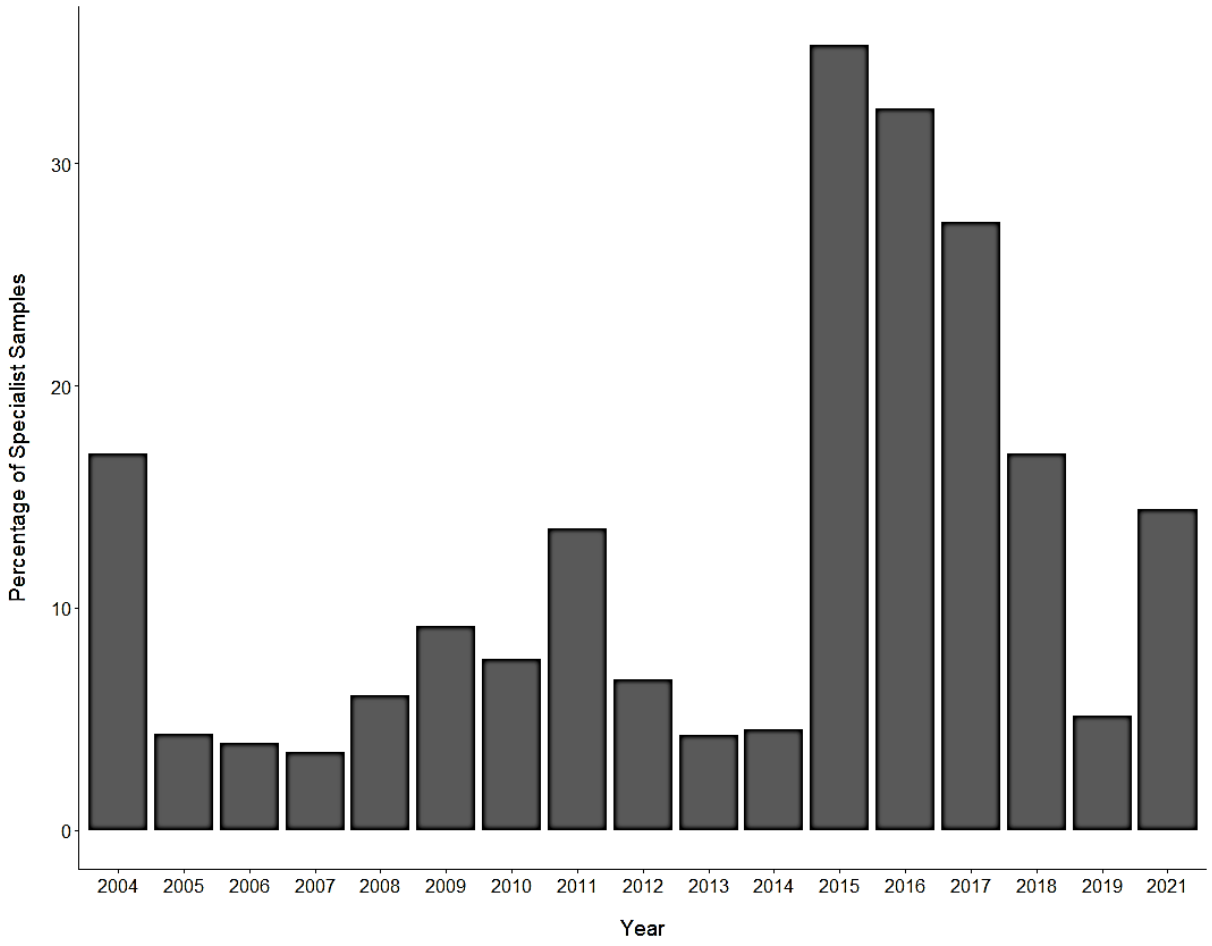

Figure 2.8. The percentage of samples per year that demonstrate a specialized diet ($PS_i \leq 0.50$). A total of 179 samples had a PS_i value of ≤ 0.50. Samples were collected from Western Hudson Bay between 2004 and 2021, with no sampling occurring during 2020.

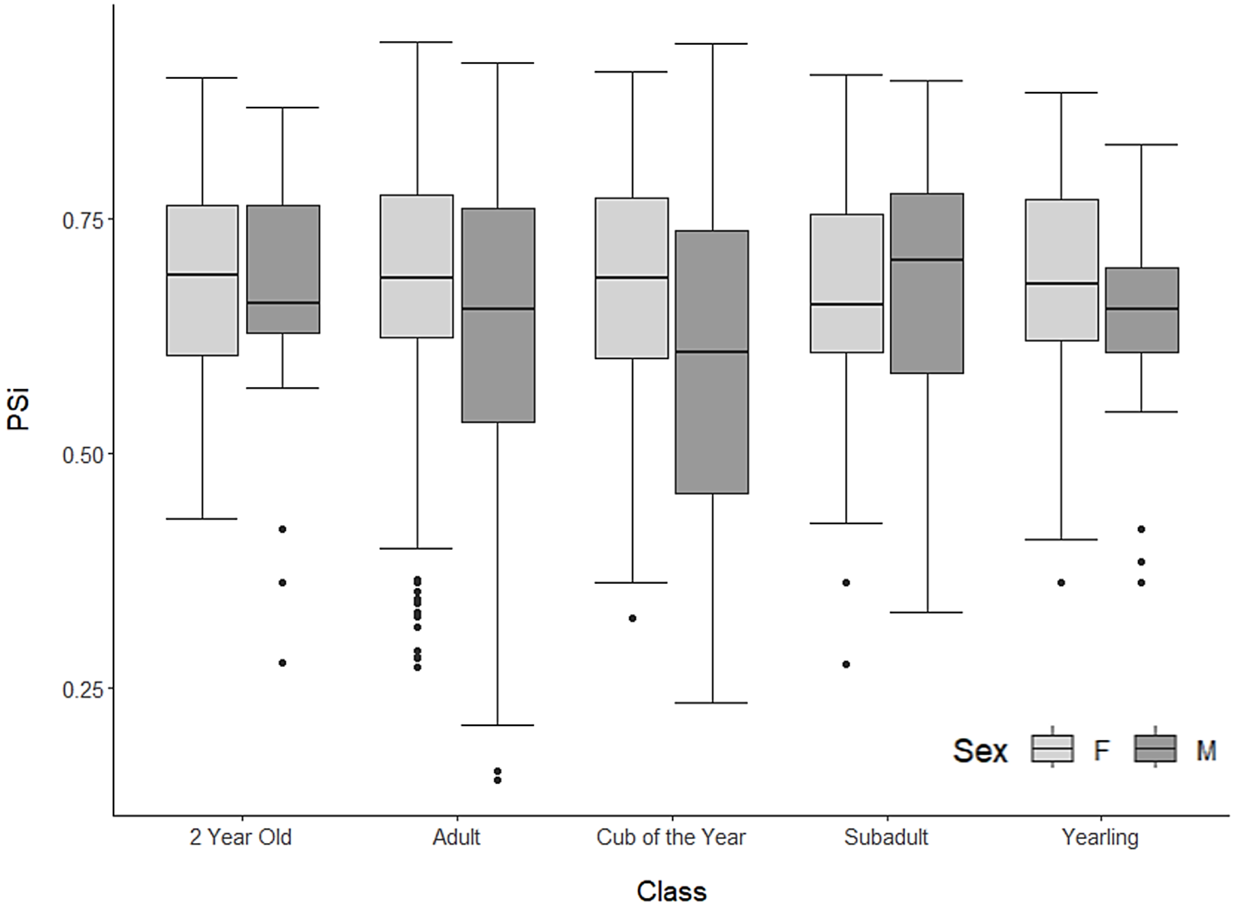

Figure 2.9. *PS_i* values for male and female polar bears across all age classes. Age class did not have a significant effect on *PS_i* ($\chi^2 = 5.26$, df = 4, p = 0.26), while sex was shown to significantly affect *PS_i* ($\chi^2 = 24.05$, df = 1, $p < 0.05$). Male bears have lower mean *PS_i* values for all age classes, apart from subadult bears in which the female bears demonstrate a lower mean *PS_i*.

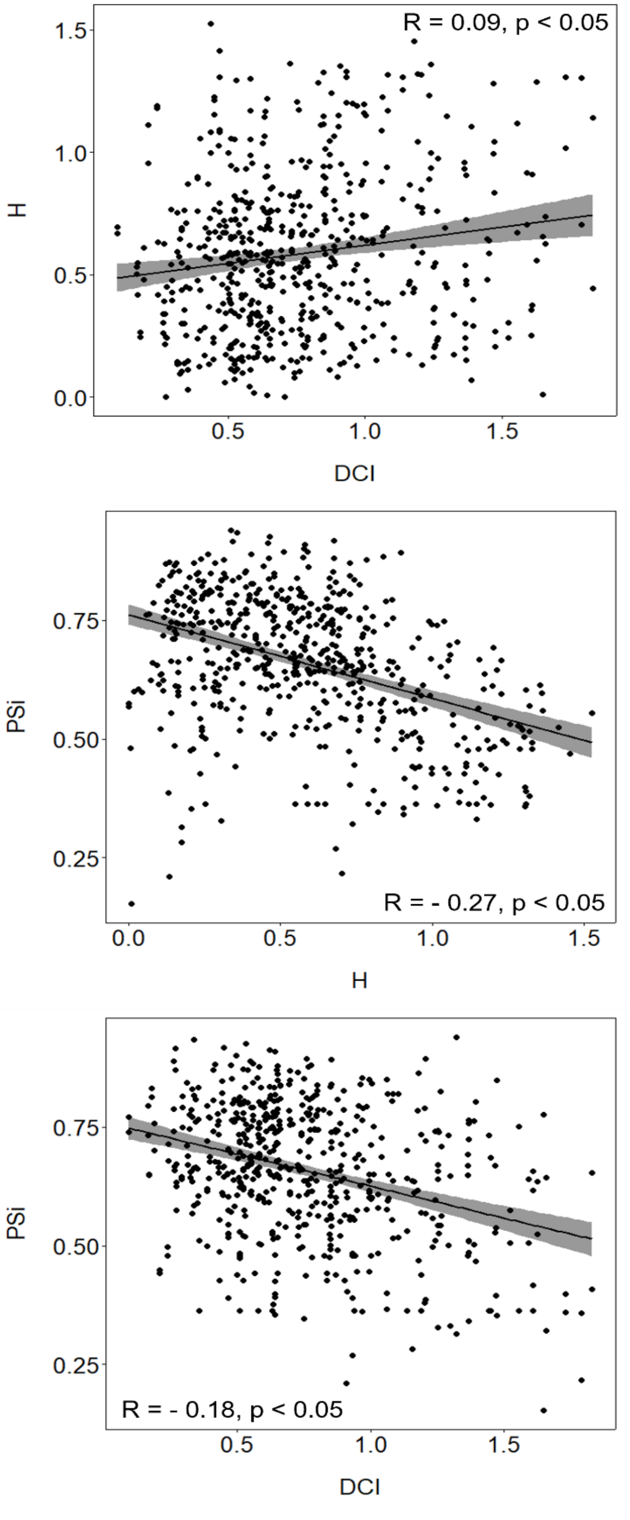

Figure 2.10. A comparison of the dietary metrics used to assess the foraging habits of polar bears in Western Hudson Bay between 2004 and 2021. No sampling was conducted in 2020. Correlation coefficients were derived from the Kendall Rank Correlation test. Only repeat-sampled bears (n = 221) were included to allow for a meaningful comparison between dietary metrics.

Chapter III – General Conclusion

Summary

Polar bears exhibit highly variable, individual foraging behaviours. Many individuals display broad dietary niches with generalist foraging strategies, while others display limited dietary niches with specialist foraging strategies (Thiemann et al. 2011). This thesis investigated the extent and drivers of individual dietary specialization in the Western Hudson Bay subpopulation over time, addressing the following hypotheses: (1) Individual specialization will be present in the population because polar bears exhibit characteristics that encourage specialization, such as intraspecific competition, low interspecific competition, and behavioural plasticity (Araújo et al. 2011). (2) Adult male bears will show the highest degree of individual specialization because their large body size allows them to exploit prey unavailable to other age and sex classes. (3) Solitary females will exhibit a greater degree of dietary specialization than females with dependent cubs because mothers will avoid areas with infanticidal males, limiting their access to a range of prey types. (4) In years where sea ice break-up occurs later, higher levels of dietary specialization will be observed, as bears can remain on the ice and hunt, allowing for selective feeding. (5) When the previous year's NAO is high, the degree of specialization will be higher due to increased competition. (6) When snow depth is lower, seal recruitment and survival will decrease, resulting in greater intraspecific competition among bears, and thus, a greater degree of specialization.

Diet composition was quantified for each bear sampled between 2004 and 2021, and final diet estimates were used to calculate the dietary niche breadth (*H'*), the dietary change index (*DCI*), and the proportional similarity index (PS_i) for each sample. PS_i was used to indicate the degree of individual specialization and was compared across age, sex, and reproductive classes. Environmental indices, including the Arctic and North Atlantic Oscillations, snow depth, and sea ice break-up, were investigated as potential extrinsic drivers of specialization. The results of this thesis provide an update on the foraging habits of polar bears in Western Hudson Bay while establishing an understanding of the prevalence and drivers of individual specialization within the population over time. Understanding the foraging habits of polar bears at both the individual and population levels will facilitate more accurate predictions of polar bear responses to continued climatic warming.

Diet estimates were best estimated using the average mink-derived calibration coefficients (Thiemann et al. 2008) consistent with several studies on polar bear diet composition across the Canadian Arctic (Thiemann et al. 2008, 2011; Galicia et al. 2015, 2021; Sciullo et al. 2017). Although the novel grizzly bear-derived (*Ursus arctos*) calibration coefficients (Thiemann et al. 2022) reflected diagnostically sound estimates, the overestimation of harbour seal in the Dog Food + Anchovy method and the substantially large proportion of ringed seal in the Dog Food + Salmon method are less ecologically plausible than proportions derived using the mink estimates. Similarly, the simultaneous method (Bromaghin et al. 2017) estimates did not align closely with the mink estimates. Thus, the average mink method was used to estimate diet. This thesis compared diet estimates produced using tested calibration coefficients with novel feeding trial and empirically derived calibration coefficients. My findings suggest that the grizzly-derived and simultaneously estimated calibration coefficients could become commonplace with continued testing and usage in future QFASA research.

Previous studies have quantified the diets of polar bears in Western Hudson Bay, highlighting the prevalence of ringed and bearded seals (Thiemann et al. 2011; Sciullo et al. 2017). My results indicated similar trends, with ringed and bearded seals serving as primary prey. Harbour seal, beluga whale, harp seal, and walrus each contributed smaller proportions to the diets. As the length of the open-water period trends longer each year, open-water species like harbour seals may be favoured over ice-dependent species like the ringed seal (Stirling and Derocher 1993). This trend was seen in the temporal diet data, with increases in harbour and harp seal in years where ringed seal abundance was low. Bearded seal consumption also showed a marked increase throughout the study, consistent with previous studies of polar bear diet composition (Sciullo et al. 2017).

Dietary niche breadth is often influenced by phenotypic constraints such as age and sex, with large-bodied individuals exhibiting greater dietary diversity than smaller conspecifics. Larger individuals typically have greater energetic requirements, which can be met with dietary flexibility (Clutton-Brock et al. 1987). My results were consistent with these findings, with adult male polar bears exhibiting the largest dietary diversity. Adult male bears are approximately twice the size of females, enabling them to hunt various prey types of differing sizes, thus increasing their dietary niche breadth. Adult male bears also had the most temporally variable diets compared to bears of other sex and age classes due to their substantial size, encouraging dietary flexibility (Thiemann et al. 2011). Adult females with or without cubs had temporally consistent diets, suggesting a limitation in their foraging habits due to their diminutive stature or avoidance of large infanticidal males (Taylor et al. 1985; Stirling and Derocher 1993).

Similar to previous studies, my results showed evidence of individual specialization, driven by factors such as age, sex, snow depth, sea ice break-up, and the North Atlantic Oscillation (Thiemann et al. 2011; Balme et al. 2020), which resulted in differential effects on the degree of specialization. Although the drivers were directly related to the degree of specialization, they served as indirect measures of an individual's learned hunting abilities (Coleman and Wilson 1998), sexual size dimorphism (Clutton-Brock et al. 1987), behavioural plasticity (Kobler et al. 2009), the abundance or distribution of prey (Araújo et al. 2011), and intraspecific competition (Bolnick et al. 2003, 2010; Svanbäck and Bolnick 2007), which have been documented as driving forces of individual specialization. Thus, this study has contributed to understanding the complex interactions of intrinsic and extrinsic drivers of individual dietary specialization. Further research will be required to understand the nature of individual specialization and its long-term implications on individual bears as climate warming intensifies.

Implications for Conservation

The polar bear relies on the sea ice as its primary habitat, where it spends time hunting, mating, and travelling (Stirling and Derocher 1993). Likewise, the polar bear's primary prey, the ringed seal, relies heavily on the sea ice for birthing and nursing their pups (Smith and Stirling 1975). Annual variations in the abundance and seasonal distribution of Arctic sea ice have been found to impact the survival and reproductive success of polar bears and ringed seals as a result of their reliance on the sea ice (Stirling and Latour 1978; Smith et al. 1991; Ferguson et al. 2005). With predicted annual declines in sea ice loss and an increased open water period, polar bears may be adversely affected, undergoing habitat degradation and food insecurity as their primary prey suffers from declines in body condition, natality, and survival (Stirling and Derocher 1993; Ferguson et al. 2005, 2017).

Climate-induced changes in sea ice have resulted in changes to polar bear foraging habits (e.g., Franz et al. 2022). As their ice-dependent prey species experience physiological stress, declines in body condition, and declining survival, intraspecific competition will be favoured as polar bears compete for a limited number of seals (Araújo et al. 2011; Thiemann et al. 2011). Increased intraspecific competition may lead to an increase in interindividual variation in foraging habits, whereby some individuals may choose to specialize on alternative prey species such as bearded seals (Thiemann et al. 2011). As more individuals specialize on alternative prey species, the resulting population would become a heterogeneous mixture of dietary generalists and specialists, occupying distinctive or minimally overlapping dietary niches.

This study identified the extent of dietary specialization within the Western Hudson Bay subpopulation and investigated the intrinsic and extrinsic drivers associated with specialization. Determining the factors responsible for increased interindividual variation in foraging habits will contribute to our understanding of the factors influencing individual fitness, which is vital to the conservation and management of polar bears in Western Hudson Bay. Continued monitoring efforts are necessary to ensure interindividual variation in foraging behaviours is considered when modelling responses of polar bears to future climatic warming.

Future Research

My thesis provided the first look at the extrinsic drivers of dietary specialization for polar bears in Western Hudson Bay. Although identifying intrinsic and extrinsic drivers of specialization will contribute to more effective management of polar bears in Western Hudson Bay, this study was limited to only one of 19 subpopulations across the circumpolar north. Further research should explore individual specialization across spatial scales to understand the extent of specialization across the Arctic. Continuing to assess and document the foraging habits of polar bears across the Arctic will allow for spatial comparisons of individual specialization between subpopulations.

Given that only one subpopulation was investigated in this thesis, it is likely that there may be other variables driving individual specialization across the polar bear's range. For example, in a large felid, intraspecific competition explained very little of the observed dietary specialization (Balme et al. 2020), unlike observed trends in specialization in this study. Instead, ecological opportunity and an individual's home range were reasonable predictors of specialization (Balme et al. 2020). An individual's home range size could impact the degree of specialization, with more extensive home ranges (Robertson et al. 2015) and home ranges boasting greater prey diversity (Cloyed and Eason 2016), resulting in increased specialization as a result of ecological opportunity. The quality and number of resources within the home range may also serve as a driver of specialization, with lower-quality home ranges encouraging intraspecific competition, which has been shown to drive individual specialization (Araújo et al. 2011; Robertson et al. 2015). Due to the considerable variation in polar bear home range size, it is plausible that an individual's home range size or prey availability could influence their degree of specialization (McCall et al. 2015) and should be investigated further.

My results indicated significant variation in the contributions of various prey types to polar bear diets. This study suggests that patterns in foraging habits depended on the availability and distribution of a prey species, with declines in primary prey driving individual specialization. However, this study was limited by a lack of prey abundance and distribution data. Without a thorough understanding of spatiotemporal trends affecting prey availability, it will be difficult to predict how the foraging habits of polar bears may change due to climate warming. Future research should continue to monitor trends in the distribution, abundance, and survival of key prey species of the polar bear to ensure the effective management of polar bears and their prey.

Although we can estimate an individual's diet 30-90 days before sampling (Thiemann et al. 2022), without tracking individual bears, we cannot know where they were while foraging on the sea ice. Movement data has been linked to studies on polar bear foraging (e.g., Togunov et al.

2022), as these studies can reveal spatial differences in foraging habits. Future research could begin to link movement data with specialization data to determine if spatial patterns of individual specialization emerge within a subpopulation. Since patterns of prey abundance and distribution have been shown to influence specialization within a population, it would follow that areas with high prey diversity or low prey abundance may result in a hotspot of dietary specialization.

In summary, my work confirmed previous findings regarding intrinsic drivers of specialization while providing novel insights into the environmental variables driving specialization within the subpopulation. This study was also the first to explore the effects of reproductive status on dietary specialization in the polar bear. Although this study provides an up-to-date account of the foraging habits and extent of individual specialization within the subpopulation, further research should examine spatiotemporal trends and potential drivers of dietary specialization across the Arctic.

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