# POLAR BEAR (*URSUS MARITIMUS*) FORAGING ECOLOGY IN WESTERN HUDSON BAY

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A DISSERTATION SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

**DOCTOR OF PHILOSOPHY**

GRADUATE PROGRAM IN BIOLOGY
YORK UNIVERSITY
TORONTO, ONTARIO
SEPTEMBER, 2017

## Abstract

The ecological response to climate change is expected to be especially pronounced across the circumpolar Arctic. Predicted declines in sea ice extent and seasonal duration are expected to affect the foraging ecology of marine species, particularly polar bears (*Ursus maritimus*) that rely on stable sea ice patterns for various aspects of their life history. The goal of this thesis was to quantify body condition and characterize diet composition of polar bears in western Hudson Bay over a broad temporal scale (2004-2014), and identify potential environmental factors that may influence dietary shifts in one of the southernmost subpopulations of this species.

Body condition was higher in adult and subadult females than males, consistent with energetic demands of gestation and lactation. Body condition also declined over time in adult and subadult males and females and was influenced by sea ice breakup and freeze-up dates. These trends suggest that the historical climate-driven declines in polar bear body condition documented in western Hudson Bay have continued. Variation in diet composition and dietary niche breadth across age, sex and reproductive groups suggest foraging behaviour is structured by energetic demands, intraspecific competition and sexual body-size dimorphism. Specifically, variation in diet and niche breadth across females was influenced by age (experience), energetic state and avoidance behaviours. Variation in diet composition and niche breadth between male and female bears, however, was more likely structured by body size, whereby capture of larger prey types and a broader range of prey species occurred with increasing body size. Body condition was positively related to niche breadth in adult males but negatively related to niche breadth in females with dependents, suggesting that less-selective foraging (scavenging) does not benefit body condition among reproductive females. Inter-annual fluctuations in diet composition reflected shifts in local prey availability during the study period, and sea ice breakup date influenced the diets of subadults and family groups, suggesting an increased sensitivity to sea ice conditions. Therefore, inter-annual variability in diet and declines in polar bear body condition likely reflect contemporaneous changes in sea ice availability and population demography, and have implications for the long-term conservation of this subpopulation.

# Acknowledgments

***This thesis is dedicated to the bears,***
***who let us take a small piece of them for the sake of research***

The completion of this research would not have been possible without the many people I have worked with during my time at York University and provided guidance along the way.

A special thank you to the Inuit hunters of Nunavut for the collection of fat samples from marine mammals harvested during annual subsistence hunts. This research could not have been made possible without the support of: Natural Sciences and Engineering Research council (NSERC, Canada), Environment and Climate Change Canada, Fisheries and Oceans Canada, Nunavut Wildlife Management Board, Earth Rangers Foundation, Isdell Family Foundation, Manitoba Sustainable Development, Parks Canada Agency, Schad Foundation, Wildlife Media Inc., the Northern Scientific Training Program (NSTP) and York University.

Thank you to Adrienne Dome and Cristalina Del Biondo who assisted me tremendously with program inquiries, funding applications and general guidance during my time at York. Thank you to Dr. Suzanne Budge and Christopher Barry (Dalhousie University) for assistance with gas chromatography and Dr. Evan Richardson (Environment and Climate Change Canada) for assistance with sea ice data. A special thank you to Dr. Steven Ferguson for providing marine mammal samples and providing important suggestions to manuscripts.

Thank you to all of the individuals I have met during my field seasons and to the entire community of Churchill, Manitoba for allowing myself and my colleagues the privilege of pursuing research in your backyard. Thank you to the Churchill Northern Studies Center and all of the researchers, volunteers and students for providing a very comfortable, entertaining and of course, educational experience during my stay. A special thank you to Dr. Nick Lunn for

providing invaluable feedback and suggestions on this project as well as all manuscripts, and for the many great memories I will forever cherish from the field.

I would like to thank my lab colleagues (past and present) for always keeping me entertained over the years. I am especially grateful for my lab mate and friend, Melissa Galicia who has been there through the joys (many) and sorrows (many more) of graduate school - I have made a lifelong friend in you and am grateful for the many laughs we shared.

I would also like to thank my two committee members: Dr. Bridget Stutchbury and Dr. Roberto Quinlan for providing guidance and suggestions that contributed significantly to the development of this thesis and its improvement. Your guidance and contributions are greatly appreciated. I would like to express thanks to my supervisor, Dr. Gregory Thiemann for giving me the opportunity to pursue research in the field of marine mammals and fulfill my lifelong dream. In addition to taking me on as a graduate student and providing me with much guidance and suggestions during my degree, Dr. Thiemann presented me with the opportunity to embark on the most extraordinary of field research experiences and aided in my professional development via conference support and lecture experience from which I learned a great deal and am extremely grateful.

Finally, I would like to thank the most important people in my life who have provided me with strength, patience and encouragement: my mom Fiorella, dad Nick, brother Timmy and best friend Matty. You were always there to lend an ear to anything I had to say, and kept me on my toes by frequently asking when I'll be "done." When I needed words of encouragement, reassurance or even a distraction, you were always up for the job. I cannot put into words how appreciative I am to have you in my life. I hope I can make all of you proud.

## Table of Contents

## List of Tables

CHAPTER II

CHAPTER III

CHAPTER IV

## List of Figures

### CHAPTER I

### CHAPTER II

### CHAPTER III

## CHAPTER IV

## Table of Abbreviations and Acronyms

| Acronym | Meaning |
|---|---|
| AIC | Akaike Information Criteria |
| $AIC_c$ | Akaike Information Criteria for small sample size |
| ANOVA | Analysis of Variance |
| BIA | Bioelectrical Impedance Analysis |
| COY | Cub-of-the-year (<1 year old) |
| FA | Fatty Acid |
| FAME | Fatty Acid Methyl Ester |
| MANOVA | Multivariate Analysis of Variance |
| NMI-FA | Non-methylene Interrupted Fatty Acid |
| PC | Principal Component |
| PCA | Principal Component Analysis |
| QFASA | Quantitative Fatty Acid Signature Analysis |
| SEM | Standard Error of the Mean |
| SLEN | Straight Line Body Length |
| SVL | Snout to Vent Contour Length |
| VIF | Variance Inflation Factor |
| WH | Western Hudson Bay |

# CHAPTER I

# Introduction to Predator Foraging Behaviour & Polar Bear Ecology

## Background

Predator-prey interactions are the subject of many ecological theories involving diet and foraging. The manner in which organisms respond to shifts in their environment and alter behaviour to maximize foraging efficiency is termed foraging ecology and involves a dynamic relationship between predator and prey populations. Apex predators are found in the upper trophic level of the food web, and their diet selection and foraging behaviour can structure communities and influence ecosystem functioning through top down effects (Borrvall & Ebenman, 2006; Sih, 2011). Ultimately, foraging behaviours and diet selection are shaped by natural selection to promote the survival of individuals who possess distinct behavioural characteristics that serve to increase fitness (Sih, 2011). Environmental shifts over a broad temporal scale may alter predictable foraging behaviour as well as predator-prey interactions. It is therefore important to understand the factors that influence the foraging ecology of apex predators, as their success in specific environments may have subsequent effects on community and ecosystem dynamics.

### Predation and food web ecology

The role of predation and the dynamics of predator-prey relationships are fundamental to studying food web ecology. The influence of predation by species in upper trophic levels can structure the processes and interactions that occur among species at lower trophic levels, thus influencing community dynamics. Predation is perceived to influence community structure via two contrasting yet influential processes, including both (i) lethal effects, and (ii) non-lethal or risk effects (Lima, 1998; Creel & Christianson, 2007). Direct lethal effects involve the mortality of individuals from a population via predation by individuals from upper trophic levels, directly affecting prey population abundance. Predation can significantly influence prey population size, for example, predation by cougars (*Puma concolor*) in south-central British Columbia was found to negatively affect population abundance and growth rates of two primary prey species, mule deer (*Odocoileus hemionus*) and white tailed deer (*Odocoileus virginianus*) (Robinson, Wielgus & Gwilliam, 2002). In this case, predation was a direct link to increased mortality of prey species and consequently influenced population size.

In contrast, indirect predation effects may involve prey behavioural or physiological changes in response to predation pressure that do not necessary result in direct mortality. The presence of predators in a habitat can result in changes to life history, distribution, habitat use, foraging and movement patterns in prey species (Ludwig & Rowe, 1990; McNamara & Houston, 1994; Lima, 1998; Creel & Christianson, 2007). Cumulatively, such changes in prey behaviour can be energetically costly and results in increased vigilance and a reduction in foraging time (Schmitz, Beckerman & O'Brien, 1997). Changes to herbivore feeding patterns as a result of predation risk can consequently alter the degree of herbivory and distribution of plant species (Schmitz *et al.*, 1997). For example, wolves have an important effect on prey populations through both direct predation as well as indirect risk effects. Changes in ungulate behaviour in response to wolf presence includes shifting distribution away from central wolf territory and reducing localized grazing intensity (Ripple *et al.*, 2001; Ripple & Beschta, 2004). Furthermore, the presence (or absence) of wolves in an ecosystem has been directly linked to changes in plant community structure. For example, multiple studies from differing habitats have showed that the absence of wolves resulted in a depression in plant growth rate (Mclaren & Peterson, 1994; White *et al.*, 1998) due to an increase in ungulate population size. Thus, the foraging behaviour of predators can exert strong top-down effects through a combination of both direct mortality and indirect risk effects that cumulatively structure community dynamics and predator-prey interactions.

Studying predator foraging behaviour is therefore crucial for a better understanding of food web dynamics and the influence of extrinsic factors such as environmental stochasticity on community structure. Furthermore, implementing suitable conservation strategies for protection of habitat and species is dependent upon a solid understanding of predator-prey dynamics and their response to broad-scale environmental change.

## Foraging ecology of predators

Predator diet selection and foraging behaviour is governed by interspecific competition, intraspecific competition, environmental heterogeneity and prey availability and behaviour (Sih, 2011). A predator's response to shifts in the aforementioned factors, particularly prey availability, is predicted by optimal foraging theory whereby the decision and preference to forage on certain prey is a function of multiple interacting variables including relative encounter rate, probability of attack, capture success and probability of consumption (MacArthur & Pianka, 1966; Chesson, 1983; Sih, 1993). Predator foraging behaviour and diet composition are thus influenced by prey behaviour and availability. For example, during periods of reduced primary prey availability, South American sea lions (*Otaria flavescens*) shifted their diet and foraging behaviour, whereby females increased time spent hunting at sea and less time on shore with pups, increasing vulnerability to predation (Soto, Trites & Arias-Schreiber, 2006). Diet breadth of adults also broadened to encompass a larger array of prey species during periods when primary prey was low, and shifted back to a selective diet when prey populations recovered (Soto *et al.*, 2006).

Optimal foraging theory also suggests that predators should invest energy on attack and capture of only the most "profitable prey" (Scheel, 1993; Sih, 1993, 2011; Karanth & Sunquist, 1995; Estes *et al.*, 2003), or prey that provides the greatest caloric return relative to energy expended in search time, capture, and handling (Stephens & Krebs, 1986; Krebs & Davies, 1993; Drickamer, Vessey & Jakob, 2002). The occurrence of other "less profitable" prey in the same habitat will have no influence on a predator's decision to shift diet and foraging behaviour, irrespective of their abundance (Schoener, 1971; Charnov, 1976; Krebs & Davies, 1993; Sih, 1993). For example, diet composition of the common dolphin (*Delphinus delphis*) was most reflective of prey species that provided the greatest energetic return including lancet fish (*Notoscopelus kroeyeri*), despite its low relative abundance in the environment (Spitz *et al.*, 2010). Furthermore, predators with high energetic demands (high basal metabolic rate, large body size, mobile) in particular, must focus foraging efforts on prey with a high caloric return to support their energetically expensive mode of living (Spitz *et al.*, 2012). In this case, a shift in predator diet will only occur if the encounter rate of the most profitable prey has declined considerably, often due to changes in environmental conditions.

Predators may shift foraging strategies in response to environmental change and inter/intra specific interactions, known as behavioural plasticity (Komers, 1997). Foraging strategies may become increasingly flexible and alternate foraging methods may develop to broaden ecological niches when: (i) competition amongst individuals is strong, (ii) environmental conditions fluctuate (resource availability or habitat composition), and (iii) phenotypic variation exists among individuals that can result in differences in behaviour (Klopfer & MacArthur, 1960; Partridge & Green, 1985; Komers, 1997; Estes *et al.*, 2003; Matich, Heithaus & Layman, 2011). The evolution of alternate foraging strategies is more likely to develop when strong intraspecific competition is coupled with weak interspecific competition, resulting in the divergence of foraging strategies within a population (Estes *et al.*, 2003). The shift to alternate foraging strategies, however, will involve a combination of interacting factors including predator experience in search and handling (Werner, Mittelbach & Hall, 1981; Bolnick *et al.*, 2003), prey availability, environmental heterogeneity and competitive interactions with other individuals (Bolnick *et al.*, 2003). Diet composition in gray wolf packs, for example, was highly variable as a function of age, body size and position in the pack's social hierarchy (Urton & Hobson, 2005). Lone wolves were found to have broader diets and their ability to most effectively hunt and capture prey was thought to be reduced when lacking the cooperation of the pack, resulting in opportunistic foraging on other prey such as smaller mammals, fish and birds (Urton & Hobson, 2005). Learning behaviour from mother to kin or among individuals in a group is also hypothesized to be an important factor involved in successful foraging (Estes *et al.*, 2003). If individuals become increasingly specialized to a particular prey type, minor fluctuations in prey availability may hinder adaptation to other food sources if foraging skills have become specialized in pursuit, capture and consumption (Bolnick *et al.*, 2003). It is important to note, however, that foraging plasticity can be energetically expensive as well. Sudden changes in diet composition requires a rapid response by an organism's digestive physiology, morphology and anatomy to allow for the implementation of a new behaviour (i.e., capture and consumption of a different prey species). Consequently, this additional energetic expenditure may negatively affect reproduction and growth (Komers, 1997).

### Polar bear ecology and western Hudson Bay

Few species have evolved to exist in extreme environments, including the Arctic which is characterized by high seasonal variation in snow, temperature and ice cover. Polar bears (*Ursus maritimus*) reside in 19 discrete subpopulations across the circumpolar Arctic and are considered apex predators reliant on the marine environment, particularly sea ice, for foraging, breeding, migration and denning (Amstrup, 2003). Because much of their life history is dependent upon sea ice dynamics, polar bears often migrate to areas with high productivity such as shallow areas near shore, and their distribution varies seasonally based on ice melt patterns (Amstrup, 2003).

Western Hudson Bay (WH) is one of the southernmost subpopulations of polar bears and encompasses approximately 435,000 km$^2$ including regions of Ontario, Manitoba and Nunavut (Atkinson, Garshelis & Hedman, 2012) (Fig. 1). Ice coverage in Hudson Bay follows a predictable pattern of melt and freeze-up, and timing of such events consequently drive multiple aspects of polar bear foraging behaviour. Onset of freeze-up varies from November to December, and during the ice-covered season, bears migrate onto the sea ice for foraging and breeding (Kovacs *et al.*, 2011). During this time, polar bear diets are comprised mainly of ringed seal (*Pusa hispida*) and bearded seal (*Erignathus barbatus*) with opportunistic foraging on harbour seal (*Phoca vitulina*), harp seal, (*Pagophilus groenlandica*), walrus (*Odobenus rosmarus*) and beluga whale (*Delphinapterus leucas*) (Iverson, Stirling & Lang, 2006; Thiemann *et al.*, 2007a; Thiemann, Iverson & Stirling, 2008a). The on-ice foraging season is crucial for survival as bears use this time to accumulate energy reserves to be later mobilized during the fasting season (Stirling & McEwan, 1975; Stirling & Archibald, 1977; Best, 1985). Peak foraging occurs during the April-June seal pupping period, when seal pups are weaned and their inexperience in predator avoidance in conjunction with high population abundance make them ideal prey, providing a high caloric return comprised of up to 50% fat by wet weight (Stirling & McEwan, 1975; Stirling & Archibald, 1977; Stirling & Øritsland, 1995). Target prey include seals under two years of age due to small body size and easy capture, accounting for over 80% of seal kills by polar bears (Stirling & McEwan, 1975). Following this peak foraging period, ice melt begins to occur in June and July, with counter clockwise currents and wind patterns causing initial melt along the eastern coast of Hudson Bay, later followed by ice melt in more northerly waters (Stirling *et al.*, 2004). This pattern allows for remnant ice to be distributed along the western and southwestern coasts of Hudson Bay when polar bears begin to migrate onto land where they will remain until subsequent ice freeze-up.

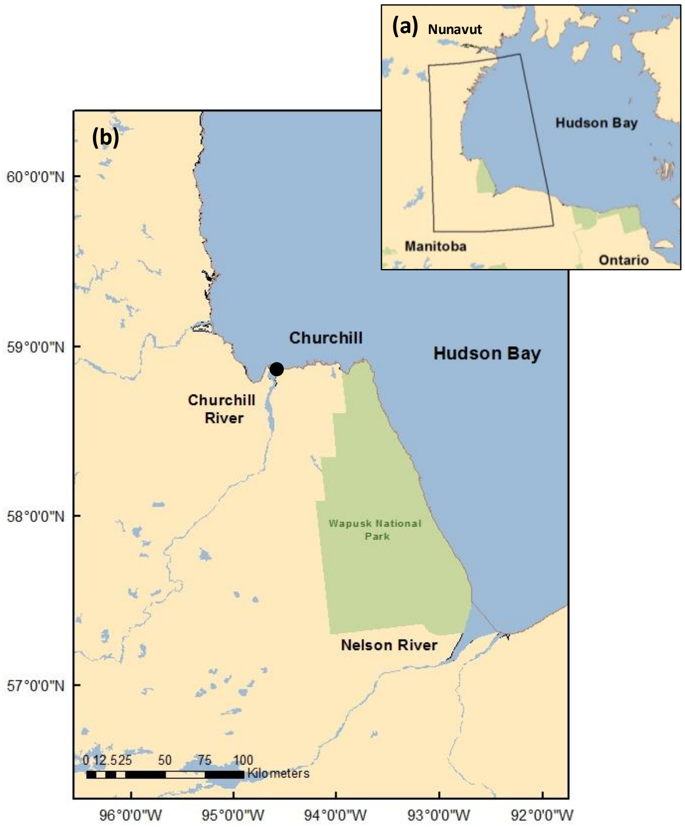

**Figure 1.** (a) Map of the Hudson Bay region with solid line outlining the management zone of the Western Hudson Bay polar bear subpopulation; (b) geographic area between Churchill and

Nelson River (including Wapusk National Park) where bears were annually surveyed and captured via helicopter. Location of Churchill, Manitoba represented with ●

While bears remain on shore, energy expenditure is minimal and individuals do not typically engage in aggressive interactions, mating or migratory behaviour. Individuals experience an approximate four month fast during which terrestrial foraging on berries, kelp, goose eggs and other scavenging may occur (Lunn & Stirling, 1985; Ramsay & Hobson, 1991; Derocher, Andriashek & Stirling, 1993; Pilfold *et al.*, 2016). Pregnant females experience a prolonged fasting period of approximately eight months on shore, including denning, gestation and early lactation (Ramsay & Stirling, 1986). Spatial segregation between solitary males, solitary females and family groups (females with dependent offspring) occurs on shore, whereby males reside near coastal areas while family groups and females move further inland (Latour, 1981; Derocher & Stirling, 1990a; McCall *et al.*, 2016). On shore distribution patterns of bears are likely to be a function of energy conservation and avoidance behaviour (Taylor, Larsen & Schweinsburg, 1985; Derocher & Stirling, 1990b), as past observations indicate the potential for male cannibalism on subadults, females and cubs (Taylor *et al.*, 1985; Stirling & Ross, 2011). Movement patterns at the end of the open water season are towards northern coastlines where ice freeze-up occurs first (Cape Churchill), allowing for early access to their foraging habitat (Stirling & Archibald, 1977; Stirling *et al.*, 2004). It is increasingly evident that much of the life history and behavioural patterns of polar bears is reliant upon environmental patterns including ice formation, (Peacock *et al.*, 2010).

Polar bears are considered specialized predators, with diets consisting of high energy marine mammal blubber and individuals often abandon lower energy protein and muscle components to consume only fat (Stirling, 1974; Amstrup, 2003). This adaptive behaviour is beneficial as lipid metabolism releases water therefore hydrating the individual, while protein catabolism requires significant water intake (Nelson *et al.*, 1983), which is difficult to acquire as individuals must expend energy to melt snow or ice. Past studies on polar bear foraging indicate considerable variation in individual prey species consumption, likely associated with fluctuating environmental conditions  (Thiemann *et al.*, 2007a, 2008a, 2011a). Changing sea ice conditions are thought to result in increased opportunistic foraging (scavenging) and behavioural plasticity during periods in which primary prey is less available (Regehr *et al.*, 2007; Thiemann *et al.*, 2007a, 2008a). For example, subordinates (younger inexperienced bears, females with cubs) may scavenge on leftover seal carcasses (Stirling & McEwan, 1975; Derocher, Lunn & Stirling, 2004), indicating the potential for adaptability during periods of shifting prey availability. Scavenging on alternate prey can also occur on shore, for example through increased predation on bird nesting colonies (Iverson *et al.*, 2014; Dey *et al.*, 2016). Prey availability is suspected to have an important effect on polar bear foraging behaviour and diet composition, as distribution and abundance are likely to alter length of foraging time, techniques used and energy expended for search, capture and handling.

Identifying factors that can influence polar bear foraging behaviour can serve as a useful indicator of individual and population level health. For example, seasonal or inter-annual fluctuations in body condition can be indicative of broad scale ecological change that may affect species' ability to successfully forage and ultimately affect survival. Because adipocytes (fat cells) swell and shrink as an organism fattens and thins (e.g., during fasting periods) (Iverson, 2008), adipose tissue retrieved from polar bears can be used as an index of overall fatness and indicator of body condition (Thiemann, Iverson & Stirling, 2006; Stirling, Thiemann & Richardson, 2008).

## Diet composition & fatty acid analysis

Understanding diet composition of apex predators is important for identifying broad scale environmental change that may be occurring and its effect on food web dynamics. Past methods used to determine predator diet included locating and identifying kill remains, direct predation observations, analyzing stomach contents and scat collection (Thiemann, 2008). Although these methods can provide information on predator-prey interactions and recent consumption events, they provide little insight into the age and sex class of both forager or prey species when consumed over a broad temporal scale, beyond the most recent foraging event (Thiemann, 2008). For example, a predator's rapid digestion of soft-bodied prey may render only hard parts available for scat analysis, generating bias in diet estimates (Iverson *et al.*, 2004). Further, scat analysis, stomach contents and direct observation of foraging only provide a snapshot of diet composition, thus cannot provide insight into seasonal or inter-annual fluctuations (Iverson *et al.*, 2004). Assessing polar bear diet using the aforementioned methods is also difficult as prey carcasses may be scavenged or cached by other predators and home ranges are broad and often too remote to observe predation events (Iverson *et al.*, 2004). Stable isotope analysis has been used to assess diet of predators by quantifying isotopic ratios of nitrogen and carbon in various tissues including hair, blood, and lipid (Bentzen *et al.*, 2007; Cherel *et al.*, 2007; Horton *et al.*, 2009). Although stable isotope analysis can provide insight into the trophic level of consumer species, it limits its analysis to only two chemical elements.

Fatty acid analysis has been more recently used to determine diet of apex predators including black bears (Iverson, McDonald & Smith, 2001b), polar bears (Grahl-Nielsen *et al.*, 2003; Iverson *et al.*, 2006; Thiemann *et al.*, 2006, 2007a, 2008a), seals and whales (Hooker *et al.*, 2001; Grahl-Nielsen *et al.*, 2003; Herman *et al.*, 2005; Beck *et al.*, 2007; Thiemann, Iverson & Stirling, 2008b; Rosen & Tollit, 2012). Fatty acids (FA) are found in the lipid of consumers and can be distinguished between dietary and endogenous sources based on fatty acid chain length and the number and position of double bonds (Olsen, 1998; Iverson *et al.*, 2004; Budge, Iverson & Koopman, 2006; Iverson, 2008; Thiemann, 2008). Fatty acids typically possess 14 to 24 carbon atoms, 0 to 6 double bonds, a methyl group on one end and a carboxyl group on the other (Iverson, 2008). Consumer fatty acids that are biosynthesized are simpler short chain structures with no double bonds (saturated) (Iverson, 2008). In contrast, primary producers can produce long-chain unsaturated fatty acids, particularly algal species that can be consumed by upper trophic level species (Iverson, 2008). FA derived from diet (prey) are predictably assimilated into adipose tissue and remain for a period of weeks to months, thereby reflecting diet composition over ecologically relevant timescales (Budge *et al.*, 2006; Iverson, 2008; Thiemann, 2008). Determining diet composition via FA analysis requires sampling adipose tissue depots that contain energy reserves (Thiemann, 2008), rather than those involved in structure or other functions (i.e., muscle and fat deposits affiliated with the kidney, heart or extremities) (Budge *et al.*, 2006; Thiemann, 2008).

Diet composition of apex predators can be investigated using FA analysis in both a qualitative and quantitative manner. Firstly, “qualitative analysis” compares FA across groups of predators or individuals of different age and sex within species, and although this technique does not identify quantitative proportions of specific prey items, it can identify spatiotemporal variability in diet in relation to various environmental factors (Budge *et al.*, 2006; Iverson, 2008; Thiemann, 2008). Secondly, specific prey items may also possess novel FA that are uncommon and therefore can be used to identify the consumption of specific or rare prey types (known as biomarkers) (Budge *et al.*, 2006; Thiemann *et al.*, 2007a). For example, non-methylene interrupted fatty acids (NMI-FA) are unusual polyunsaturated FA that can only be synthesized by mollusk species. Consequently, bottom feeding species that specialize in this diet, including bearded seal and walrus, will possess greater proportions of NMI-FA and can be identified in predator diets (Thiemann *et al.*, 2007a). Finally, the most robust method of using FA to determine diet is through quantitative fatty acid signature analysis (QFASA), in which each FA consumed by the predator is identified and measured to create a profile or “signature” (Iverson *et al.*, 2004). This technique then models each individual predator's FA signature as a linear combination of multiple prey species that reduces the distance between the observed and modeled predator signatures (Iverson, 2008). Some FA will be metabolized by the predator while others will be biosynthesized (produced by the predator itself); therefore a predator’s FA signature will never exactly match its diet (Iverson *et al.*, 2004). To correct for the potential of certain FA appearing in higher or lower amounts in the predator signature than is actually represented in the diet, calibration coefficients are derived based on metabolic patterns observed in captive animal feeding studies to determine the relative “weight” of each FA (Iverson *et al.*, 2004; Iverson, 2008; Thiemann, 2008). Ultimately, QFASA estimates the relative abundance (proportion) of each prey species in the individual predator diet (Iverson *et al.*, 2004; Thiemann, 2008). Since Arctic species comprise simple food webs with few trophic interactions, determining diet of polar bears using FA analysis is relatively simple as the number of prey species is minimal (2 to 8 species) (Thiemann, 2008). If individuals are sampled both inter-annually and across a wide geographic range, this technique can provide an indication of shifts in prey species consumption across broad temporal and spatial scales.

### Possible effects of climate change

Shifts in sea ice habitat and climate have become evident across the Arctic with potential negative implications for polar bear survival. Between 1971 and 2001, air temperatures have increased by approximately 0.5° C per decade in Hudson Bay (Gagnon & Gough, 2005) with significant declines in sea ice extent, thickness and seasonal duration resulting in shifts in both ice freeze-up and breakup dates, specifically in WH (Hochheim, Barber & Lukovich, 2010; Hochheim & Barber, 2014). Consequently, sea ice breakup in WH has been occurring approximately 2.5 to 3 weeks earlier than 30 years ago (Gagnon & Gough, 2005; Stirling & Parkinson, 2006; Hochheim & Barber, 2014). Furthermore, changes in seasonal ice melt also results in increased sea ice fragmentation (Mauritzen *et al.*, 2003a). Earlier spring ice melt may negatively influence polar bear foraging behaviour, whereby individuals have less time to forage on fat rich prey prior to the fall fasting season (Derocher *et al.*, 2004; Regehr *et al.*, 2007). Both maternal body condition and fluctuating environmental conditions, for example, may negatively affect cub survival (Derocher & Stirling, 1996; Regehr *et al.*, 2007). Mean female body mass in WH bears has shown a steady decline since 1980 with the potential for effects on population growth rate, as adult females weighing less than 189 kg may not be able to produce offspring (Derocher, Stirling & Andriashek, 1992). Moreover, litter mass, body size of cubs and number of offspring has shown marked declines in years following reduced ice availability (Rode, Amstrup & Regehr, 2010), thereby affecting reproductive output. Due to extensive field research, WH serves as a microcosm from which a great deal of information regarding the potential effects of climate change on polar bear foraging behaviour, body condition and ultimately survival can be retrieved and used to project future change in High Arctic subpopulations.

## Dissertation outline

The overall objective of this research is to investigate polar bear foraging behaviour and the underlying mechanisms that may be structuring intraspecific variation in prey selection and body condition. As WH is an area of continuous polar bear research over the past several decades, I use this subpopulation to study seasonal and inter-annual fluctuations in diet composition and body condition and employ environmental data to identify the possible link between changes in sea ice habitat and polar bear foraging.

In Chapter 2, I investigate body condition in WH polar bears over a broad temporal scale. Multiple metrics have been used to quantify body condition in polar bears across their circumpolar range (Thiemann *et al.*, 2006; Stirling *et al.*, 2008; Molnár *et al.*, 2009; Obbard *et al.*, 2016); however, the accuracy and comparable practicality of these metrics for use in the field has not been assessed. In this study, I compare body condition in polar bears of differing age class, sex and reproductive status as measured by six condition metrics. I also explore the use of a relatively new technique never before performed on WH polar bears, known as bioelectrical impedance analysis (BIA) and evaluate its utility and feasibility in the field compared to other common metrics. As body condition of polar bears is collected over a broad temporal scale (2004-2014), I also evaluate seasonal and inter-annual trends and discuss my results in relation to variability in sea ice conditions. This study serves as a contemporary investigation of WH polar bear body condition and an individual- and population-level response to the broad scale environmental changes occurring in the Arctic.

In Chapter 3, I investigate diet composition of 374 WH female polar bears across age and reproductive status. Sex and age based differences in polar bear diet composition have been identified (Thiemann *et al.*, 2007a, 2008a, 2011a); however, less is known regarding the intraspecific variability in foraging behaviour and prey selection among females based on age and reproductive status. In this study, I use QFASA to derive diet estimates of solitary adult females, females supporting yearlings, females supporting cubs-of-the-year (COY) and subadults and compare individual prey consumption and foraging behaviour. I also investigate inter-annual trends in diet composition across each group over a ten year period in relation to timing of sea ice breakup. My results are discussed in light of what is known regarding female polar bear foraging behaviour as well as known changes in prey availability in Hudson Bay.

In response to the inter-annual fluctuations in both polar bear body condition (Chapter 2) and diet composition (Chapter 3) that have occurred during the past decade, I use Chapter 4 to examine the possible relationship between diet selection and body condition across age and sex classes in WH polar bears. As polar bears are a sexually size dimorphic species, I compare diet composition and dietary niche breadth across sex to determine if differing body size and energetic demands influence diet selection and is consequently reflected in body condition. Past research suggests diet selection influences body condition in mammals (Litvaitis, Clark & Hunt, 1986; Crête & Huot, 1993; Iverson, Arnould & Boyd, 1997a; Beck, Bowen & Iverson, 2003); however little is known regarding how polar bear foraging habits may contribute to stored energy (body condition). I discuss my results in the context of known patterns in polar bear foraging behaviour and life history that may vary with age and sex.

In the concluding Chapter 5, I summarize my main findings and general conclusions. I also discuss this research in a broader context regarding polar bear foraging behaviour, body condition and possible adaptive responses to continued declines in sea ice habitat occurring across the Arctic. Further, I highlight specific aspects of polar bear foraging ecology that require continued research and discuss the implications of climate warming on WH polar bear survival and continued conservation of this species across the Arctic.

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# CHAPTER II

# Comparative assessment of metrics for monitoring the body condition of polar bears in western Hudson Bay

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Original manuscript citation:

Sciullo, L., Thiemann, G.W., Lunn, N.J. (2016). Comparative assessment of metrics for monitoring the body condition of polar bears in western Hudson Bay. *Journal of Zoology*. **300**: 45-58.

## Abstract

Many species experience prolonged periods of fasting due to changes in habitat and food availability. Metrics that quantify energy reserves available during these periods allow for a better understanding of the interaction between environmental change and species survival. Body condition of polar bears has been assessed using morphometric and subjective indices, lipid content of adipose tissue, body composition models and, recently, bioelectrical impedance analysis (BIA). We assessed the utility of BIA and examined correlations among condition metrics for 134 free-ranging polar bears on shore in western Hudson Bay in fall 2012-2013 and spring 2013-2014. We also examined long-term inter-annual and seasonal trends from 736 bears handled in 2004-2014. Total body fat, as estimated from BIA, was correlated with adipose tissue lipid content, energy density, and fatness index, but not storage energy or skull width. Body condition was higher in adult and subadult females than males, consistent with energetic demands of gestation and lactation. Adult females had higher body fat in the fall than spring, and body fat decreased with increasing number of dependent offspring. Long-term trends indicated a decline in body condition for all adult and subadult males and females. Although there were similar patterns among BIA and other established metrics, its limitations in the field suggest that BIA may not be the most efficient method of monitoring body composition in polar bears in comparison to other modeled metrics, such as energy density. Declines in polar bear body condition over time may be a reflection of contemporaneous changes in sea ice availability and population demography, and thus have implications for the long-term conservation of this subpopulation.

**Key Words:** bioelectrical impedance analysis, lipid content, energy storage, body fat, *Ursus maritimus*, western Hudson Bay

## Introduction

Various measures of body condition are used in ecological research to assess the health and nutritional status of individuals, providing insight into biological interactions between organisms and their environment. Body condition in mammals is thought to improve with increased fat stores, which are used for the provision of energy during periods of food shortage (Pitts & Bullard, 1968; Lindstedt & Boyce, 1985). Condition has been quantified in a range of species to better understand relationships with heritability from parent to offspring (Gosler & Harper, 2000), reproductive success and breeding (Chastel, Weimerskirch & Jouventin, 1995; Simard *et al.*, 2014), and behaviour and energetics (Gallagher *et al.*, 2014; Richard *et al.*, 2014). Given the close relationship between habitat quality and foraging success (Kitaysky, Wingfield & Piatt, 1999; Taylor *et al.*, 2001; Maceda-Veiga, Green & De Sostoa, 2014), body condition can serve as an early indicator of broad scale ecological and environmental change, including reduction in habitat quality or food availability. Accurately measuring body condition can thus provide important insights into fundamental ecological processes relevant to the conservation and management of wildlife populations.

Many mammalian species undergo considerable fluctuations in body composition as energy stores are accumulated and mobilized in response to seasonal conditions and life history patterns. For example, mammalian overwinter survival is linked to fall body size and fat stores in both hibernating (Murie & Boag, 1984; Hilderbrand *et al.*, 2000) and non-hibernating species (Festa-Bianchet *et al.*, 1997; Cook *et al.*, 2004; Rödel *et al.*, 2004). Many species endure prolonged seasonal fasts, or periods of reduced foraging, associated with breeding and reproduction. Consequently, the acquisition of mates (Byers *et al.*, 2005; Byers, Byers & Dunn,

2006) and production and weaning of offspring (Farley & Robbins, 1995; Samson & Huot, 1995) may require large energy stores. Thus, fat and energy reserves in an organism are closely tied to biological fitness.

Morphometric relationships between body length and mass have been used as proxies of body condition in small mammals (Krebs & Singleton, 1993; Schulte-Hostedde, Millar & Hickling, 2001), large felids (Marker & Dickman, 2003), ungulates (Festa-Bianchet *et al.*, 1997), and ursids (Cattet *et al.*, 2002; Derocher, Wiig & Anderson, 2002; Rode, Amstrup & Regehr, 2010). Subjective indices of overall fatness, based on thickness of subcutaneous fat depots, have also been used in large mammals (Audige, Wilson & Morris, 1998; Stirling, Thiemann & Richardson, 2008; Wijeyamohan *et al.*, 2015). Adipocytes expand more rapidly than they proliferate during periods of lipid deposition, and shrink during fasting periods when lipid is mobilized (Schemmel, 1976; Pond, Mattacks & Ramsay, 1992). Therefore, adipose tissue lipid content, relative to water and non-fat components, reflects overall fatness in birds (Johnson *et al.*, 1985), cetaceans (Aguilar & Borrell, 1990; Gómez-Campos, Borrell & Aguilar, 2011), pinnipeds (Beck, Smith & Hammill, 1993), and polar bears (*Ursus maritimus*) (Thiemann, Iverson & Stirling, 2006; McKinney *et al.*, 2014).

Measures of body composition can also quantify energy stores and provide a more detailed representation of body condition. Body composition measures may involve destructive techniques such as whole body homogenization that prevent repeated measurements (Speakman, 2001; Wirsing, Steury & Murray, 2002). Conversely, non-lethal techniques, such as isotope dilution (Parker *et al.*, 1993; Farley & Robbins, 1994; Arnould, 1995) and mathematical models (Molnár *et al.*, 2009), allow for measurements of the same individual over time. Bioelectrical impedance analysis (BIA) has emerged as a relatively rapid, non-invasive and repeatable measure of body composition (Kushner, 1992; Gales, Renouf & Worthy, 1994). BIA is based on the principle that lean mass contains more water and electrolytes compared to fat (Lukaski *et al.*, 1986; Lukaski, 1987). Transmission of an electrical current through the organism will have greater resistance through fat tissue and more conductivity through lean mass (Hilderbrand, Farley & Robbins, 1998), with body water and body fat being inversely related (Farley & Robbins, 1994). BIA has been used to quantify fatness in a range of species, including humans (Lukaski *et al.*, 1985), porcupines (*Erethizon dorsatum*; Barthelmess, Phillips & Schuckers, 2006), pinnipeds (Gales *et al.*, 1994), skunks (*Mephitis mephitis;* Hwang, Larivière & Messier, 2005), raccoons (*Procyon lotor*; Pitt, Larivière & Messier, 2006), horses (*Equus* species; Latman *et al.*, 2011), and ursids (Hilderbrand *et al.*, 2000; Gau & Case, 2002; Robbins *et al.*, 2012).

Similar to other ursids, polar bears alternate between periods of hyperphagia and fasting and experience seasonal cycles in fatness (Derocher *et al.*, 1990; Atkinson & Ramsay, 1995; Thiemann *et al.*, 2006). In the Western Hudson Bay subpopulation, individuals are forced to migrate to shore as sea ice habitat melts each summer. Progressively earlier sea ice breakup over the last several decades (Gough, Cornwell & Tsuji, 2004; Gagnon & Gough, 2005; Hochheim & Barber, 2014) has shortened the spring foraging period and negatively influenced body condition (Stirling, Lunn & Iacozza, 1999; Derocher, Lunn & Stirling, 2004; Regehr *et al.*, 2007). Simultaneously, progressively later freeze-up in the fall (Hochheim & Barber, 2014) has extended the time bears spend on shore, without access to marine mammal prey. Several studies have reported terrestrial feeding during the onshore period (Derocher, Andriashek & Stirling, 1993; Gormezano & Rockwell 2013) and have suggested that terrestrial foods could offset nutritional deficits from reduced on-ice foraging (Gormezano & Rockwell 2015). However, empirical support for this hypothesis is still lacking (Hobson, Stirling & Andriashek 2009; Rode *et al.*, 2015). Monitoring polar bear body condition over time may provide an indication of large scale ecological change in this subpopulation and inform bioenergetic models aimed at predicting the demographic effects of future climate change (Molnár *et al.,* 2010, 2011).

Despite its use in quantifying fatness in many species, BIA has yet to be applied to polar bears in western Hudson Bay. This technique may be useful as it directly quantifies total body fat in a manner that is relatively quick, non-invasive, and non-destructive. The objectives of this study were to (i) comparatively assess BIA with other established condition metrics among age and sex classes and evaluate its utility and feasibility in the field; (ii) assess potential contribution of terrestrial feeding to overall body condition on shore; and (iii) evaluate inter-annual trends (2004-2013) in body condition in relation to polar bear life history patterns and long-term changes in sea ice.

## Materials and Methods

### *Capture of free-ranging polar bears*

Polar bears were captured in an approximate 12 000 km$^2$ area in northeastern Manitoba between the Churchill and Nelson Rivers and throughout Wapusk National Park of Canada during the fall open water (September) and spring ice covered (February-March) seasons 2004-2014. Spring captures consisted of family groups, with females and cubs exiting dens and migrating onto the sea ice. Bears were located from a Bell 206B helicopter and immobilized via remote delivery of a 1:1 combination of tiletamine hydrochloride and zolazepam hydrochloride (Telazol®, Fort Dodge Laboratories, Fort Dodge, Iowa, USA or Zoletil®, Virbac S.A., Carros, France) following standard protocols (Stirling, Spencer & Andriashek, 1989). Individuals were marked with uniquely numbered plastic tags in each ear and tattoos on the inside of the upper lip. A vestigial premolar was extracted for aging (Calvert & Ramsay, 1998) for independent bears not previously handled. Bears were classified into the following age classes: cub of the year (COY, <1 year), yearling (dependent 1-2 years), subadult (independent bears 2-4 years), and adult (5+ years). We measured axillary girth (cm), straight-line body length (tip of the nose to the last vertebra of the tail, cm), and zygomatic skull width (mm) on each bear in sternal recumbency. Skull measurements have been found to fluctuate with demographic and environmental factors (food availability, diet composition, and habitat) in both subadult and adult life stages of brown bears (*U. arctos*) (Mowat & Heard, 2006; Zedrosser, Dahle & Swenson, 2006) and polar bears (Rode *et al.*, 2010). We scored each bear on a fatness index from 1 to 5 based on visual observation and palpation of subcutaneous fat on the dorsal side and rump (Stirling *et al.*, 2008). Body mass was estimated using regression equations based on axillary girth and straight-line body length (Thiemann *et al.*, 2011). All bears (excluding spring COY) were sampled for adipose tissue lipid content using an 8 mm biopsy taken approximately 15 cm lateral to the base of the tail. Samples were stored frozen (-20°C) in air-tight cryogenic vials until analysis. We recorded evidence of terrestrial foraging (e.g., remnants of berries or vegetation around the mouth or presence of feces).

We collected BIA measurements on a subset of bears captured in fall 2012-2013 and spring 2013-2014 using a Quantum X analyzer (RJL Systems, Clinton Township, Michigan, USA) and following the protocol (snout-to-tail method) outlined by Farley and Robbins (1994). Briefly, immobilized bears were positioned on a plastic tarp when on damp ground or snow to prevent interference with the current. Bears were placed in sternal recumbency, with hind legs fully extended and forelimbs bent at 90 degrees. A 21 gauge, 1.5" vacutainer needle was inserted in the rump approximately 3 cm on either side of the base of the tail. We attached alligator clips to both needles and on moistened gums above each canine. Resistance readings were taken twice and mean values were used for calculating percent body water and body fat using equations derived by Farley and Robbins (1994). Because the Farley and Robbins (1994) model used snout-to-vent contour length to relate total body water to BIA resistance, we estimated snout-vent contour length (SVL) from straight-line body length (SLEN) using the relationship: $SVL = 1.11 \cdot SLEN - 13.65$ based on measurements from 109 live-captured polar bears in the Chukchi Sea (U.S. Fish and Wildlife Service, unpublished data). We collected BIA readings prior to obtaining biological samples and noted any movement, irregular breathing patterns or vocalizations. Environmental conditions (e.g., precipitation, wet ground) were recorded. Bears with wet fur produced inconsistent readings and were omitted from analyses. Omitted bears included adults ($n = 11$), subadults ($n = 2$), and COY ($n = 6$). Bears measured for BIA were also weighed using an electronic load cell suspended from a tripod. Capture and handling procedures were reviewed and approved annually by the Animal Care and Use Committees at Environment Canada (Prairie and Northern Region) and York University.

### *Body condition measures & statistical analysis*

Adipose tissue biopsies were weighed after removing attached skin or muscle. Lipid was quantitatively extracted (Iverson, Lang & Cooper, 2001; Budge, Iverson & Koopman, 2006) and total lipid content expressed as percent total wet weight ± standard error of the mean. As BIA was performed on bears only in fall 2012 and 2013 and spring 2013 and 2014, a comparative analysis of body condition metrics was limited to this time period and included total body fat (estimated from BIA), zygomatic skull width (mm), fatness index, adipose tissue lipid content, and both storage energy (MJ) and energy density (MJ/kg), calculated following Molnár *et al.*

(2009). Storage energy quantifies total energy in the individual allocated to body maintenance, reproduction and growth and is derived from protein and fat. Storage energy will be affected by energy expenditure and intensity of foraging and may thus fluctuate both spatially and temporally in a population (Molnár *et al.*, 2009). Energy density accounts for the fact that, due to the costs of somatic maintenance, not all storage energy is available during fasting, and is thus defined as the ratio of storage energy to lean body mass (Molnár *et al.*, 2009). Energy density has also been used to predict polar bear survival (Molnár *et al.,* 2010) and reproduction (Molnár *et al.*, 2011) as a function of body condition. We used principal component analysis (PCA) to explore relationships among six condition metrics. Spearman correlations were used to compare body condition measures and Kruskal-Wallis ANOVA and Mann-Whitney U post-hoc tests were used to compare metrics across age and sex groups. We also used Mann-Whitney U tests to compare body condition between bears with and without evidence of terrestrial feeding.

### *Temporal trends in body condition and sea ice*

We assessed trends in body condition (fall 2004-2013) using simple linear regression models for adult and subadult males and females. Adult females were further separated depending on reproductive status and body condition metrics were compared using Kruskal-Wallis ANOVA (fall/spring, 2004-2014): (i) solitary females (fall); (ii) females with yearlings (fall); (iii) females with COY (fall); and (iv) females with COY (spring). No solitary females were handled in the spring.

We used ArcInfo (Environmental Systems Research Institute, California) to extract sea ice concentrations from 25 x 25 km resolution passive microwave satellite raster imagery (NASA Team algorithm; Cavalieri *et al*., 1996, 2012) from the National Snow and Ice Data Center

(Boulder, Colorado) for 2004-2013. Each grid cell had an associated sea ice concentration value estimating the fractional amount of sea ice covering that cell (Cavalieri *et al*., 1996). We calculated mean daily sea ice concentrations for the entire Western Hudson Bay management zone. Two metrics were derived from mean daily sea ice concentration: (i) breakup, the ordinal date in spring when sea ice reached and remained below 50% concentration for at least three consecutive days (Etkin, 1991; Gagnon & Gough, 2005; Stirling & Parkinson, 2006); and (ii) freeze-up, the ordinal date in autumn when sea ice reached and remained above 10% concentration for at least three consecutive days (Cherry *et al.*, 2013).

We used multiple linear regression to assess relationships between sea ice and each body condition metric for age/sex classes. To ensure non-collinearity among predictors, we used variance inflation factor (VIF $< 2.5$) and tolerance values ( $> 0.10$), which were supported with weak correlations between breakup and freeze-up. We used $p$ values to assess if sea ice could significantly predict body condition and compared absolute standardized $\beta$ coefficients of each predictor to assess its relative strength in the model. Positive or negative $\beta$ coefficients provided relationship direction. Statistical analyses were done using SPSS® version 22 for Windows® (IBM, Chicago, IL, USA).

## Results

### *Comparison of body condition measures*

PCA generated 2 principal components (PC) accounting for 72.6% of total variance. Metrics loaded onto PC1 (43.9% variance) were BIA, energy density, adipose tissue lipid content, and fatness index; while PC2 (28.7% variance) included storage energy and skull width.

Both BIA and energy density had the greatest loadings on PC1 (0.82 and 0.75, respectively) followed by adipose lipid and fatness index (0.70 and 0.58).

Lipid content in adipose tissue was positively correlated with total percent body fat as estimated by BIA ($r^2 = 0.34$, $p = 0.01$) (Fig. 1). Lipid content increased with energy density ($r^2 = 0.43$, $p < 0.001$) but was negatively correlated with skull width ($r^2 = -0.22$, $p = 0.01$), and did not correlate with storage energy ($r^2 = -0.06$, $p = 0.46$). BIA was significantly correlated with energy density ($r^2 = 0.49$, $p < 0.001$), but not storage energy ($r^2 = 0.16$ $p = 0.23$) or skull width ($r^2 = -0.12$, $p = 0.37$) (Fig. 2). Fatness index scores across all immobilized bears varied from 1 to 4 in the fall, with the majority of handled bears scoring 2 and 3 (42% and 51%, respectively). Fatness index scores were correlated with BIA (Spearman correlation, $r^2 = 0.33$, $p = 0.016$), but not with adipose tissue lipid content ($r^2 = 0.10$, $p = 0.25$).

All measures of body condition differed across males and females and typically increased with age class (Fig. 3). Both adipose tissue lipid content (Kruskal-Wallis, $\chi^2 = 38.8$, $p < 0.001$) and BIA ($\chi^2 = 10.58$, $p = 0.032$) differed across adult female, adult male, subadult female, subadult male and COY groups in the fall (2012-2013). Similarly, skull width ($\chi^2 = 116.6$, $p < 0.001$), storage energy ($\chi^2 = 99.3$, $p < 0.001$), and energy density ($\chi^2 = 58.9$, $p < 0.001$) also differed across age and sex groups. Both adult and subadult females had greater adipose tissue lipid content (Mann-Whitney U post-hoc, $p < 0.001$, respectively) and energy density ($p < 0.001$ and $p = 0.02$, respectively) compared to adult males (Fig. 3). Skull width and storage energy also increased with age but were greater in adult male bears compared to both adult ($p < 0.001$, respectively) and subadult females ($p < 0.001$, respectively). Fatness index scores were nearly significantly different across age and sex groups ($\chi^2 = 8.64$, $p = 0.07$) (Fig. 3).

During the study, some individuals were noted to have been foraging on terrestrial food sources (i.e., berries and vegetation). For both adult and subadult groups, skull width (Mann-Whitney U, $p = 0.37$ and $p = 0.80$, respectively), fatness index ($p = 0.89$ and $p = 0.06$), adipose tissue lipid content ($p = 0.44$ and $p = 0.46$), BIA ($p = 0.17$ and $p = 0.38$), storage energy ($p = 0.21$ and $p = 0.34$) and energy density ($p = 0.74$ and $p = 0.18$) did not differ between bears with and without signs of terrestrial feeding. Similarly, dependent COYs did not differ in body condition metrics between terrestrial foragers and non-foragers for skull width ($p = 0.31$), fatness index ($p = 0.75$), adipose tissue lipid ($p = 0.18$) and storage energy ($p = 0.09$). Energy density, however, was greater in non-foraging COY (9.51 ± 0.48 MJ/kg, mean ± SE) compared to those terrestrially feeding (8.32 ± 0.52 MJ/kg) ($p = 0.04$).

### *Adult female body condition*

Body condition metrics were higher in solitary adult females than in females with COY or females with dependent yearlings for storage energy (Mann-Whitney U, $p < 0.001$), energy density ($p < 0.001$), and fatness index ($p < 0.001$) (Fig. 4). Solitary females had greater adipose tissue lipid content than females supporting COY ($p = 0.003$), and this was nearly significant for females supporting yearlings ($p = 0.07$). BIA was not significantly different between solitary females and those with COY ($p = 0.08$), or between solitary females and those with yearlings ($p = 0.61$), although patterns were similar to other metrics (Fig. 4). Skull width was greater in females with COY ($p = 0.01$) and females with yearlings ($p = 0.05$) compared to solitary adult females in the fall (Fig. 4). Females accompanied by dependent yearlings had greater storage energy ($p = 0.001$), energy density ($p = 0.001$) and fatness index ($p = 0.02$) than females accompanied by COY, but no difference in skull width ($p = 0.92$), adipose tissue lipid content ($p = 0.51$), or BIA ($p = 0.53$) (Fig. 4).

Adult female body condition was higher in fall than in spring for multiple metrics. Solitary females in the fall, females with COY in the fall and females with yearlings in the fall had significantly greater fatness index ($p < 0.001$, $p = 0.002$ and $p < 0.001$, respectively), adipose tissue lipid content ($p < 0.001$, $p = 0.002$ and $p = 0.002$, respectively), storage energy ($p < 0.001$) and energy density ($p < 0.001$) than females with COY in the spring. However, skull width ($p = 0.72$, $p = 0.06$ and $p = 0.11$, respectively) and total body fat via BIA ($p = 0.25$, $p = 0.77$ and $p = 0.82$, respectively) did not differ statistically across season, although seasonal patterns in BIA data were similar to other metrics (Fig. 4).

Body condition in adult females was further subdivided based on litter size (solitary, single offspring, or multiple offspring; yearlings and COY combined). Overall, adipose tissue lipid content (Kruskal-Wallis $\chi^2 = 9.01$, $p = 0.011$), energy density ($\chi^2 = 56.97$, $p < 0.001$) and storage energy ($\chi^2 = 55.62$, $p < 0.001$) decreased with a greater number of offspring. A similar but not significant pattern was evident for BIA ($\chi^2 =4.74$, $p = 0.09$) (Fig. 5). Conversely, skull width was larger in females with one or more offspring compared to solitary females ($\chi^2 = 7.02$, $p = 0.03$) (Fig. 5). Fatness index scores were higher in solitary females than females with a single offspring (Mann-Whitney U post-hoc, $p < 0.001$) or females with multiple offspring ($p < 0.001$), and higher in single offspring than multiple offspring females ($p = 0.015$) (Fig. 5).

### *Inter-annual trends in body condition*

Body condition of male polar bears decreased during 2004-2013 across each age class (Fig. 6). Energy density, adipose tissue lipid content, and storage energy declined in adult male

($p < 0.001$, respectively) and subadult males ($p = 0.001$, $p = 0.017$ and $p = 0.001$, respectively) (Fig. 6), but skull width showed no change ($p > 0.05$) (Fig. 6). Similar trends were found in females across age class and status (Fig. 7). Energy density ($p = 0.015$), storage energy ($p = 0.001$) and skull width ($p = 0.015$) declined in solitary adult females, but lipid content did not ($p = 0.30$) (Fig. 7). Adult females with dependent offspring showed declines in adipose tissue lipid content ($p = 0.04$), energy density ($p < 0.001$) and storage energy ($p < 0.001$), but not skull width ($p = 0.35$) (Fig. 7). Similarly, subadult female bears declined in energy density ($p = 0.001$), adipose lipid content ($p = 0.007$), and storage energy ($p = 0.01$), but not skull width ($p > 0.05$).

Between 2004-2013, date of sea ice breakup varied from 5 June to 2 July and freeze-up from 18 November to 30 November, but showed no significant trends (linear regression, $p = 0.40$ and $p = 0.86$, respectively). Sea ice breakup and freeze-up significantly predicted lipid content ($p = 0.002$ and $p < 0.001$) and energy density ($p < 0.001$ and $p = 0.008$) in adult males, while only breakup date predicted storage energy ($p < 0.001$) and skull width ($p = 0.004$) (multiple linear regression, Table S1, Supplementary Material). Breakup and freeze-up date also predicted lipid content in subadult males ($p = 0.011$ and $p = 0.043$), while sea ice breakup date predicted both storage energy ($p = 0.002$) and energy density ($p = 0.003$). Sea ice breakup also predicted energy density ($p < 0.001$) and storage energy ($p = 0.025$) in subadult females, while both breakup and freeze-up predicted lipid content ($p < 0.01$), but not skull width ($p > 0.05$). Only lipid content in solitary adult females was significantly predicted by both sea ice breakup and freeze-up ($p = 0.015$ and $p = 0.004$). Body condition of females with dependents was predicted by sea ice conditions for lipid content (Overall Model, $p = 0.001$), energy density ($p = 0.003$) and storage energy ($p = 0.017$), and more strongly affected by freeze-up date. Overall, body condition was positively related with later breakup and negatively related with later freeze-up (standardized $\beta$ coefficients, Table S1, Supplementary Material).

## Discussion

Body condition in mammals is a complex function of both extrinsic (e.g., resource availability) and intrinsic factors (e.g., energy demand). Although our data were broadly indicative of known patterns of polar bear life history in western Hudson Bay (Stirling *et al.*, 1999; Thiemann *et al.*, 2006; Regehr *et al.*, 2007), our results provide evidence that various metrics used to date differ in their sensitivity and utility when applied to free-ranging polar bears. Our results confirm that body condition in Western Hudson Bay polar bears is highly dynamic and variable across age and sex classes, reproductive states, seasons, and years. Moreover, because polar bears in western Hudson Bay are adapted to prolonged seasonal and reproductive fasts, body condition reflects a mechanistic link between environmental conditions and demographic processes (Molnár *et al.*, 2011) and metrics of condition can serve as powerful predictors of future population trends (Molnár *et al.*, 2010).

### *BIA and body condition measures*

We found that BIA followed similar patterns in body condition as other established metrics including adipose tissue lipid content (Thiemann *et al.*, 2006; McKinney *et al.*, 2014), energy density (Molnár *et al.*, 2009), and fatness index (Stirling *et al.*, 2008), however, correlations were relatively weak ($r^2$ ranged from 0.34 to 0.49) (Fig 2). Although our estimates of total body fat may have been affected by the estimation of snout-vent contour length from straight-line body length (see Methods), the close relationship between the two length measures ($r^2$ = 0.88; U.S. Fish and Wildlife Service, unpublished data) suggests that any bias was minimal.

Since BIA uses an electric current to measure resistance through body tissue, BIA was more strongly correlated with metrics that quantify fat and energy stores (adipose tissue lipid content and energy density), compared to measures influenced by skeletal size (Fig. 1 and Fig. 2). We also found similar patterns for BIA, adipose tissue lipid, and energy density across age and sex classes (Fig. 3; Thiemann *et al.*, 2006; Stirling *et al.*, 2008) whereas morphometric-based measures, influenced by structural size, may not be representative of overall energy stores over shorter time scales (Pitt *et al.*, 2006; Barnett *et al.*, 2015). Although BIA did not differ across female reproductive status, this is likely attributable to lower sample sizes for these data. Specifically, BIA data were only available in the final two years of the study (2012-2014; Fig. 4 and Fig. 5).

Superficial fat stores are often used as an indicator of body condition in mammals (Robitaille *et al.*, 2012; Thiemann *et al.*, 2006; Stirling *et al.*, 2008), however not all energy mobilized during fasting periods will be derived from superficial fat catabolism. Metrics that quantify total energy stores (e.g., energy density) may therefore be more useful in monitoring polar bear condition. In this study, energy density consistently identified differences across age and sex classes (Fig. 3), seasonal patterns (Fig. 4 and Fig. 5), and inter-annual trends (Fig. 6 and Fig. 7). Moreover, assessing condition using energy density models is arguably easier to implement as these models require only morphological measurements. In contrast to the subjective fatness index (Stirling *et al*., 2008), which is based on palpation of superficial fat depots around the rump and hips, BIA quantifies both superficial and internal fat stores including intra-abdominal cavity and inter-muscular depots (Pond, 1992; Pond *et al.*, 1992). Although inter-muscular depots expand minimally with increasing fatness, they remain more metabolically active than larger superficial fat depots despite contrasting number and size of adipocytes between regions (Pond, 1992; Pond *et al.*, 1992). Inter-muscular depots, for example, exhibit greater glucose and lipoprotein lipase activity (Pond, Mattacks & Sadler, 1992) and are an important energy source for muscle activity (Pond, 1992). Smaller internal fat depots may be an important energy source for fasting organisms with daily energetic demands (e.g., movement) and can only be quantified by body composition analyses (e.g., BIA and energy density). Although BIA has been used in brown and black (*U. americanus*) bear studies to investigate relationships between body condition and hibernation, reproductive success (Hilderbrand *et al.*, 2000; Harlow *et al.*, 2002), and diet (Hilderbrand *et al.*, 1999; Schwartz *et al.*, 2014), our initial results suggest this technique reflects similar patterns in condition, but may not be easiest to implement on polar bears in the field.

We found that BIA measurements could be completed quickly (i.e., 5-10 minutes) and relatively non-invasively on immobilized polar bears, but readings were sensitive to capture conditions, including wet animals and wet ground. Similar to other studies (Farley & Robbins, 1994; Hilderbrand *et al.*, 1998), wet individuals generated erroneous readings due to increased conductivity around the body. The level of sedation and positioning was also found to be a factor affecting conductivity. Bears with head movement or vocalization gave variable readings, as previously reported in polar, black, and brown bears (Farley & Robbins, 1994). As young bears (i.e., COY) are necessarily administered a relatively light dose of drug (due to small body size) and recover more quickly, accurate readings may be difficult to obtain; therefore, BIA should be collected from young individuals first. Gut fill was previously thought to affect BIA measures (Hilderbrand *et al.*, 1998), however this was not evident in our study. We used evidence of foraging based on remnants of vegetation around the mouth/anus as a proxy for gut fill and found no effect on BIA. However, polar bears in this study were probably fasting or consuming limited amounts of vegetation. Polar bears actively foraging on the sea ice can consume large amounts of material (e.g., up to 20% of body mass, Best 1985) and BIA measures may thus be more strongly affected by gut fill if performed during periods of hyperphagia.

Although polar bears on shore during the ice free season are largely fasting (Stirling *et al.*, 1977; Ramsay & Stirling, 1988) some individuals forage on berries, kelp, goose eggs and other terrestrial foods (Lunn & Stirling, 1985; Ramsay & Hobson, 1991; Derocher *et al*., 1993). Although the energetic value of terrestrial foods is minimal in comparison to marine mammal prey (Rode *et al*., 2015), Gormezano & Rockwell (2015) argued that land-based food could offset the nutritional deficits arising from reduced foraging opportunities on the sea ice. We found no evidence to support this hypothesis as our results showed no relationship between body condition and terrestrial foraging. Our finding that energy density is lower in foraging COY suggests that terrestrial feeding may be associated with smaller body size and reduced energy stores in younger, small bodied bears.

### *Adult female body condition*

The consistently greater body condition of adult and subadult females across metrics (Fig. 3) suggests the potential for higher relative body fat stores in females as early as the subadult stage compared to males. It is possible that fat stores begin to accumulate earlier in females to better prepare for gestation and lactation that require large fat reserves (Ramsay & Stirling, 1986; Thiemann *et al.*, 2006). Moreover, male bears continue growth for longer periods before reaching maximum adult size compared to females (Derocher & Wiig, 2002), consequently fat store accumulation may not occur as early in life. Consistent with seasonal fasting and a *ca.* 8 month onshore period associated with denning, body condition in adult females was higher in fall than spring and was higher in solitary females than those with dependent young in the fall (Atkinson & Ramsay, 1995; Hilderbrand *et al.*, 2000; Thiemann *et al.*, 2006; McKinney *et al.*, 2014).

Energy expenditure in mammals may increase with litter size (Konig, Riester & Markl, 1988; Kenagy *et al.*, 1990), and the effects of lactation (Arnould & Ramsay, 1994) appeared to influence body condition of females supporting multiple cubs (Fig. 5). The extent of fat stores accumulated prior to fasting may dictate the likelihood of producing offspring (Atkinson & Ramsay, 1995; Samson & Huot, 1995; Belant *et al.*, 2006), date of parturition, rate of cub growth (Samson & Huot, 1995; Robbins *et al.*, 2012), litter size (Samson & Huot, 1995), and cub mass and survival (Derocher & Stirling 1996, 1998). In contrast, skull size was smaller in solitary females compared to those supporting offspring. Skeletal features may be influenced by long term nutrition (Zedrosser *et al*., 2006; Rode *et al*., 2010), and body size in bears can influence litter size and natality (Stringham, 1990). Thus, structurally larger females in our study population may have a reproductive advantage. Energy expenditures of adult females vary based on offspring needs, as storage energy, energy density and fatness index were greater in females with yearlings than COY (Fig. 4). Energetic demands of milk production for females supporting COY surpasses that of yearlings due to rapid COY growth rate and is reflected in the decline in fat content of milk over time (Arnould & Ramsay, 1994).

### *Inter-annual trends in body condition*

Temporal trends in a suite of metrics revealed a long-term decline in polar bear body condition across age and sex classes. Although a fundamental adaptation of polar bear survival involves the ability to prioritize lipid catabolism during fasting, ongoing declines in sea ice habitat are likely reflected in measures of body condition. For example, declines in body condition were found in Southern Beaufort Sea polar bears following years with reduced ice availability (Rode *et al.*, 2010). Polar bears in Southern Hudson Bay have shown declines in body condition associated with a progressively longer ice-free season (Obbard *et al.*, 2016). Past studies in western Hudson Bay have documented declines in body condition of adult males and females associated with earlier sea ice breakup, suggesting that a reduced foraging period affects nutritional condition (Stirling *et al.*, 1999). Regehr *et al*. (2007) found juvenile, subadult and senescent (>20 years) polar bear survival to fluctuate based on timing of spring melt, while Lunn *et al.* (2016) identified trends in sea ice breakup dates to reflect survival of females across all age classes. Similarly, we found sea ice to influence body condition metrics across age and sex classes. The differing response of various metrics to changing ice conditions, however, suggests that timing of breakup and freeze-up may not be the sole factors involved in influencing polar bear body condition. For example, energy density, storage energy and skull width declined over time in solitary adult females (Fig. 7) but these metrics were not predicted by sea ice breakup or freeze-up dates. This suggests that other environmental factors, in conjunction with sea ice, may be collectively influencing body condition (Rode *et al*., 2010), and environmental parameters that fluctuate with a changing climate may be more complex (Rode *et al*., 2014; Bromaghin *et al*., 2015). Although polar bear life history has evolved to enable populations to cope with fluctuating ice conditions, more frequent years of poor habitat can negatively influence body condition and survival (Stirling & Parkinson, 2006; Whiteman *et al.*, 2015).

The western Hudson Bay region is undergoing considerable environmental change. Spring air temperatures have increased and sea ice breakup occurs approximately 3 weeks earlier than 30 years ago (Gagnon & Gough, 2005; Hochheim, Barber & Lukovich, 2010; Hochheim &

Barber, 2014). Earlier ice melt reduces the foraging window and individuals come ashore in poorer condition (Stirling *et al.*, 1999; Regehr *et al.*, 2007). Our assessment of multiple metrics of body condition indicate that the climate-driven declines in polar bear body condition initially documented in western Hudson Bay in the mid-1990s (Stirling *et al.*, 1999) have continued. It is likely that sustained reductions in body condition resulting from ongoing changes in sea ice habitat driven by a warming climate will negatively affect population vital rates and subsequently, the abundance of polar bears in western Hudson Bay.

## Acknowledgments

This research was supported by the Natural Sciences and Engineering Research Council (NSERC, Canada), Environment and Climate Change Canada, the Churchill Northern Studies Centre, Earth Rangers Foundation, Isdell Family Foundation, Manitoba Conservation and Water Stewardship, Parks Canada Agency, Schad Foundation, Wildlife Media, Inc., York University and the Northern Scientific Training Program (NSTP). Thanks to Dr. K. Rode (U.S. Geological Survey) and Dr. E. Regehr (U.S. Fish and Wildlife Service) for sharing morphometric data on polar bears in the Chukchi Sea. Dr. Rode also provided valuable comments on an earlier version of the manuscript. Thanks to Dr. E. Richardson (Environment and Climate Change Canada) for calculating sea ice metrics, as well as the many field assistants, helicopter crews and colleagues who contributed to the collection of data from this subpopulation of polar bears over the years.

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## Figures and Tables

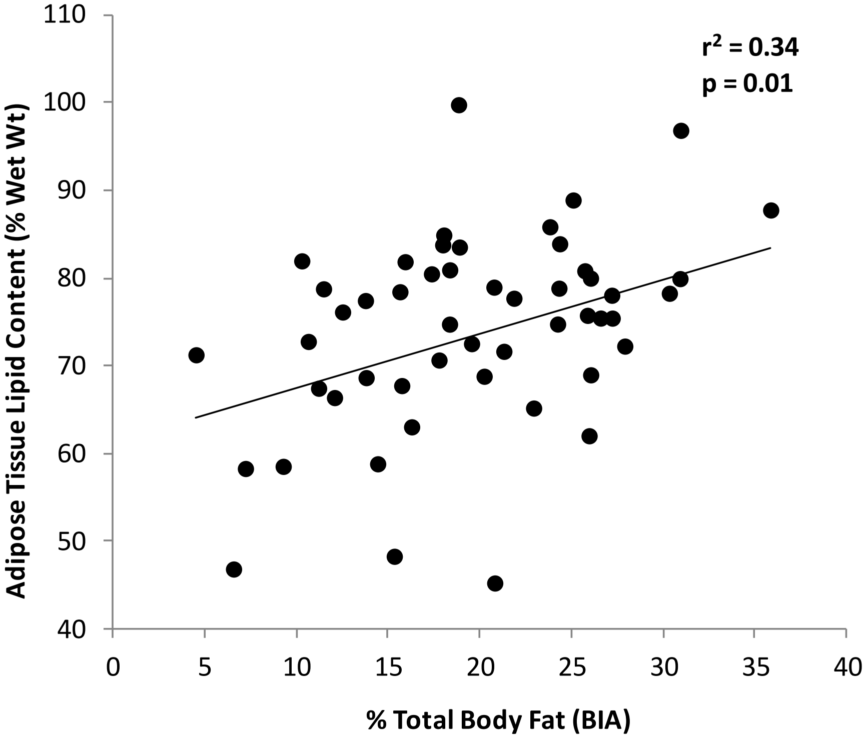


**Figure 1.** Relationship between adipose tissue lipid content (% wet weight) and percent total body fat (calculated from bioelectrical impedance analysis, BIA) for n = 52 Western Hudson Bay polar bears in fall 2012 and 2013.

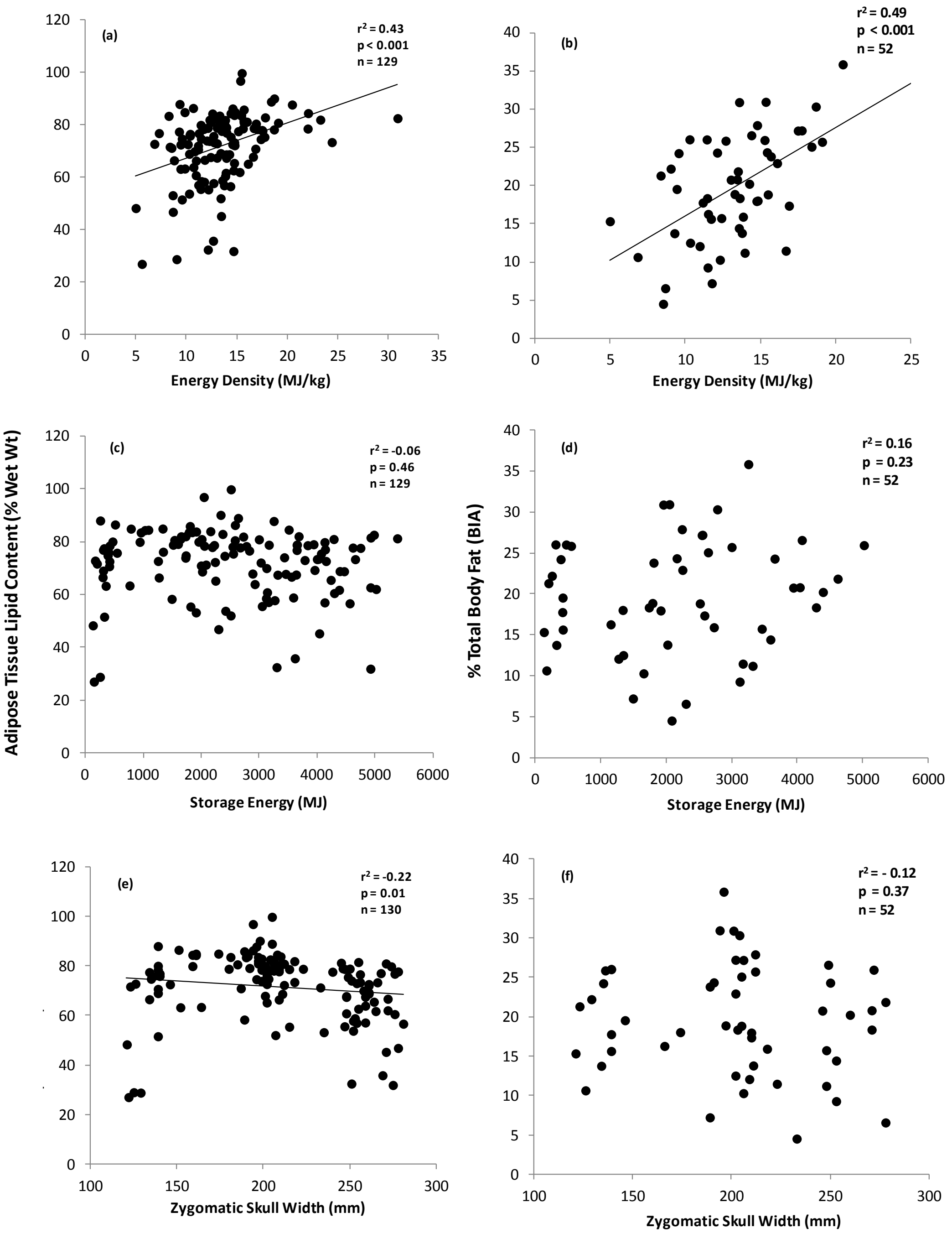


**Figure 2.** Relationship of adipose tissue lipid content (left) and total body fat (BIA) (right) with energy density (a, b), storage energy (c, d) and zygomatic skull width (e, f) for Western Hudson Bay polar bears in fall 2012 and 2013.

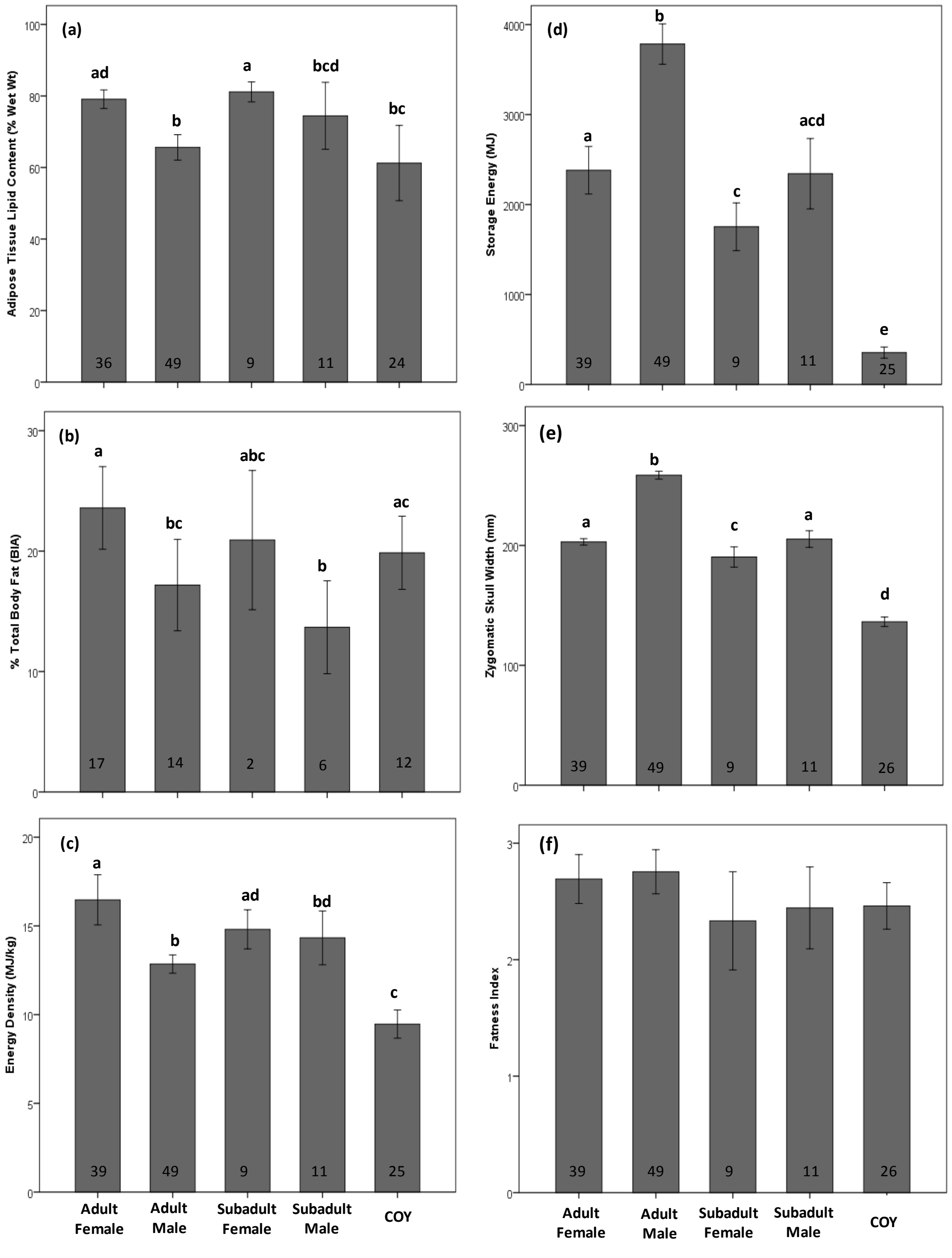


**Figure 3.** Mean (SE) measures of body condition of adult female, adult male, subadult female, subadult male, and cub-of-the-year (COY) polar bears in the fall season in western Hudson Bay, 2012 and 2013: (a) adipose tissue lipid content; (b) total body fat derived via BIA; (c) energy

density; (d) storage energy; (e) skull width; and (f) fatness index. Different letters indicate statistical differences between age and sex groups within each body condition metric.  Numbers within bars indicate sample size.

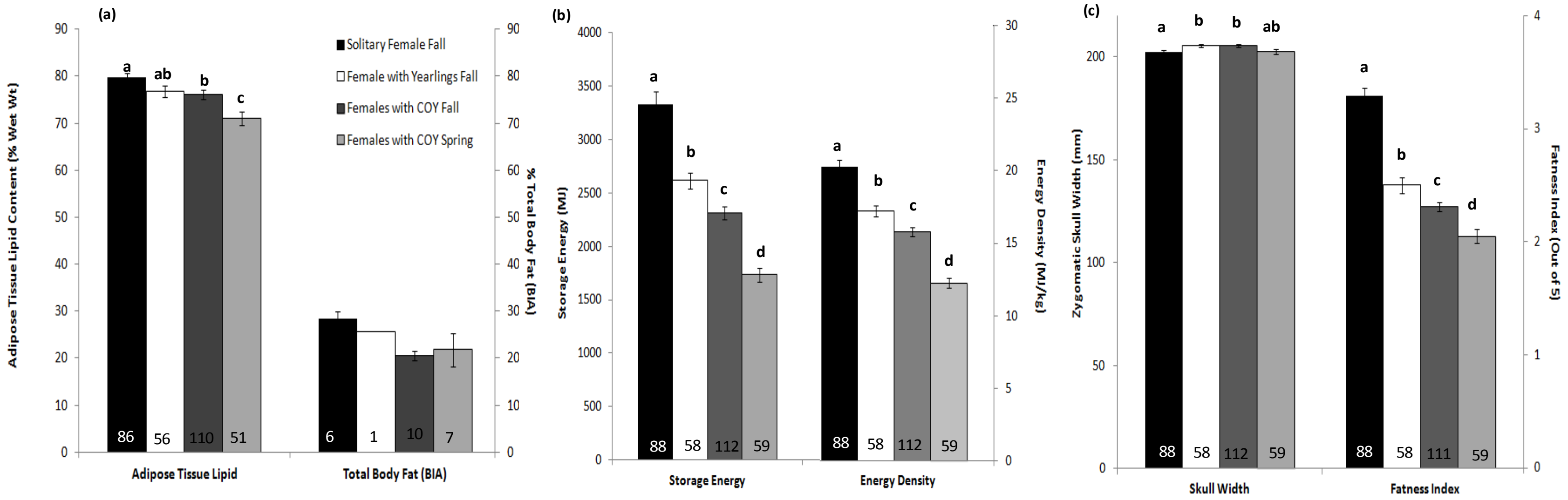


**Figure 4.** Mean (SE) measures of body condition of solitary female (fall), female accompanied by dependent yearlings (fall), female with COY (fall) and female with COY (spring) polar bears in western Hudson Bay (2004-2014) for: (a) adipose tissue lipid content and total body fat BIA; (b) storage energy and energy density; and (c) skull width and fatness index. Total body fat (BIA) was measured in fall 2012 and 2013 and in spring 2013 and 2014. Statistical differences between female status/season within each body condition metric indicated by different letters and symbols. Numbers within bars indicate sample size.

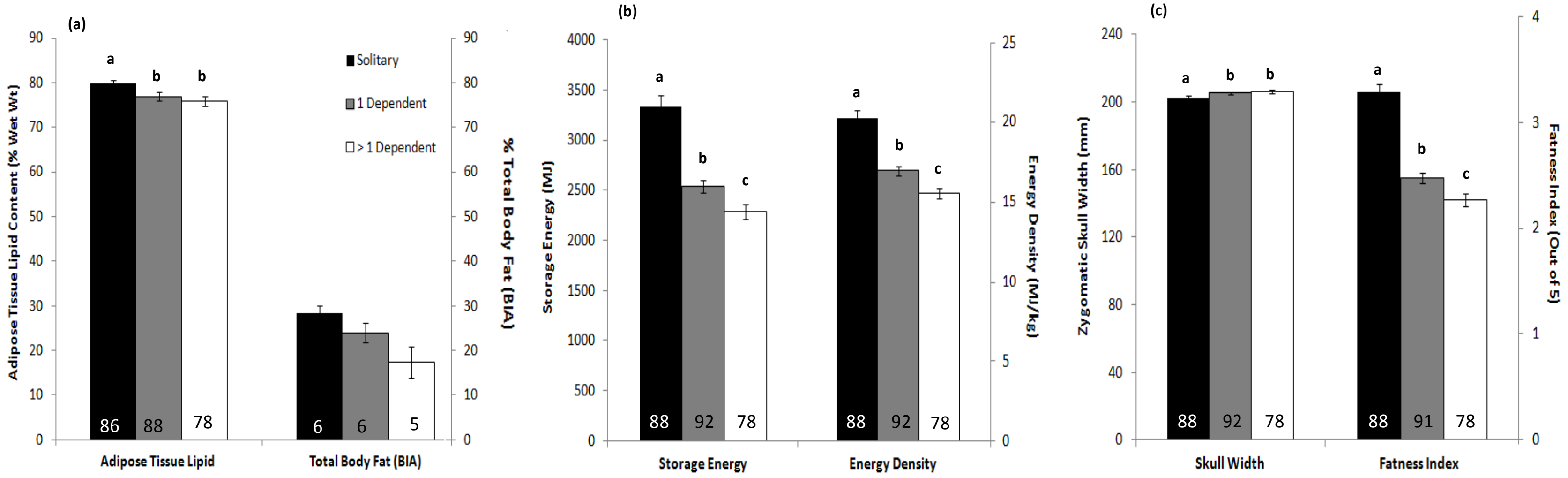
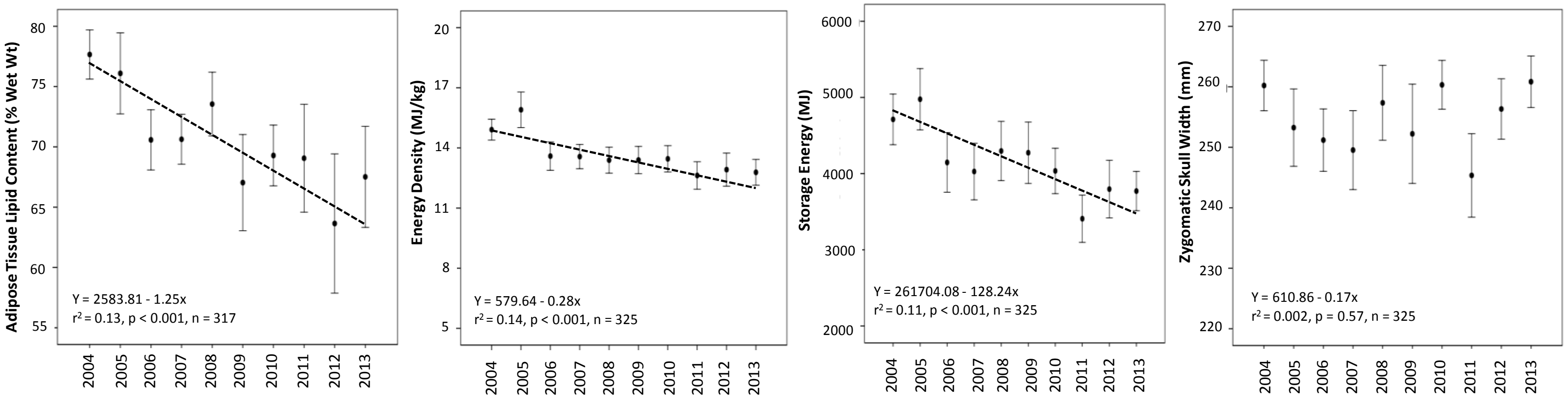


**Figure 5.** Mean (SE) measures of polar bear body condition for solitary females, females with 1 dependent offspring, and females with >1 dependent offspring in the fall 2004-2013 in western Hudson Bay for: (a) lipid content and total body fat BIA; (b) storage energy and energy density; (c) skull width and fatness index. Total body fat (BIA) was measured in the fall 2012 and 2013. Statistical differences between females within each body condition metric are indicated by different letters and symbol. Numbers within bars indicate sample size.

(a) Adult Male



(b) Subadult Male

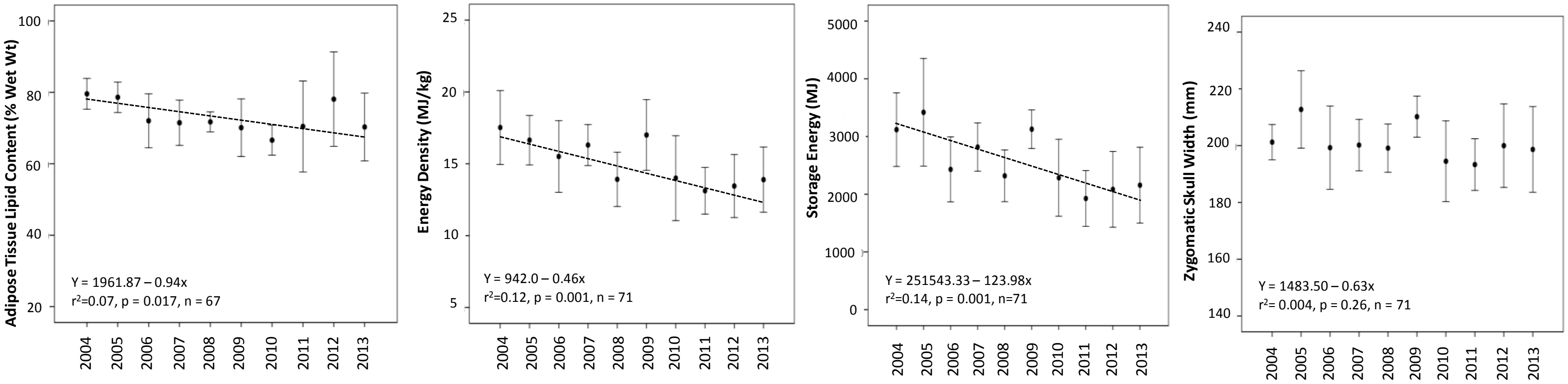
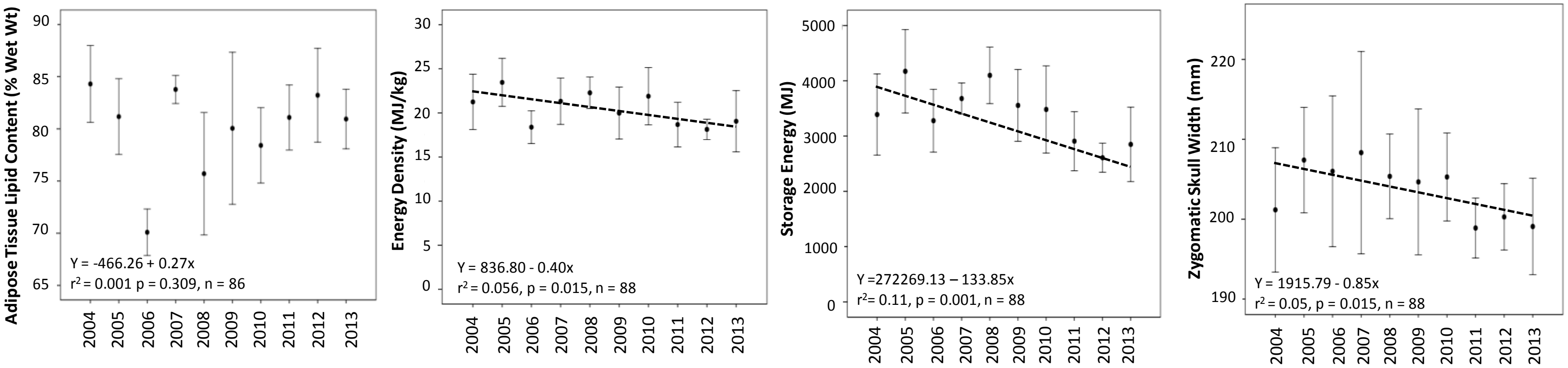
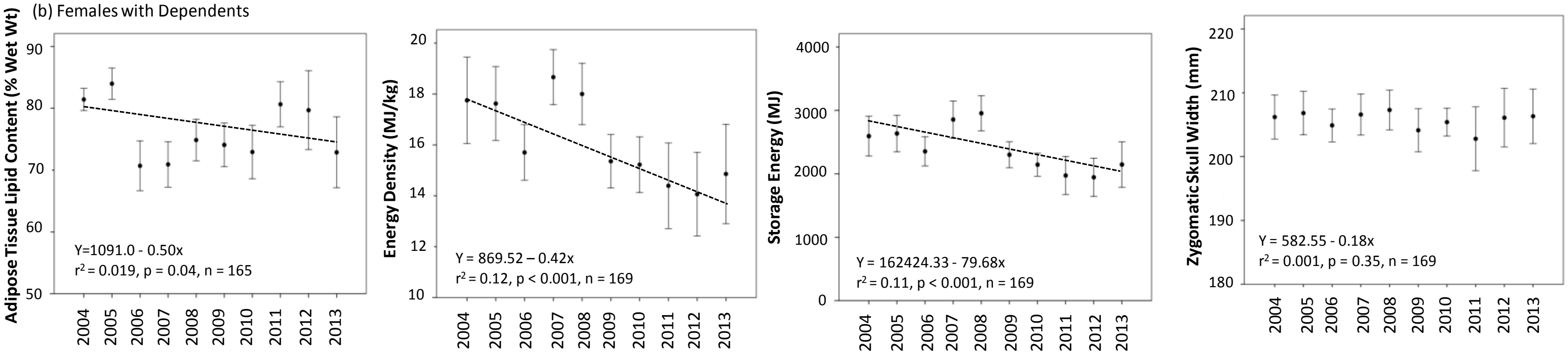


**Figure 6.** Temporal trends in mean (SE) body condition measures for (a) adult male, and (b) subadult male (independent age 2-4 years) polar bears in western Hudson Bay in the fall 2004-2013.

(a) Solitary Adult Female



(b) Females with Dependents



(c) Subadult Female

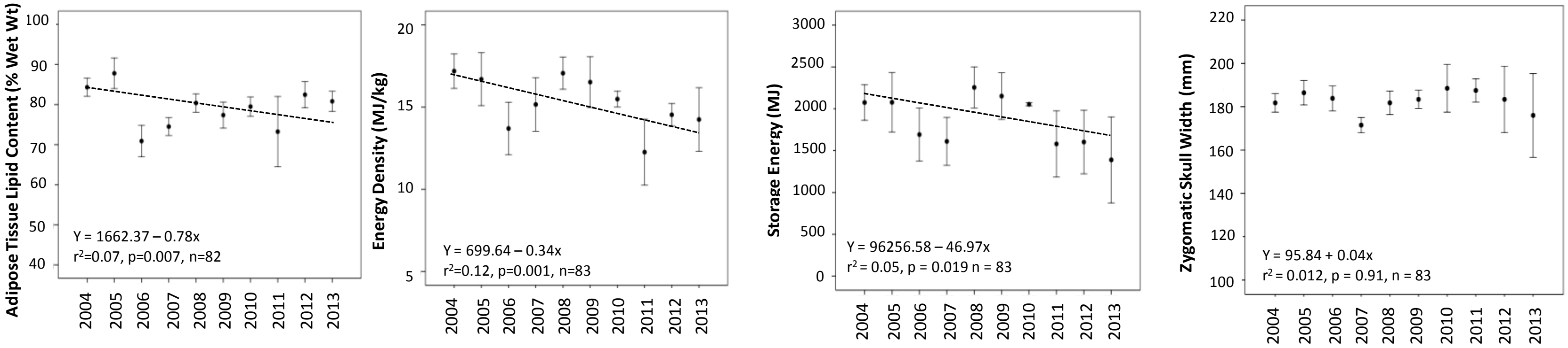


**Figure 7.** Temporal trends in mean (SE) body condition measures for (a) solitary adult female, (b) female with dependent offspring (both yearling and COY), and (c) subadult female (independent age 2-4 years) polar bears in western Hudson Bay in the fall 2004-2013.

## Supplementary Information

**Table S1.** Multiple linear regression results examining relationship between sea ice (breakup and freeze-up date) and adipose tissue lipid content, energy density, storage energy and skull width in different age/sex classes for polar bears captured during the fall season in western Hudson Bay from 2004-2013. Model *F* statistics, *p*-values and adjusted $r^2$ are reported along with standardized β coefficient values (and direction of relationship, positive or negative) for both breakup and freeze-up date in each model. * denotes a significant relationship between sea ice and each body condition metric. Ŧ indicates which predictor variable (breakup or freeze-up) had the greatest effect on the dependent variable (comparing *β* value). Sample sizes shown in Figure 6 and Figure 7.

| | | **Multiple Regression Model** | | **Standardized $\beta$ Coefficient ($p$ value)** | |
|---|---|---|---|---|---|
| | ***F*** | ***p*** | **Adjusted $r^2$** | **Breakup** | **Freeze-up** |
| **Adult Male** | | | | | |
| Adipose Lipid* | 11.48 | < 0.0001 | 0.062 | 0.181 (0.002) | - 0.245 (< 0.0001) † |
| Energy Density* | 11.47 | < 0.0001 | 0.061 | 0.254 (< 0.0001) † | - 0.149 (0.008) |
| Storage Energy* | 12.20 | < 0.0001 | 0.065 | 0.275 (< 0.0001) † | - 0.089 (0.112) |
| Skull Width* | 4.16 | 0.016 | 0.019 | 0.165 (0.004) † | - 0.036 (0.531) |
| **Subadult Male** | | | | | |
| Adipose Lipid* | 4.89 | 0.011 | 0.106 | 0.309 (0.011) † | - 0.242 (0.043) |
| Energy Density* | 4.81 | 0.011 | 0.098 | 0.348 (0.003) † | - 0.121 (0.294) |
| Storage Energy* | 5.29 | 0.007 | 0.109 | 0.365 (0.002) † | - 0.113 (0.326) |
| Skull Width | 1.13 | 0.327 | 0.004 | 0.178 (0.144) | 0.011 (0.928) |
| **Solitary Adult Female** | | | | | |
| Adipose Lipid* | 4.96 | 0.009 | 0.085 | 0.305 (0.015) | - 0.364 (0.004) † |
| Energy Density | 0.49 | 0.611 | 0.012 | 0.125 (0.330) | - 0.045 (0.727) |
| Storage Energy | 0.46 | 0.628 | 0.012 | 0.085 (0.507) | 0.030 (0.818) |
| Skull Width | 1.30 | 0.277 | 0.007 | 0.023 (0.857) | 0.159 (0.213) |
| **Adult Female with Dependents** | | | | | |
| Adipose Lipid* | 6.84 | 0.001 | 0.066 | 0.210 (0.013) | - 0.297 (0.001) † |
| Energy Density* | 6.10 | 0.003 | 0.057 | 0.132 (0.113) | - 0.290 (0.001) † |
| Storage Energy* | 4.15 | 0.017 | 0.036 | 0.099 (0.239) | - 0.242 (0.004) † |
| Skull Width | 0.57 | 0.566 | 0.005 | 0.039 (0.651) | - 0.092 (0.287) |
| **Subadult Female** | | | | | |
| Adipose Lipid* | 9.92 | < 0.0001 | 0.190 | 0.412 (< 0.0001) † | - 0.370 (0.001) |
| Energy Density* | 8.05 | < 0.0001 | 0.160 | 0.460 (< 0.0001) † | -0.164 (0.138) |
| Storage Energy* | 3.23 | 0.045 | 0.052 | 0.266 (0.025) † | 0.018 (0.879) |
| Skull Width | 0.79 | 0.455 | -0.005 | -0.072 (0.533) | 0.150 (0.213) |

# CHAPTER III

# Intraspecific and temporal variability in the diet composition of female polar bears in a seasonal sea ice regime

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Original manuscript citation:

Sciullo, L., Thiemann, G.W., Lunn, N.J., Ferguson, S.H. (2017). Intraspecific and temporal variability in the diet composition of female polar bears in a seasonal sea ice regime. *Arctic Science.* **In Press.**

## Abstract

Predator foraging behaviour is influenced by a suite of intrinsic and extrinsic factors, including energetic requirements, resource availability, and habitat conditions. Polar bears (*Ursus maritimus*) are specialized predators of marine mammals and are adapted to a seasonal sea ice regime in much of their range. We used quantitative fatty acid signature analysis (QFASA) to estimate the diet composition of 374 female polar bears from 2004 to 2014 in western Hudson Bay, Canada. Ringed seal (*Pusa hispida*) was the dominant prey species, followed by bearded seal (*Erignathus barbatus*) and harbour seal (*Phoca vitulina*), with minimal consumption of beluga whale (*Delphinapterus leucas*), harp seal (*Pagophilus groenlandica*) and walrus (*Odobenus rosmarus*). Solitary adults and females supporting yearling cubs consumed more bearded seal than did subadults or females with cubs-of-the-year (COY). Subadults may be too small or inexperienced to capture bearded seals and females with COY may avoid offshore pack ice where densities of bearded seals, and potentially infanticidal adult male polar bears, may be highest. A relatively high dietary diversity in subadults and females supporting COY suggests less selective foraging and opportunistic scavenging. Overall, bears consumed more harbour seal and less ringed seal in congruent years suggesting variable local prey availability. Date of sea ice breakup influenced the diet of subadults and family groups more so than solitary females, suggesting differential sensitivity to sea ice conditions. Inter-annual variability in diet may be a consequence of differing responses of polar bears and multiple prey species to sea ice conditions in Hudson Bay.

**Keywords:** foraging ecology, polar bear (*Ursus maritimus*), quantitative fatty acid signature analysis, western Hudson Bay

## Introduction

An organism's foraging behaviour is determined by intrinsic and extrinsic factors. Success in the capture and consumption of prey is a function of individual traits (e.g., morphology, energetic state, life history) and environmental conditions (e.g., resource availability, competition) (Sih, 2011). Foraging efficiency is optimized when net energy gain is maximized, translating into greater individual reproductive success and survival (Stephens & Krebs, 1986; Stephens, Brown & Ydenberg, 2007; Sih, 2011). However, resources are often neither evenly distributed in an environment nor found in consistent seasonal or annual abundance (Drickamer *et al.*, 2002). Consequently, foragers must modify behaviour by altering prey selection based on availability, or forage in an alternate habitat, both of which can influence net energy gain (Schoener, 1971; Drickamer *et al.*, 2002).

Intraspecific interactions among predators can affect both foraging success and prey selection. Such interactions can result in the diets of weaker competitors being broader, whereas more dominant individuals can specialize on high value prey (Sih, 1993), thereby partitioning resources (prey type) among predators. Subordinate individuals may avoid dominant conspecifics while foraging, which may reduce foraging efficiency or alter diet composition (Lima & Dill, 1990; Sih, 1993). Such avoidance behaviour may stimulate individuals to broaden their dietary niche (Sih, 1993), engage in scavenging behaviour, travel further distances for prey, or forage in less productive habitats. A growing body of evidence has documented resource partitioning across a broad range of environments and taxa, including invertebrates (Townsend & Hildrew, 1979), fish (Grossman, 1986; Matich *et al.*, 2011), terrestrial carnivores (Karanth & Sunquist, 1995), and marine mammals (Cooper *et al.*, 2009; Weise, Harvey & Costa, 2010). Divergence in prey selection can also occur as a function of age- or sex-specific differences in morphology, breeding behaviour, and energetic demands (Bolnick *et al.*, 2003). For example, sex differences in diet composition have been observed in birds (Lewis *et al.*, 2002), primates (Boinski, 1988) and marine mammals (Beck et al., 2005, 2007; Thiemann et al., 2007). Moreover, diet composition may vary across females of the same species based on social hierarchy (primates: Whitten, 1983), predation risk to females with offspring (ungulates: Bøving and Post, 1997), and reproductive status of lactating females (pinnipeds: Merrick and Loughlin, 1997).

Polar bears (*Ursus maritimus*) are marine top predators that use annual sea ice as their primary habitat for hunting marine mammal prey (Stirling & Derocher, 1993; Amstrup, 2003). The seasonal life history of polar bears is largely dependent upon consumption of high energy prey to support periods of fasting, migration, breeding and, for adult females, maternal care. Past studies have shown that polar bears feed primarily on ringed seal (*Pusa hispida*) and bearded seal (*Erignathus barbatus*), and to a lesser extent on harp seal (*Pagophilus groenlandica*), harbour seal (*Phoca vitulina*), walrus (*Odobenus rosmarus*) and beluga whale (*Delphinapterus leucas*) (Thiemann *et al.*, 2008a). In Hudson Bay, Canada, polar bears experience a seasonal sea ice regime, during which foraging is primarily limited to the ice-covered season (Stirling *et al.*, 1977; Ramsay & Hobson, 1991). Since marine mammals are unevenly distributed and densities can fluctuate both spatially and temporally (Stirling, Kingsley & Calvert, 1982; Kingsley, Stirling & Calvert, 1985), bears can often travel long distances while foraging (Ferguson *et al.*, 1999; Amstrup *et al.*, 2000, 2001).

On-ice foraging is particularly crucial for pregnant females who require substantial energy stores (i.e., fat) to support gestation, parturition, and lactation, which occurs during an 8-month onshore period following sea ice melt in late summer (Stirling *et al.*, 1977; Atkinson &

Ramsay, 1995). Terrestrial feeding during the onshore period may be minimal and does not appear to provide energetic value to improve body condition (Rode *et al.*, 2015; Pilfold *et al.*, 2016; Sciullo, Thiemann & Lunn, 2016). Moreover, females with dependent cubs require considerable energy to support the energetic demands of lactation through the approximately 2.5 year period of maternal care (Derocher & Stirling, 1995). Aggressive interactions and infanticide by adult male bears (Taylor *et al.*, 1985) can drive spatial separation during periods of foraging (Stirling *et al.*, 1993) and may thus be reflected in diet composition.

Recent changes in sea ice, including progressively earlier breakup and later freeze-up, have been linked to declines in body condition, reproductive success, and survival of female bears in the Western Hudson Bay (WH) subpopulation (Stirling, Lunn & Iacozza, 1999; Lunn *et al.*, 2016; Sciullo *et al.*, 2016). Progressively earlier ice breakup can shorten the period of polar bear hyperphagia that is associated with the peak of seal pupping in the spring (Stirling & Øritsland, 1995). Sea ice cover and breakup have also been linked to changes in prey life history and survival. Declines in ringed seal pregnancy rate have been observed during years with earlier ice breakup, in conjunction with increased frequency of diseased seals (Ferguson *et al.*, 2016). The behaviour and distribution of harbour seals vary with sea ice breakup and freeze-up date (Bajzak *et al.*, 2013). Sea ice phenology may thus be associated with changes in prey distribution or availability, altering polar bear foraging behaviour and diet composition. Since the demographic effects of sea ice loss on polar bears are expected to be driven by changes in feeding opportunities, diet composition may reflect broader ecological trends relevant to the conservation and management of the species.

Our objective was to characterize the diet composition of WH female polar bears using quantitative fatty acid signature analysis (QFASA; see Iverson et al. 2004; Thiemann et al. 2008) and assess long-term temporal trends in diet potentially affected by sea ice conditions. We hypothesized that female diet composition would vary according to age and reproductive status, as individuals would exploit resources differently based on foraging experience, energetic requirements, or avoidance of adult males. We further hypothesized that the dietary niche of females supporting dependent cubs would be broader in comparison to solitary females due to less selective foraging to offset higher energetic demands. Finally, we hypothesized that the diet composition of all females would be influenced by the timing of sea ice breakup, reflecting the effects of ongoing environmental changes in Hudson Bay (Gagnon & Gough, 2005; Hochheim *et al.*, 2010; Hochheim & Barber, 2014).

## Methods

### *Sample collection*

Samples were collected during the fall (late August – September) 2004 to 2014 from free-ranging polar bears handled in northeastern Manitoba (Fig. 1) as part of a long-term study of the population ecology of WH polar bears (Ramsay & Stirling, 1988; Stirling *et al.*, 1999; Lunn *et al.*, 2016). A vestigial premolar was extracted from previously unmarked bears older than one year for age determination (Calvert & Ramsay, 1998). Adult bears were 5 years and older, and subadults were independent bears 2-4 years. Ages of cubs-of-the-year (COY; approximately 9 months old in fall) and yearling cubs (approximately 21 months old) were based on body size and dentition. Family groups consisted of an adult female with one or more dependent COY or yearlings. We collected a subcutaneous adipose tissue sample from each adult and subadult using an 8 mm disposable biopsy punch (Miltex Inc., York, PA, USA) inserted ca. 15 cm lateral to the base of the tail (Thiemann *et al.*, 2006). Biopsies were stored in labelled cryogenic vials at -20°C until analysis. All capture and handling procedures were reviewed and approved annually by

Animal Care and Use Committees at Environment and Climate Change Canada, and York University.

We also collected 248 full-depth blubber samples from six potential polar bear prey species taken in Inuit subsistence hunts from 1994-1996 and 2001-2009. Prey samples were thought to be representative of those available to WH polar bears, and included ringed seal (~ 65 kg), bearded seal (300 kg), harbour seal (87 kg), harp seal (110 kg), walrus (1040 kg) and beluga whale (1500 kg) of all age and sex classes (Fig. 1). Blubber samples were wrapped in aluminum foil and stored in Whirl-Pak bags at -20°C until analysis.

### *Laboratory analysis*

Lipid was extracted from adipose tissue biopsies after removing any attached skin or muscle. Prey blubber was subsampled (*ca*. 0.5 g) through the full depth of the sample, avoiding any exposed and potentially oxidized surfaces. We extracted lipid from all samples using methods outlined by Iverson, Lang and Cooper (2001). Fatty acid methyl esters (FAME) were prepared from extracted lipid using sulfuric acid as a catalyst (Budge *et al.*, 2006). We analyzed each sample in duplicate and identified and quantified > 70 fatty acids (FA) via temperature-programmed gas-liquid chromatography using a Perkin Elmer Autosystem II capillary gas chromatograph and flame ionization detector (Agilent Technologies, Palo Alto, California, USA). FA were identified using the nomenclature A:Bn-X, indicating the length of the carbon chain (A), number of double bonds (B), and the position of the first double bond relative to the terminal methyl group (-X). Each FA was expressed as mass percent of total FA ± SEM.

### *QFASA and diet modelling*

We estimated polar bear diet composition using the QFASA model developed by Iverson et al. (2004) and applied to polar bears as described elsewhere (e.g., Thiemann et al., 2008; Galicia et al., 2016). Briefly, QFASA models the FA profile (or "signature") of a predator as a linear combination of mean prey signatures and then determines the proportional combination that minimizes the distance between the observed and modelled predator, after accounting for patterns of FA metabolism. To account for these metabolic patterns, we used calibration coefficients derived from captive mink (*Mustela vison*) fed a marine-based diet (Thiemann *et al.*, 2008a). We modified the original Iverson et al. (2004) QFASA model to use the Aitchison distance between modeled and observed predator signatures (Bromaghin et al., 2015, 2016). Diets of polar bears were estimated using 30 FA derived primarily from diet (Iverson *et al.*, 2004). We excluded 20:1n-11 as this FA appeared to contribute to confounding among prey species (Galicia *et al.*, 2015). Adipose FA profiles provide insight into the integrated diet composition of individuals over the weeks to months prior to sampling (Iverson *et al.*, 2004). Our diet estimates therefore reflect foraging behaviour of females on the sea ice from late winter through early summer. Although the onshore period is associated with a metabolic fasting state in WH bears (Stirling *et al.*, 1977), individuals were sampled early in the fall season (August - September) and any fasting-associated changes in FA stores would be minimal. All QFASA estimates were generated in R (version 3.2.4, The R Foundation for Statistical Computing, 2005) using the package QFASA.

### ***Statistical analysis***

We compared diet estimates of females across the following age and reproductive classes: (1) solitary adult; (2) adult with COY; (3) adult with yearlings; and (4) subadult. Since diet composition of individual bears did not necessarily include all prey species, diet data were not normally distributed. We therefore used randomization-permutation MANOVA to test for intraspecific differences in diet composition (randomly permuting factor levels 10 000 times) (Anderson, 2001a, 2001b). We also used one-way permutation ANOVA to test *post hoc* differences in the proportion of each prey type across groups. We used simple linear regression to test for inter-annual changes in diet composition for each age and reproductive class. Adult females supporting either yearling or COY were pooled for inter-annual comparisons due to small sample sizes in each year. We used Spearman-rank correlations to assess the relationship between ringed seal and harbour seal consumption across all females and in each group. We used the Shannon-Wiener Index ($H'$) to estimate dietary diversity in females using the formula:

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

where $p_j$ represents the proportion of prey type $j$ in the diet, summed across all $S$ prey types. Differences in dietary diversity across female groups were assessed using one-way ANOVA.

Following Lunn et al. (2016), we used ArcInfo (Environmental Systems Research Institute, California) to extract sea ice concentration from 25 x 25 km resolution passive microwave satellite raster imagery from the National Snow and Ice Data Center (NASA Team algorithm; Cavalieri et al., 1996, 2012) for 2003-2014. We calculated mean daily sea ice concentration from the fractional amount of sea ice covering each of 381 grid cells that provided complete coverage of the WH management zone (PBSG, 2015). From these data, we determined spring sea ice breakup as the ordinal date when sea ice reached and remained below 50% concentration for a minimum of three consecutive days (Gagnon & Gough, 2005; Stirling & Parkinson, 2006). To assess if environmental factors influenced diet composition, we performed multiple linear regression using the current year's sea ice breakup date (*breakup*), the previous year's breakup date (*lag breakup*), and *year* for each prey species in each female group. Since the spring period of hyperphagia likely overlaps the period when sea ice melt is at 50% (May-June), we used the current year's sea ice breakup date as a predictor in determining diet composition, while *year* was included in the model to reflect potential cumulative effects of multiple environmental factors that may fluctuate over time. As abundance and availability of prey may be affected by seal reproductive success from the previous year, we also used *lag breakup* as a covariate to assess prior-year habitat effects on diet composition. The assumption of non-collinearity among predictor variables was met using a variance inflation factor $< 2.5$ and tolerance values $> 0.10$, and correlation coefficients between independent variables remained $< 0.50$. *P*-values for each predictor variable were used to determine the relationship between predictors and consumption of each prey species, while standardized $\beta$ coefficients provided the strength of each predictor in the model. Statistical analyses were performed in R (Version 3.2.4, The R Foundation for Statistical Computing, 2005) and SPSS® version 22 for Windows® (IBM, Chicago, USA).

## Results

### *Diet composition*

Across all female polar bears, ringed seal contributed the most to polar bear FA signatures (mean ± SEM: 57.2 ± 0.8%) (Fig. 2a), and did not differ significantly across age class or reproductive status (one-way permutation ANOVA, $p = 0.59$) (Fig. 2b). Bearded seal was also consumed in relatively high proportion across all females (15.6 ± 0.8%) (Fig. 2a). Mean bearded seal consumption was higher among solitary adult females than subadults ($p = 0.02$) (Fig. 2b). Bearded seal was also found more frequently in the diets of solitary adults (82% of bears) compared to females supporting COY (74%), females supporting yearlings (66%) and subadults (63%).

Harbour seal was consumed in similar proportions to bearded seal across all females (15.4 ± 0.5%) (Fig. 2a), however this component of the diet did not differ across age class or reproductive status ($p = 0.67$). Similarly, beluga whale was consumed in minor proportions across all females (6.6 ± 0.4%) (Fig. 2a), and did not differ across female groups ($p = 0.07$). Harp seal and walrus were consumed in lowest proportions across all females (3.5 ± 0.4% and 1.3 ± 0.08%, respectively) (Fig. 2a), and significantly differed across age class and reproductive status ($p < 0.01$ and $p = 0.03$, respectively). Specifically, subadult females consumed more harp seal (6.1 ± 1.4%) than both solitary females (2.0 ± 0.3%) ($p < 0.01$) and females with yearlings (2.5 ± 0.5%) ($p = 0.03$). Walrus was found in higher proportions in solitary adult females compared to females supporting yearlings ($p < 0.01$), but not females supporting COY ($p = 0.40$) or subadults ($p = 0.10$) (Fig. 2b). Family groups only differed in their consumption of walrus with adults supporting COY consuming greater proportions than those supporting yearlings ($p < 0.01$). Overall, walrus was found more often in the diets of solitary adult females (90% of bears) than subadults (72%).

Dietary diversity did not differ significantly across age and reproductive status (ANOVA, $F = 1.57$, $p = 0.18$). Dietary diversity, however, varied considerably among individual bears, both within and across age and reproductive status ($H'$ range: 0.25-1.43, Table 1) and was most variable in females with COY (Table 1).

*Temporal trends in diet*

Female diet composition varied over time across age and reproductive groups. Bearded seal consumption increased in solitary females (linear regression, $R^2 = 0.16$, $p < 0.01$), females with dependents ($R^2 = 0.21$, $p < 0.01$) and subadults ($R^2 = 0.17$, $p < 0.01$) (Fig. 3). Conversely, beluga whale decreased over time in solitary females ($R^2 = -0.27$, $p < 0.01$), females with dependents ($R^2 = -0.38$, $p < 0.01$) and subadults ($R^2 = -0.20$, $p < 0.01$). Harp seals remained relatively low in proportion throughout the study, and consumption increased over time in solitary females ($R^2 = 0.06$, $p < 0.01$), but not in females with dependents ($p = 0.21$) or subadults ($p = 0.71$). Similarly, walrus contributed minimally to female polar bear diet and only increased over time in subadult females ($R^2 = 0.08$, $p < 0.01$) (Fig. 3).

Ringed seal consumption showed no directional trend in solitary females ($p = 0.21$), females with dependents ($p = 0.14$) or subadults ($p = 0.94$), however consumption ranged from 48.4% (2009) to 64.8% (2014) (Fig. 3). Consumption of harbour seal declined in solitary females ($R^2 = -0.26$, $p < 0.01$), females with dependents ($R^2 = -0.20$, $p < 0.01$) and subadults ($R^2 = -0.05$, $p = 0.01$), with the lowest proportion observed in 2013 (solitary 4.8%, family 4.5%, and subadult 3.8%). Years in which harbour seal consumption was greatest (for example, 2005 and 2009), were paralleled with declines in ringed seal consumption (Fig. 3). Consumption of ringed seal and harbour seal were inversely related across the entire study period (2004-2014) (Spearman-rank correlation, $r_s = - 0.29$, $p < 0.001$) although the relationship appeared weaker after 2009. In 2004-2009, ringed seal and harbour seal consumption were negatively correlated in solitary females (Spearman-rank correlation, $r_s = - 0.39$, $p = 0.01$), females with dependents ($r_s = - 0.35$, $p < 0.01$), and subadults ($r_s = - 0.43$, $p < 0.01$) (Fig. 4a). Consumption of ringed and harbour seal during the last stage of the study (2010 - 2014) was not significantly correlated across females in any group ($p > 0.05$) (Fig. 4b).

### *Diet composition and timing of sea ice breakup*

Although date of sea ice breakup varied from 5 June to 2 July (ordinal date: 156 - 183) over the period 2004 - 2014, there was no directional trend (linear regression, $F = 0.75$, $p = 0.40$) (Fig. 5). Overall, only *year* affected diet composition of solitary females, specifically in their consumption of harbour seal, bearded seal, beluga whale and harp seal (Table 2). For adult females accompanied by dependent offspring, *breakup date*, *lag breakup* and *year* had a significant effect on both harbour seal and beluga whale consumption, while only *year* influenced consumption of bearded seal (Table 2). Among females with dependents, *breakup date* and *lag breakup* was negatively related to ringed seal consumption (Table 2). Subadults were similarly influenced by *breakup date, lag breakup* and *year* in beluga whale consumption, while harbour seal was affected by *breakup date* and *lag breakup* (Table 2).

## Discussion

Our results suggest that the diets of WH female polar bears are dependent on age and reproductive status and that ongoing ecological change in the region has potentially contributed to long-term variability in foraging habits. Dietary differences among age and reproductive classes of females may be a function of alternate space-use strategies, prey selection, or both. Our results reveal intra-population variability in WH polar bears and suggest a complex interaction between sea ice habitat and predator-prey dynamics.

### *Diet composition*

Our results are consistent with past studies that have identified ringed and bearded seals as the most common prey of polar bears in WH and throughout most of their circumpolar range

(Derocher, Wiig & Anderson, 2002; Iverson *et al.*, 2006; Thiemann *et al.*, 2008a; Galicia *et al.*, 2015). Ringed seals are likely the primary prey because of their ubiquitous distribution across the Arctic, high abundance, and relative ease of capture (Stirling & McEwan, 1975). The highest consumption of bearded seal by solitary adult females and the lowest consumption by subadults (Fig. 2) is consistent with the use of offshore pack ice by these large-bodied seals (Kovacs, Lydersen & Gjertz, 1996; Chambellant, Lunn & Ferguson, 2012a; Pilfold, Derocher & Richardson, 2014). Specifically, subadult female bears may be too small or inexperienced to hunt even juvenile bearded seals. Pack ice is frequented by adult male polar bears (Stirling *et al.*, 1993) and females with dependent cubs may avoid adult males to minimize the risk of infanticide (Derocher and Stirling, 1990; Pilfold *et al*., 2014; Taylor *et al*., 1985). Stirling *et al*. (1993) found that solitary adult females and females with older dependents (two year old cubs) foraged along the floe edge adjacent to adult males, consistent with our observation of higher bearded seal consumption among solitary females and females with yearlings (Fig. 2).

The consumption of other prey species, including harp seal, beluga whale and walrus, suggests opportunistic foraging and locally variable availability. Scavenging on beluga whales, for example, has been recorded across the Arctic (Freeman, 1973; Heyland & Hay, 1976; Rugh & Shelden, 1993). Similarly, walrus has been detected in the diets of polar bears in Foxe Basin and Gulf of Boothia (Galicia *et al*., 2016; Thiemann *et al*., 2007, 2008) and bears have been observed both scavenging and actively hunting walrus throughout the High Arctic and Chukchi Sea (Calvert & Stirling, 1990; Kochnev, 2005). Polar bears are sexually size dimorphic (Derocher *et al*., 2005) and female bears in our study were presumably limited to scavenging walrus, which have only been observed to be successfully hunted by adult male polar bears (Calvert and Stirling, 1990) and walrus consumption is positively correlated with adult male body size (Thiemann *et al*., 2007). WH polar bears have large home ranges (Mauritzen *et al.*, 2003a; Parks, Derocher & Lunn, 2006; McCall, Derocher & Lunn, 2015) and can access walrus colonies in northern and eastern parts of Hudson Bay. Overlapping use of prey resources by bears in adjacent subpopulations is reflected in similar diet composition of bears (specifically, ringed seal and walrus proportions) from western Hudson Bay and southern Foxe Basin (Galicia *et al.*, 2016).

The large range we observed in female dietary diversity implies substantial individual variation in prey selection or space-use strategies. Females with COY and subadults had a higher than expected diet diversity and are likely scavenging on a broader range of prey types (Thiemann *et al.*, 2011a). Parks *et al.* (2006) and McCall *et al.* (2015) found that family groups travel further on the sea ice compared to solitary females, which is consistent with less selective foraging habits. Females supporting COY may be in an energy deficit in spring following the maternal denning period and thus be motivated to forage widely (Ricklefs, Konarzewski & Daan, 1996; Parks *et al.*, 2006). As long distance migration can be energetically expensive in polar bears (Hurst *et al*., 1982a, 1982b) and can fluctuate with sea ice dynamics (Mauritzen *et al.*, 2003b), females with dependents may experience a trade-off between the need to forage widely and the need to avoid potentially infanticidal males.

### *Temporal trends in diet*

We documented long term variability in diet composition among female WH polar bears. Ringed seal consumption varied over time, consistent with documented changes in seal density in our study area (Chambellant *et al.*, 2012a; Young, Ferguson & Lunn, 2015; Ferguson *et al.*, 2016). Spring aerial surveys in WH showed an overall decline in ringed seal density from 2007 to 2009 (Young *et al.*, 2015) and the lowest seal densities in 2009 and 2013 (Chambellant *et al.*, 2012a), matching our results of reduced ringed seal consumption during these years (Fig. 3). Moreover, although we found bearded seal consumption to increase over time, reduced consumption was observed from 2007 to 2008 across all groups, consistent with a decline in density observed in 2008 (Chambellant *et al.*, 2012a). The distribution of ringed and bearded seals, and thus their availability to polar bears, is influenced by timing of ice breakup, snow depth, and ice cover and habitat conditions were notably poor in 2008 (Chambellant *et al.*, 2012a).

We detected an inverse relationship in the consumption of harbour seal and ringed seal: years marked with a decline in the proportion of ringed seal (2005, 2009) were matched by an increase in the proportion of harbour seal (Fig. 3; Fig. 4a). Both ringed and harbour seals coexist along the western and southern shore of Hudson Bay (Stirling, 2005), and both are available to WH polar bears. However, timing of ice breakup can dictate when female bears begin moving into coastal habitat (Derocher & Stirling, 1990b; Stirling *et al.*, 1999; Bajzak *et al.*, 2013; Cherry *et al.*, 2013; McCall *et al.*, 2016) allowing them access to harbour seals concentrated in coastal habitat with shallow, nutrient rich rivers and estuaries (Mansfield, 1967; Stirling, 1997; Derocher *et al.*, 2004; Stewart & Barber, 2010; Bajzak *et al.*, 2013). Ringed and harbour seal consumption, however, uncoupled during the final years of the study (2010 - 2014) (Fig. 4a), when timing of sea ice breakup exhibited greater inter-annual variability (Fig. 5). Even during years of later sea ice breakup, harbour seal consumption was high while ringed seal declined (Table 2), suggesting that sea ice dynamics such as proportion of land fast ice along the coast, changes in the shore lead system, and timing of ice breakup may influence harbour seal presence along the coast and affect availability to polar bears (Bajzak *et al.*, 2013).

Sporadic dietary shifts in polar bears may be a consequence of ephemeral prey availability and opportunistic foraging (e.g. Galicia *et al*., 2016). For instance, the observed decrease in bearded seal and increase in beluga consumption in 2004 and 2005 may be related to local entrapment of beluga whales (Freeman, 1973; Heide-Jørgensen *et al.*, 2002) that overwinter in parts of Hudson Bay (S. Ferguson, unpublished data) (Luque & Ferguson, 2010). The expansion of killer whale (*Orcinus orca*) distribution in response to reduced sea ice cover has been associated with increased predation of beluga whales in both northwestern and western Hudson Bay (Higdon & Ferguson, 2009; Westdal *et al.*, 2016). Killer whale presence can drive beluga into shallow waters, making them more accessible to polar bears (Smith & Sjare, 1990; Westdal *et al.*, 2016). In 2004 and 2005, an increase in the number of killer whales in WH (see Higdon and Ferguson, 2009; Richard, 2005) may have resulted in increased beluga whale predation and, as a consequence, increased carrion for polar bears.

### *Diet composition and timing of sea ice breakup*

Timing of sea ice breakup has been found to predict overall body condition in polar bears (Sciullo *et al.*, 2016), suggesting a decrease in foraging success associated with reduced feeding time. Our results suggest the effects of sea ice on diet composition are more variable. Date of *breakup*, *lag breakup* and *year* influenced diet composition of subadult females and females with young, while only *year* influenced the diet of solitary females (Table 2). Subadult females and females with dependents may be especially sensitive to habitat conditions because of their smaller absolute energy stores and higher energetic requirements, respectively, relative to solitary adult females. Responses to changes in sea ice availability will also differ across prey species (Chambellant *et al*., 2012a, 2012b; Johnston *et al.*, 2005; Smith and Harwood, 2001). Earlier ice breakup, for example, can negatively affect ringed seal recruitment and pup survival with negative consequences for abundance the following year (Ferguson, Stirling & McLoughlin, 2005). Numerical responses of prey to sea ice conditions may explain the effect of *lag breakup* on subadult and family group diet composition. *Year* was found to significantly influence diet composition across all groups, which suggests that unidentified habitat conditions contributing to the variability in prey selection are not completely reflected in the timing of breakup. Long term trends suggest that consumption of ringed seal may be less variable over time relative to other prey, including bearded seal, harbour seal, and beluga whale. The reasons for the apparent constraint on ringed seal consumption are not immediately clear, but the ubiquitous distribution and relatively high abundance of ringed seal in Hudson Bay may maintain this species as the primary polar bear prey. Proportional consumption of alternative prey species, however, may be more strongly related to sea ice conditions and prey availability (Thiemann *et al*. 2008).

Ongoing changes in sea ice habitat may alter predator-prey interactions in complex ways, including functional and numerical responses in polar bears across the Arctic (Ferguson, Taylor & Messier, 2000; Mauritzen *et al.*, 2003a). Our results suggest that prey selection in females is influenced by age and reproductive status, and the avoidance of potentially predatory adult males. Polar bears use sea ice as foraging habitat and sea ice conditions are thus likely to affect foraging success and diet composition. The inter-annual variability in diet composition we detected may be driven by habitat-mediated changes in prey availability, polar bear behaviour, or both. Understanding how prey density and polar bear foraging are linked to sea ice characteristics will be essential to understanding and predicting how Arctic marine food webs will respond to long term climate warming.

## Acknowledgements

We are very grateful to the Inuit hunters of Nunavut for the collection of fat samples from marine mammals harvested during annual subsistence hunts. S. Budge, C. Barry (Dalhousie University) and M. Galicia (York University) assisted with chromatographic analyses. Thanks to E. Richardson (Environment and Climate Change Canada) for calculation of sea ice metrics and S. Lang (Dalhousie University) for help with QFASA diet modelling. Thank you also to the many researchers, field assistants and helicopter personnel that assisted over the years in the capture and handling of polar bears in western Hudson Bay. This study was supported by the Natural Sciences and Engineering Research council (NSERC, Canada), Environment and Climate Change Canada, Fisheries and Oceans Canada, Nunavut Wildlife Management Board, Churchill Northern Studies Centre, Earth Rangers Foundation, Isdell Family Foundation, Manitoba Sustainable Development, Parks Canada Agency, Schad Foundation, Wildlife Media Inc., Northern Scientific Training Program (NSTP), and York University.

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## Figures and Tables

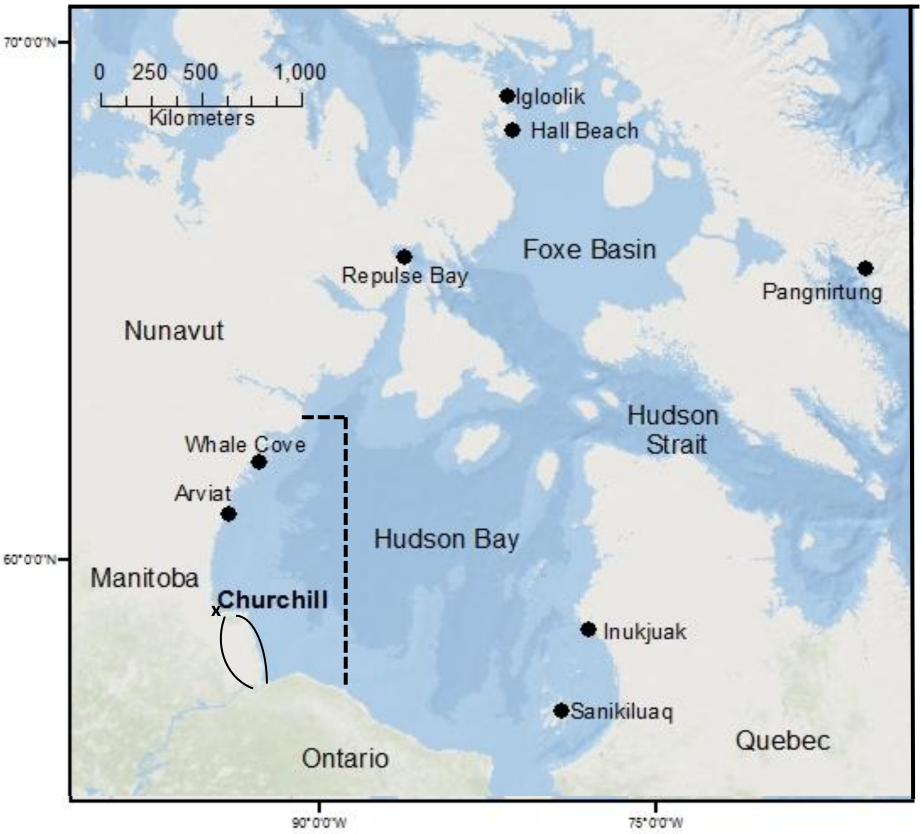

**Figure 1.** Hudson Bay, Canada showing the location where polar bears (n=374) were captured south of Churchill, Manitoba, 2004-2014. The management boundary of the Western Hudson Bay polar bear subpopulation is shown as a dashed line. Prey samples were collected from community subsistence harvests: Arviat - ringed seal (n = 98), bearded seal (n = 33), harbour seal (n = 17); Pangnirtung - harp seal (n = 42); Hall Beach and Igloolik - walrus (n = 21); and, Inukjuak, Sanikiluaq, Repulse Bay, and Whale Cove - beluga whale (n = 37).

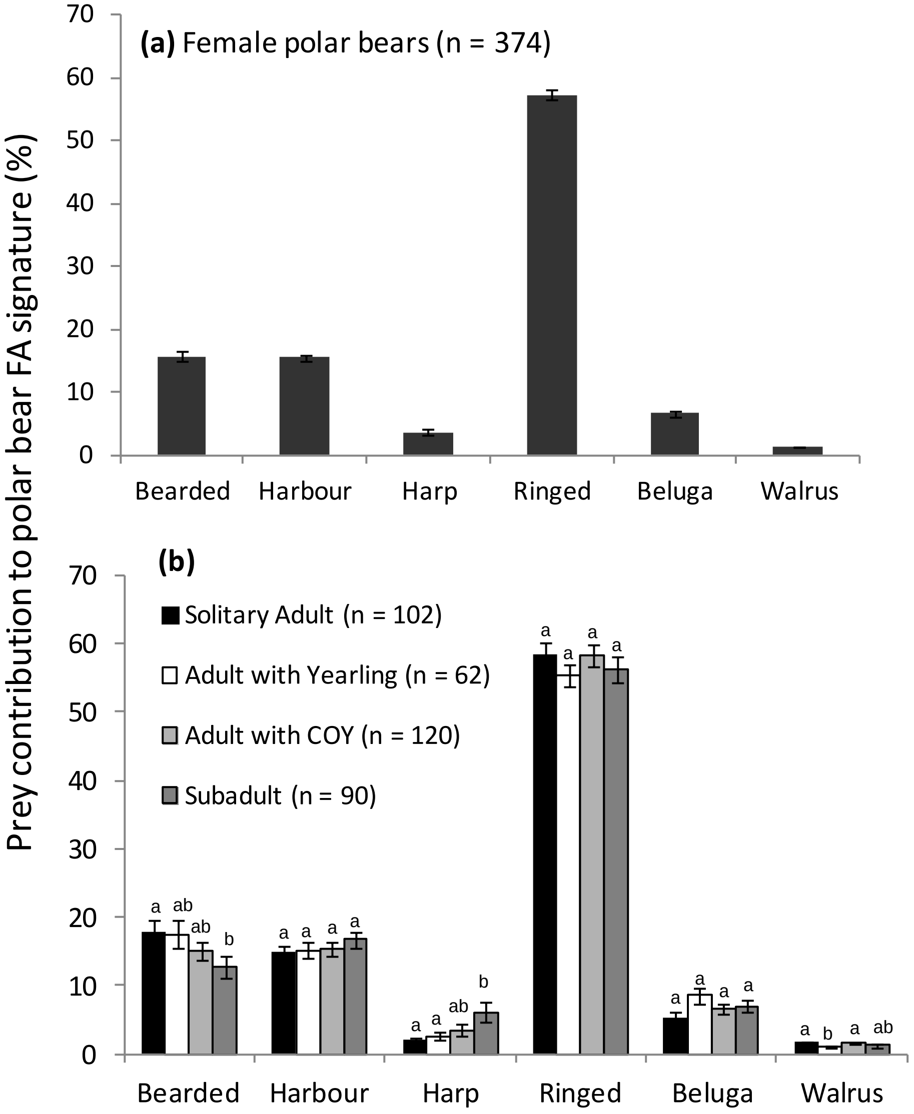

**Figure 2.** Diet composition of Western Hudson Bay female polar bears captured in fall, 2004-2014 (a) pooled and (b) by age and reproductive status. Each prey species' biomass contribution to individual diet composition is represented as a mean ± SEM. Different letters indicate statistical differences between age and reproductive status within each prey species.

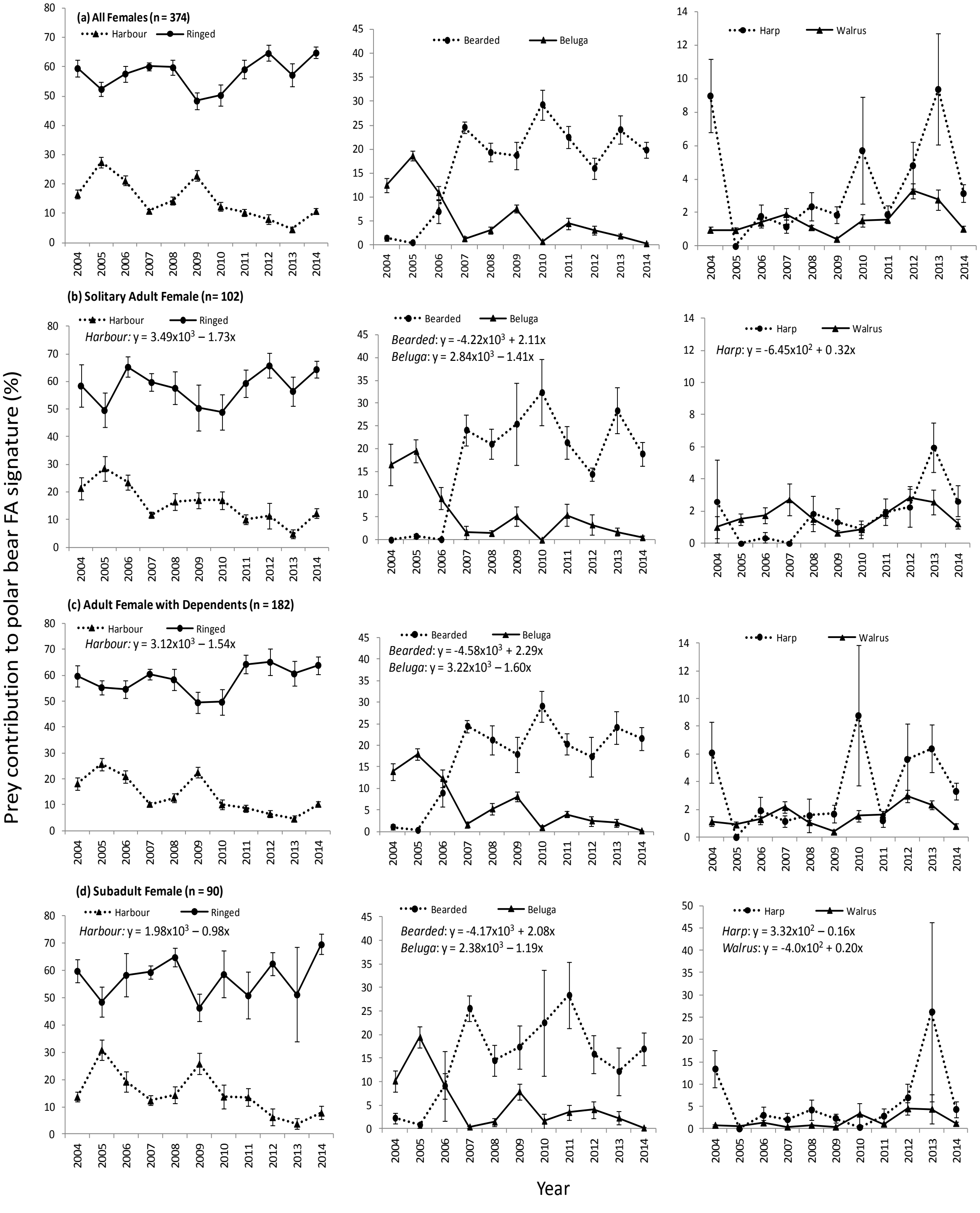

**Figure 3.** Diet composition of Western Hudson Bay female polar bears captured in fall, 2004-2014 (a) pooled and (b-d) by age and reproductive status. Prey species contributing to overall diet composition include ringed seal and harbour seal (left panel), bearded seal and beluga whale

(middle panel), and harp seal and walrus (right panel). Note differing scales across y-axis. Diet estimates are expressed as mean ± SEM. Significant linear regression equations are indicated for each prey species.

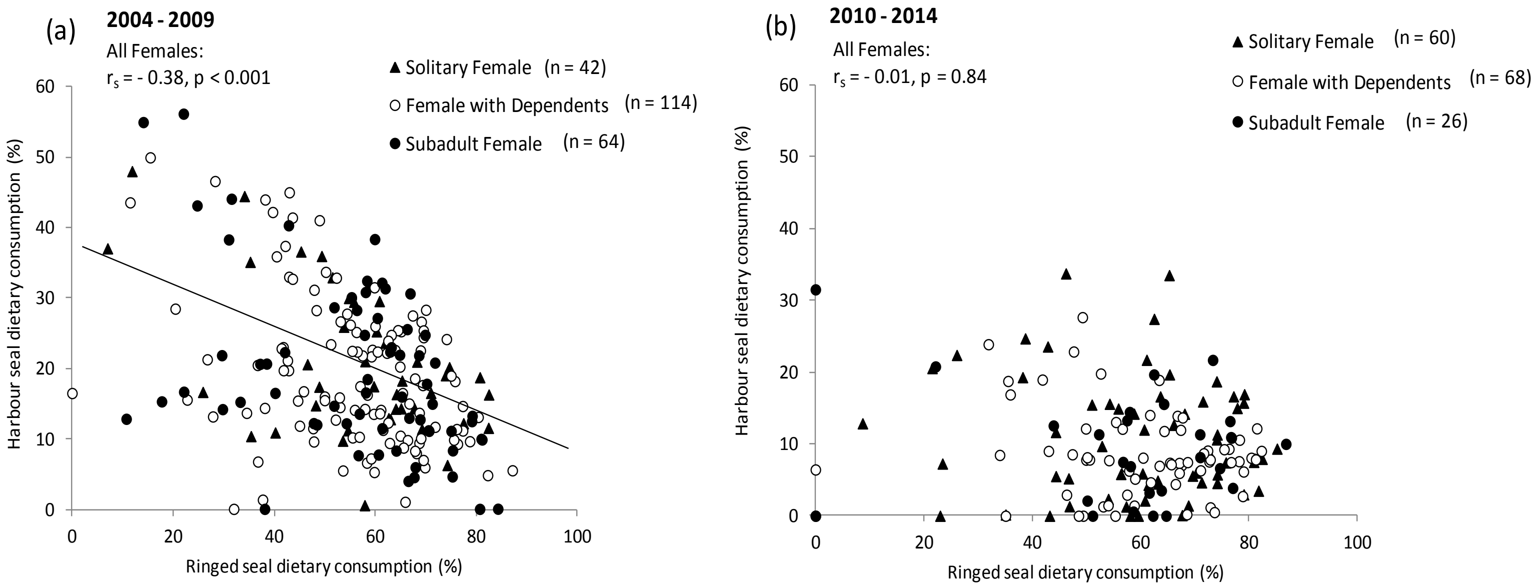

**Figure 4.** Relationship between consumption of ringed seal versus harbour seal for solitary females (▲), females with dependent offspring (○) and subadults (●) captured in the fall, (a) 2004 - 2009 and (b) 2010 - 2014 in western Hudson Bay. Consumption of harbour seal and ringed seal across all females during the entire study period (2004 - 2014): $r_s$ = - 0.29, $p$ < 0.001.

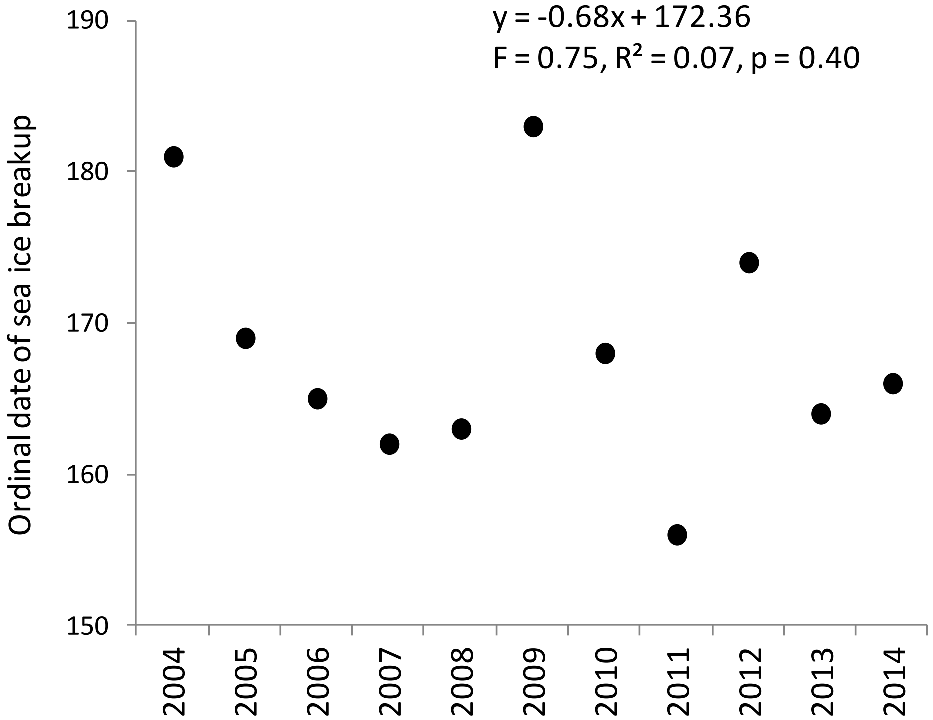

**Figure 5.** Timing of sea ice breakup (50% sea ice concentration) in the Western Hudson Bay management zone (PBSG, 2015), 2004 to 2014.

**Table 1.** Shannon-Wiener Diversity Index (*H'*) values (mean ± SEM) for 374 female polar bears captured in western Hudson Bay in fall 2004 - 2014. Minimum and maximum individual observations of diet diversity are indicated as well as absolute differences in diversity index.

| **Age and Reproductive Status** | ***H'* Mean ± SE** | **Range [absolute difference]** |
|---|---|---|
| Solitary adult female (n=102) | 0.97 ± 0.017 | 0.50 - 1.28 [0.78] |
| Adult female with yearling cubs (n=62) | 1.04 ± 0.019 | 0.63 - 1.42 [0.79] |
| Adult female with cubs-of-the-year (n=120) | 0.98 ± 0.018 | 0.25 - 1.40 [1.15] |
| Subadult female (n=90) | 0.97 ± 0.021 | 0.40 - 1.43 [1.03] |

**Table 2.** Multiple linear regression models examining the effect of ice *breakup* date, *lag breakup* date and *year* on consumption of prey species for female polar bears including solitary adults, family groups (adult females supporting dependents), and subadults captured between 2004 - 2014 in western Hudson Bay. * represents the significant predictor variable in each model.

| | Multiple Regression Model | | | β Coefficient (p significance) | | |
|---|---|---|---|---|---|---|
| **Solitary** n = 102 | *F* | *p* | *Adj.* $r^2$ | Breakup Date | Lag Breakup | Year |
| Ringed seal | 2.40 | 0.07 | 0.040 | - 0.11 (0.27) | -0.23 (0.02) | 0.06 (0.54) |
| Harbour seal | 13.63 | <0.001 | 0.273 | 0.14 (0.12) | 0.12 (0.16) | -0.46 (<0.001)* |
| Bearded seal | 7.82 | <0.001 | 0.168 | 0.001 (0.99) | 0.13 (0.15) | 0.43 (<0.001)* |
| Beluga whale | 13.59 | <0.001 | 0.272 | 0.07 (0.44) | 0.09 (0.30) | -0.50 (<0.001)* |
| Harp seal | 2.83 | 0.04 | 0.052 | 0.03 (0.74) | -0.02 (0.83) | 0.28 (0.006)* |
| Walrus | 1.06 | 0.36 | 0.002 | -0.15 (0.15) | -0.07 (0.46) | 0.04 (0.67) |
| **Family** n = 182 | | | | | | |
| Ringed seal | 4.23 | 0.006 | 0.051 | -0.21 (0.01) | -0.21 (0.006)* | 0.04 (0.51) |
| Harbour seal | 22.76 | <0.001 | 0.265 | 0.27 (<0.001) | 0.17 (0.01) | -0.38 (<0.001)* |
| Bearded seal | 17.73 | <0.001 | 0.217 | -0.09 (0.18) | 0.02 (0.78) | 0.44 (<0.001)* |
| Beluga whale | 40.73 | <0.001 | 0.397 | 0.15 (0.01) | 0.12 (0.04) | -0.57 (<0.001)* |
| Harp seal | 1.25 | 0.29 | 0.004 | 0.12 (0.14) | 0.06 (0.44) | 0.12 (0.10) |
| Walrus | 3.79 | 0.01 | 0.044 | -0.23 (0.004)* | -0.08 (0.28) | 0.06 (0.41) |
| **Subadult** n = 90 | | | | | | |
| Ringed seal | 1.79 | 0.15 | 0.026 | -0.22 (0.08) | -0.26 (0.03) | -0.03 (0.73) |
| Harbour seal | 8.52 | <0.001 | 0.202 | 0.33 (0.006) | 0.45 (<0.001)* | -0.19 (0.06) |
| Bearded seal | 7.58 | <0.001 | 0.182 | -0.17 (0.13) | -0.08 (0.44) | 0.37 (0.001)* |
| Beluga whale | 14.22 | <0.001 | 0.308 | 0.30 (0.006) | 0.38 (<0.001) | -0.39 (<0.001)* |
| Harp seal | 1.10 | 0.35 | 0.003 | 0.02 (0.84) | -0.17 (0.14) | 0.002 (0.98) |
| Walrus | 2.84 | 0.04 | 0.059 | 0.02 (0.86) | 0.01 (0.87) | 0.30 (0.008)* |

# CHAPTER IV

# Diet composition and dietary niche breadth predict body condition in a sexually size dimorphic marine carnivore

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This manuscript has been reprinted by permissions from its co-authors GW Thiemann and NJ Lunn from a manuscript in preparation for submission (see Appendix A).

## Abstract

Age- and sex-specific energetic demands may influence intraspecific patterns of foraging in animals. In sexually size dimorphic species, resource partitioning and patterns of prey selection should be reflected in dietary niche breadth and diet composition, and consequently influence body condition. We examined diet composition, niche breadth and body condition of polar bears (*Ursus maritimus*), a sexually size dimorphic marine predator, to determine if differences in energetic demands and body size among age, sex and reproductive classes influence diet. We used quantitative fatty acid signature analysis (QFASA) to generate estimates of polar bear diet from 2004-2014 in western Hudson Bay, and found that fatty acid signatures and diet composition differed among adult male and female bears as well as among females of different reproductive stages (solitary or accompanied by dependents). Consumption of prey types fluctuated over time, and although ringed seal (*Pusa hispida*) remained relatively consistent, significant increases in consumption occurred in bearded seal (*Erignathus barbatus)*, harp seal (*Pagophilus groenlandica)* and walrus (*Odobenus rosmarus)*. Adult males consumed both a greater proportion of larger-bodied prey types, as well as a broader range of prey species compared to females and subadults. Dietary niche breadth increased with increasing body size (mass) in all bears. Body condition was inferred from adipose tissue lipid content and was significantly related to the proportional consumption of bearded seal, harbour seal (*Phoca vitulina*) and niche breadth (in adult males); bearded seal, ringed seal and niche breadth (in solitary females); and beluga whale (*Delphinapterus leucas*), ringed seal and niche breadth (in females with dependents). Body condition was positively related to niche breadth in adult males but negatively related to niche breadth in females with dependents, suggesting that less-selective foraging (e.g., scavenging) does not benefit body condition among reproductive females. Given that body condition is a key determinant of reproduction and survival in polar bears, our results reveal functional relationships between environmental conditions (i.e., prey availability) and polar bear demography.

**Keywords:** body condition, body size, diet, foraging ecology, niche breadth, sexual size dimorphism, *Ursus maritimus*

## Introduction

An organism's ability to successfully locate, capture and consume prey is essential to its reproductive success and survival. Foraging behaviour is based on a suite of intrinsic characteristics (e.g., sex, age, morphology, physiology, energetic state) interacting with the external environment (Sih, 2011). An organism's behavioural response to environmental heterogeneity will vary among individuals and can result in intraspecific variation in foraging behaviour (Sih, 1993).

Age- and sex-specific patterns in foraging behaviour have been well-documented across taxa, including ungulates (Ruckstuhl, 1998; Kie & Bowyer, 1999), reptiles (Paulissen, 1987), birds (Lewis *et al.*, 2002; Weimerskirch *et al.*, 2009) and marine mammals (Le Boeuf *et al.*, 1993; Breed *et al.*, 2006). For example, in sexually size dimorphic species, the larger sex may consume a greater proportion of the same prey types or a greater array of different prey types (broadening niche breadth) than the smaller-bodied sex (Clutton-Brock, Iason & Guinness, 1987; Dickman, 1988; Costa, 2009). Similarly, larger bodied individuals may have a wider geographic range (Lindstedt & Boyce, 1985; Kelt & Van Vuren, 1999) and travel greater distances to locate diverse prey. Energetic requirements needed to satisfy a larger body size may work to structure sex-specific foraging behaviour (Clutton-Brock *et al.*, 1987; Main & Coblentz, 1990). Reproductive demands have also been found to affect sex differences in foraging behaviour. Pregnant females or those females supporting dependent offspring have greater energetic demands compared to males or non-reproductive females and will select foraging habitat and prey to maximize energy intake while minimizing reproductive risks (Clutton-Brock & Parker, 1992). For example, Kie and Bowyer (1999) found that female white-tailed deer (*Odocoileus virginianus*) supporting dependent offspring selected for densely covered foraging habitat to avoid predators, thus partitioning resources between the sexes. Sex-based differences in body size and energy requirements can result in niche divergence, whereby intraspecific competition is reduced as a result of sex-specific differences in resource selection (Schoener, 1969).

Accurate determination of foraging behaviour and diet is often essential for a quantitative understanding of animal ecology. Quantitative fatty acid signature analysis (QFASA) (Iverson *et al.*, 2004) is an especially powerful tool for estimating predator diets, particularly in marine environments, in which a broad range of long-chain polyunsaturated fatty acids can be traced from prey to predator (Ackman, 1989). QFASA is based on the knowledge that dietary fatty acids are predictably incorporated into predator tissues over ecologically relevant periods of time (weeks to months) (Iverson *et al.*, 2004). QFASA estimates require data on the fatty acid composition of all potential prey and an understanding of fatty acid-specific patterns of metabolism in the predator (Iverson *et al*., 2004). In the absence of such data, predator fatty acids alone can be used to identify intraspecific differences in predator diets across temporal and spatial scales (Cooper *et al*., 2009; Iverson *et al*., 1997; Thiemann *et al*., 2007b).

The polar bear (*Ursus maritimus*) is a sexually size dimorphic marine predator, with males achieving an adult body mass roughly twice that of females through both higher growth rate and a prolonged period of growth (Atkinson, Stirling & Ramsay, 1996b; Derocher & Stirling, 1998; Derocher & Wiig, 2002). Despite pronounced differences in body size between males and females, body condition (fatness) does not follow a similar pattern. Fatness varies based on sex and reproductive status of females, where females supporting dependent offspring have less body fat compared to solitary females, due to the higher energetic demands of lactation and provisioning of young (Pond, Mattacks & Ramsay, 1992; Atkinson & Ramsay, 1995; Thiemann *et al.*, 2006; Sciullo *et al.*, 2016). Further, pregnant females often have higher proportional adiposity than any other group (Atkinson & Ramsay, 1995; Atkinson, Nelson & Ramsay, 1996a).

Throughout their circumpolar range, polar bears rely on ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) as their primary prey (Stirling & Archibald, 1977; Thiemann *et al.*, 2008a). Polar bears may also prey on other locally available marine mammals including harp seal (*Pagophilus groenlandicus*), harbour seal (*Phoca vitulina*), beluga whale (*Delphinapterus leucas*) and walrus (*Odobenus rosmarus*) (Thiemann *et al.*, 2008a). In western Hudson Bay (WH), the sea ice melts completely in summer, which forces polar bears onshore and limits their access to marine mammal prey. While on shore, polar bears must rely on stored energy for at least 4 months during the ice-free period and up to 8 months for females entering terrestrial maternity dens in the fall (Stirling *et al.*, 1977; Atkinson & Ramsay, 1995). Sea ice conditions in WH have changed over the past 40 years, such that progressively earlier breakup and later freeze-up (Gagnon & Gough, 2005; Hochheim & Barber, 2014) have shortened the on-ice foraging period in the spring and forced bears to fast for longer periods onshore while relying on smaller fat stores (Stirling *et al.*, 1999; Sciullo *et al.*, 2016). Reduced body condition has been associated with declining reproductive success, survival, and abundance in WH polar bears (Regehr *et al.*, 2007; Lunn *et al.*, 2016). Although earlier studies have suggested that males and females in WH differ in their on-ice foraging habits (e.g., Thiemann *et al.*, 2008), little is known about how polar bear diets may have changed since 2004 or how foraging habits contribute to the stored energy (i.e., body condition) that is essential to their survival and reproduction.

We used QFASA to estimate diet composition of WH polar bears across age and sex class and identify inter-annual patterns in prey consumption. We also examined how prey selection and dietary niche breadth may be related to polar bear body condition. We hypothesized that differences in diet and niche breadth would be influenced by sex- and age-specific differences in body size and energetic requirements. We expected males to have a broader dietary niche compared to females due to larger body size allowing for capture of larger prey (Thiemann *et al.*, 2008a). We further hypothesized that females supporting dependent offspring would also consume a broad range of prey types, compared to solitary females, to offset the high energetic demands of lactation (Sciullo *et al.*, in press). Finally, we expected the relationship between diet, niche breadth and body condition to differ across sex, with males expected to benefit from consumption of a broader range of prey types and females more likely to specialize on available small-bodied prey.

## Methods

### *Study site and sample collection*

We captured free-ranging polar bears on shore in northeastern Manitoba, between the Churchill and Nelson rivers, in August and September from 2004 to 2014 as part of a long-term research program on polar bear ecology in WH (Ramsay & Stirling, 1988; Lunn *et al.*, 2016). Bears were located from a Bell 206B JetRanger helicopter and captured using standard chemical immobilization techniques (Stirling, Spencer & Andriashek, 1989; Cattet *et al*. 1999). We uniquely marked all bears with plastic ear tags and identifying tattoos on the inside of the upper lip. The age of bears greater than one year was determined by counts of cementum growth layer groups (Calvert & Ramsay, 1998). Ages of cubs-of-the-year (COY; approximately 9 months old in fall) and yearling cubs (approximately 21 months old) were based on body size and dentition. Bears 5 years and older were considered adults, and subadults were independent bears 2-4 years old. We estimated body mass using regression equations (Thiemann *et al.*, 2011b) based on straight-line body length (nose tip to last vertebra of the tail, cm) and axillary girth (cm) for each bear in sternal recumbency. We collected a subcutaneous adipose tissue sample (skin to muscle) from each bear using an 8 mm biopsy punch (Miltex Inc., York, PA, USA) inserted ca. 15 cm lateral to the base of the tail. Biopsies were sealed in cryogenic vials and stored at -20°C until analysis. All capture and handling procedures were reviewed and approved annually by the Animal Care and Use Committees at Environment and Climate Change Canada and York University.

### *Laboratory analysis*

We removed any attached skin or muscle from adipose tissue biopsies and weighed the remaining tissue. We quantitatively extracted lipid using methods outlined by Iverson, Lang & Cooper (2001). Lipid content was expressed as percent total wet weight ± standard error of the mean (SEM). Adipose tissue lipid content values were used as an index of overall fatness (body condition) in each bear (Thiemann *et al.*, 2006; Stirling *et al.*, 2008; McKinney *et al.*, 2014).

We derived fatty acid methyl esters (FAME) from each lipid sample using sulfuric acid as a catalyst (Budge *et al.*, 2006) and identified > 70 fatty acids (FA) via temperature-programmed gas-liquid chromatography using a Perkin Elmer Autosystem II capillary gas chromatograph and flame ionization detector (Agilent Technologies, Palo Alto, California, USA). We identified FA using the standard nomenclature of A:Bn-X, where A is the length of the carbon chain, B is the number of double bonds, and n-X indicates the position of the first double bond relative to the terminal methyl group. FAME samples were analyzed in duplicate and we manually verified FA identifications using Varian Star 6.41 Chromatography Workstation software (Varian Inc., 2004). Each FA was expressed as mass percent of the total FA ± 1 SEM.

### *Diet modelling*

We estimated polar bear diet composition using QFASA (Iverson *et al*., 2004). In brief, this technique models each predator FA profile (or "signature") as a linear combination of mean prey signatures. The diet of each predator is estimated as the proportional combination of prey types that minimizes the distance between observed and modeled predator signatures. To account for FA-specific metabolism (e.g., biosynthesis) in the predator we used calibration coefficients derived from a terrestrial carnivore, mink (*Mustela vison*), fed a controlled marine-based diet (Thiemann *et al.*, 2008a).

We used the Aitchison distance (Bromaghin *et al.*, 2015, 2016) and 30 FA derived primarily from diet (Supplementary Material, Table S1) (Iverson *et al.*, 2004, Galicia *et al.*, 2015; Sciullo *et al.*, in press) to generate QFASA diet estimates. We used FA signatures of relevant prey species as previously outlined in Sciullo *et al*. (in press). Since predator FA profiles can reflect integrated diet of individuals up to several months prior to sampling (Iverson *et al*., 2004), diet estimates of bears captured on land during the fall likely reflect foraging behaviour during the previous months while on the sea ice. All QFASA estimates were calculated using the QFASA package in R (v 3.2.4, The R Foundation for Statistical Computing, 2005).

### *Statistical analyses*

To examine differences in FA signatures and diet estimates, polar bears were separated into five groups based on age, sex and reproductive status (denoted as 'age/sex group' from this point forward): adult male, solitary adult female, adult female accompanied by dependent offspring, subadult male and subadult female.

We used principal component analysis (PCA) as an exploratory tool to assess patterns in FA signatures across polar bear age/sex group. We used a total of 38 extended dietary FA (Supplementary Material, Table S1) derived both from diet and biosynthesis (Iverson *et al.*, 2004). To improve normality, we used a log- transformation on all FA data using the equation: $\chi_{trans} = \ln(\chi_i / c_r)$, where $\chi_{trans}$ is the log transformed FA; $\chi_i$ is the proportion of FA $i$, and $c_r$ is a constant reference FA (18:0) (Budge *et al.*, 2002; Iverson, Frost & Lang, 2002). We then used PCA components that accounted for > 70% of total variance (Jolliffe 2002) to assess differences across age/sex group and across collection year using multivariate analysis of variance (MANOVA).

Diet estimates derived from QFASA were not normally distributed, as diet composition of individual bears did not always include all potential prey types (i.e., some individuals consumed zero biomass of a particular prey species). To account for this, we used randomization-permutation tests to examine dietary differences across age/sex groups (Anderson, 2001a, 2001b; Thiemann *et al.*, 2008a). We used two-way randomized-permutation MANOVA (with 10 000 permutations) to test for differences in overall diet composition across age/sex group and across collection year. Post-hoc tests for each prey type between age/sex group were completed using one-way permutation ANOVA. To assess trends in the consumption of each prey species over time (year), we used Spearman-rank correlations within each age/sex group.

We calculated dietary niche breadth for each individual polar bear using Levins (1968) formula:

$$B = \frac{1}{\sum p_i^2}$$

where B is the dietary niche breadth of an individual, and $p_i$ is the proportion of prey species *i* in the diet. Niche breadth values range from 1 to the maximum number of prey categories (n=6). To allow for comparisons of niche breadth across age/sex group when different number of prey types were consumed, we calculated standardized dietary niche breadth (Colwell & Futuyma, 1971; Iriarte *et al.*, 1990), as follows:

$$B_{sta} = \frac{(B_{obs} - B_{min})}{(B_{max} - B_{min})}$$

where $B_{sta}$ is the standardized niche breadth, $B_{obs}$ is the observed niche breadth, $B_{min}$ is the minimum niche breadth (consumption of only one prey type, =1), and $B_{max}$ is the maximum number of prey types consumed. Values of $B_{sta}$ range from 0 (narrow, specialist diet) to 1 (broad, generalist diet). Differences in niche breadth across age/sex group were assessed using Mann-Whitney U Tests. We used Spearman-rank correlations to assess the relationship between individual prey consumption, dietary niche breadth, adipose tissue lipid content and body mass for each age/sex group.

To investigate the relationship between diet composition and variability in adipose tissue lipid content, we used generalized linear models in a model competition framework based on Akaike's information criteria (AIC). We used a step-wise method in model construction, in which separate regression models for lipid content with each separate prey type was constructed first, prior to combining multiple parameters (prey types) (Pilfold *et al.*, 2015). Models were then built combining multiple prey types with significant *p*-values ≤ 0.05. Model selection followed a backward-elimination method, removing parameters with the lowest Wald $\chi^2$ value until the remaining covariates produced a *p*-value ≤ 0.05. We used Akaike's information criterion, corrected for small sample size ($AIC_c$; Burnham and Anderson, 2002) to compare candidate models. Since models with $\Delta AIC_c$ < 2 imply substantial empirical support for the particular model (Burnham & Anderson, 2002), this measure was used to select best fitting models and are reported in the results, however all models constructed are available in Supplementary Information, Table S2. We used a Pearson's correlation < 0.80 and collinearity index < 15 to ensure non-collinearity among covariates (Rode *et al.*, 2010). Tolerance values remained > 0.10 and variation inflation factor < 3.5. All statistical analyses were conducted using R (v 3.2.4, The R Foundation for Statistical Computing, 2005) and SPSS® version 22 for Windows® (IBM, Chicago, USA).

## Results

### *Intraspecific variation in FA signatures*

A PCA performed on 38 FA generated 6 principal components (PC) accounting for 85.6% of total variance. The first three PC scores accounted for 71.4% of the total variance. The FA with the greatest loadings on PC1 (44.7%) were diet-derived, polyunsaturated and monounsaturated FA and included 18:4n-1, 20:5n-3, 16:1n-7, 18:2n-4, 18:4n-3, 16:3n-6 , 20:4n-3. FA loaded onto PC2 (14.2%) consisted only of polyunsaturated FA, and included 18:2n-6 and 22:5n-3. Only diet derived polyunsaturated and monounsaturated FA loaded onto PC3 (12.4%), including 22:4n-6 and 20:1n-7. Polar bear FA signatures separated best based on age/sex group, with adult males and adult females showing separate clusters (Fig. 1a), as well as solitary females and those supporting dependents (Fig. 1b). A MANOVA carried out on three PC scores across all bears showed that FA signatures significantly differed across age/sex group (MANOVA, $\lambda = 0.58$, $p < 0.001$) and collection year ($\lambda = 0.72$, $p < 0.001$), as well as an interaction effect ($\lambda = 0.76$, $p =$

0.001). All three principal components had a significant influence on polar bear fatty acid signature for age/sex group and collection year ($p < 0.001$, respectively), but only PC1 and PC3 contributed to the interaction effect ($p = 0.008$ and $p = 0.04$, respectively).

### *Intraspecific variation and temporal trends in diet composition*

Overall diet composition differed across polar bears of different age/sex group (MANOVA, $p < 0.001$) and collection year ($p < 0.001$), with a significant interaction effect ($p = 0.001$). Ringed seal contributed the most to polar bear diets, and ranged from 36.8 ± 1.2% (adult male) to 58.3 ± 1.6% (solitary female) (mean ± SE) across all years. Adult males consumed significantly less ringed seal than solitary females (one-way permutation ANOVA, $p < 0.001$), females with dependents ($p < 0.001$), subadult males ($p < 0.001$) and subadult females ($p < 0.001$) (Fig. 2). Overall, female bears (solitary, females with dependents and subadults) consumed the greatest proportion of ringed seal (Fig. 2). Both solitary females and females with dependents consumed significantly more ringed seal than subadult males ($p = 0.02$, respectively). Ringed seal was found more frequently in the diet of solitary females (100% of bears), females with dependents (98.3% of bears) and subadult females (97.7% of bears), compared to adult males (89.4% of bears).

Bearded seal consumption varied across bears and ranged from 12.8 ± 1.5% (subadult female) to 30.9 ± 1.3% (adult male) (Fig. 2). Adult male bears consumed significantly more bearded seal than solitary females (one-way permutation ANOVA, $p < 0.001$), females with dependents ($p < 0.001$), subadult females ($p < 0.001$), and subadult males ($p < 0.001$). Further, bearded seal appeared more frequently in the diets of both adult males (83.7% of bears) and solitary females (82.3% of bears), than females with dependents (71.4% of bears), subadult females (63.3% of bears), and subadult males (72.2% of bears).

Harbour seal was found in relatively high proportion across polar bear diet, although it did not significantly differ across age/sex group ($p = 0.46$) (Fig. 2). The frequency of harbour seal present in polar bear diet was consistently high across all groups, ranging from 93.0% (subadult male) to 96.7% (females with dependents) of bears. Harp seal contribution to polar bear diet varied based on age/sex group, as adult males consumed proportionately more than solitary females ($p = 0.005$) and females with dependents ($p = 0.01$) (Fig. 2). Similarly, subadult males consumed more harp seal than solitary females ($p < 0.001$), and females with dependents ($p < 0.001$) (Fig. 2). Harp seal appeared more often in the diets of subadult and adult males (62.5% and 59.2% of bears, respectively) than all other age/sex groups (maximum of 49% of bears, for females with dependent offspring).

Consumption of both beluga whale and walrus did not significantly differ across groups ($p = 0.05$ and $p = 0.37$, respectively) (Fig. 2). However, beluga whale accounted for >15% of overall diet early in the study period (2005) across all groups, and was more frequently consumed by subadult male (77.7% of bears), subadult female (70.0% of bears) and females with dependents (77.4% of bears). On average, walrus was found in trace amounts across bears (<5% of total dietary intake), however was consumed more so by solitary adult females (90.2% of bears) and females with dependents (83.5% of bears), than adult males (76.3% of bears), subadult males (65.2% of bears), and subadult females (72.2% of bears).

Diet composition also varied over time and across age/sex group (Fig. 3). Bearded seal consumption significantly increased over time in adult males (Spearman-rank correlation, $r_s =$

0.53), solitary females ($r_s = 0.46$), females with dependents ($r_s = 0.56$) and subadults ($r_s = 0.58$) ($p < 0.001$ in all cases) (Fig. 3). Both beluga whale and harbour seal consumption declined over time in adult males ($r_s = -0.37$ and $r_s = -0.34$, respectively), solitary females ($r_s = -0.55$ and $r_s = -0.48$), females with dependents ($r_s = -0.65$ and $r_s = -0.49$) and subadults ($r_s = -0.34$ and $r_s = -0.37$) ($p < 0.001$ in all cases). Proportion of ringed seal, however, showed no significant change in adult males ($p = 0.15$), solitary females ($p = 0.11$), females with dependents ($p = 0.09$) or subadults ($p = 0.12$) (Fig. 3). Harp seal consumption increased over time in solitary females ($r_s = 0.39$) and females supporting dependents ($r_s = 0.36$) ($p < 0.001$ in all cases), but did not change significantly in adult males ($p = 0.15$) or subadults ($p = 0.41$) (Fig. 3). Walrus consumption increased in subadults during the study period ($r_s = 0.32$, $p < 0.001$) but did not significantly vary over time in adult males ($p = 0.16$), solitary females ($p = 0.50$) or females with dependents ($p = 0.08$) (Fig. 3).

### *Niche breadth, diet and body condition*

Dietary niche breadth differed in polar bears across age/sex group. Specifically, adult males and subadult males had a significantly broader dietary niche breadth than solitary adult females (Mann-Whitney, $p < 0.01$ in all cases), females with dependents ($p = 0.006$ and $p = 0.01$, respectively), and subadult females ($p = 0.003$ and $p = 0.006$, respectively) (Table 1). Dietary niche breadth also significantly increased with increasing body size (mass) across all bears (Spearman rank correlation, $r_s = 0.11$, $p = 0.003$). Although a greater proportion of adult males consumed broader range of prey types overall (Fig. 4), when niche breadth was narrow, most bears specialized on ringed seal and walrus regardless of age/sex group (significant negative Spearman-rank correlations, Table 2).

Adipose tissue lipid content was positively correlated with niche breadth in adult males (Spearman rank correlation, $r_s = 0.17$, $p = 0.002$) and negatively correlated in females supporting dependents ($r_s = -0.16$, $p = 0.03$) (Fig. 5). Lipid content, however, was not significantly related to niche breadth in solitary adult females ($p = 0.13$), subadult males ($p = 0.10$) or subadult females ($p = 0.55$).

Table 3 lists the Akaike's information criterion (AIC) values of the top regression models comparing adipose tissue lipid content with consumption of different prey types and niche breadth. For adult males, the top models significantly predicting adipose tissue lipid content consisted of bearded seal and dietary niche breadth (model 1) and bearded seal, harbour seal and niche breadth (model 2), both with $\Delta AIC_c < 2$. Conversely, lipid content in solitary adult females was predicted by niche breadth (model 1), bearded seal (model 2) and ringed seal (model 3), with $\Delta AIC_c < 2$, however none of these models were significant. Finally, variability in adipose tissue lipid content in females supporting dependents was significantly predicted by both consumption of beluga whale and niche breadth (model 1) and consumption of beluga whale, ringed seal and niche breadth (model 2), with $\Delta AIC_c < 2$.

## Discussion

In this study, sex-specific variation in polar bear fatty acid signatures reflected differences in diet composition and suggests that sexual-size dimorphism plays an important role in prey selection. Intraspecific variation in diet and niche breadth and its influence on body condition suggest that polar bears alter their foraging patterns in response to differing energetic demands associated with sex and reproduction. Relatively narrow dietary niches suggest that adult and subadult females as well as family groups may be most sensitive to changes in prey availability and the negative relationship between body condition and niche breadth suggests that increased scavenging will not likely improve fitness among females with dependent offspring.

### *Intraspecific variation in FA signature*

Polar bear FA signatures were typical of high latitude, lipid-rich marine organisms *(Iverson et al.*, 1997; Thiemann *et al*., 2007, 2008). Polar bear signatures were characterized by diet-derived, long-chain polyunsaturated fatty acids (PUFA) (Iverson *et al.*, 1997b) and showed distinct separation between adult male and adult female bears as well as among females of differing reproductive stages (Fig. 1). Intraspecific variation in FA signatures in marine carnivores reflect differences in prey selection, particularly in sexually size dimorphic species. FA signatures of other size dimorphic marine mammals, for example, have also shown significant separation between males and females, such as common dolphins (*Delphinus delphis*: Smith and Worthy, 2006), gray seal (*Halichoerus grypus*: Beck *et al.*, 2005), bearded seal (*Erignathus barbatus*) and spotted seal (*Phoca vitulina*: West *et al*., 1979).

Reproductive status of female polar bears also likely influenced FA signatures, as solitary females and females supporting dependent offspring showed distinct separation in FA composition (Fig. 1). Variation in FA composition between females of differing reproductive status has been observed in other species and may be a function of diet and energetic demands (Aguilar & Borrell, 1990; Samuel & Worthy, 2004). As energy expenditure during lactation is particularly high (Gittleman & Thompson, 1988; Oftedal, 2000), fat stores in females will be depleted rapidly and individuals require substantial calorie intake to offset rapid fat catabolism (Gittleman & Thompson, 1988). Thus, it is likely that energetic demands among females differs substantially enough to illicit differing diet compositions reflected via FA signatures.

### *Intraspecific variation and temporal trends in diet composition*

Differences in FA composition across sex and reproductive status in polar bears was also reflected in diet composition as modelled by QFASA. Our results were consistent with previous studies on polar bear foraging patterns, which show primary prey consisting of both ringed seal and bearded seal (Fig. 2) (Stirling and Archibald, 1977; Stirling and Øritsland, 1995; Thiemann *et al.*, 2008; Sciullo *et al*., in press). In this study, adult males consumed the lowest proportion of ringed seal compared to other groups, and conversely consumed the greatest proportion of bearded seal (Fig. 2). Adult males may specialize on bearded seal, a large bodied prey (~ 300 kg), compared to young smaller bodied bears with greater size constraints (Thiemann *et al*., 2007, 2011). However, we also found that both adult males and solitary adult females more frequently consumed bearded seal compared to females with dependents and subadults. Although female polar bears are on average smaller in body size than males (Derocher, Andersen & Wiig, 2005), solitary females have been observed foraging in similar habitat alongside males (Stirling *et al.*, 1993), consistent with our results of similar frequency in bearded seal consumption. However, the lower consumption of bearded seal compared to males, suggests females may be limited to hunting smaller, juvenile bearded seals or scavenging the carcasses of seals killed by adult male bears. Scavenging may be an important foraging strategy for females preparing for reproduction as it may require less energy expenditure compared to active hunting (Carbone, Teacher & Rowcliffe, 2007; Mattisson *et al.*, 2016).

Similar to bearded seal, harp seal was consumed more frequently in adult and subadult males than females. Harp seal is also a broadly distributed large bodied prey, however is more prominent in the eastern Arctic (DFO, 2011) and likely consumed as opportunistic prey (Iverson *et al*., 2006; Thiemann *et al.*, 2008). Similarly, active hunting of polar bears on walrus and beluga whale has been infrequently observed (Freeman, 1973), and thus opportunistic scavenging is more probable (Freeman, 1973; Heyland & Hay, 1976; Rugh & Shelden, 1993), characteristic of the low proportional consumption of such prey species observed in this study (Fig. 2). As male polar bears are capable of travelling long distances while on the sea ice (Amstrup *et al.*, 2001), migration beyond the WH management zone and towards the eastern Arctic may be possible for some individuals, increasing the likelihood of encountering such prey species. Future telemetry based studies, however, are necessary to better understand adult male movement patterns and its relationship to foraging behaviour.

Prey consumption fluctuated over time across all polar bear age/sex groups (Fig. 3). Ringed seal consumption was consistent over the study period, with inter-annual fluctuations, however showed no significant directional trend (Fig. 3). Similar results were found in other studies (Sciullo *et al*. in press; McKinney *et al*., 2009; Thiemann *et al*., 2008) and suggests that although ringed seal life history, body condition, abundance and survival may fluctuate annually in response to environmental change (Chambellant *et al.*, 2012a; Young *et al.*, 2015; Ferguson *et al.*, 2016), this particular prey species continues to be the most readily available and easily captured prey item. Thus, although changes to sea ice in Hudson Bay have been observed to influence ringed seal, the effects on its proportional contribution to polar bear diet may have a delayed effect and thus not yet observed via diet analyses.

We found consumption of bearded seal increased across all groups from 2004-2014, a marked increase from past studies that have observed a decline in bearded seal contribution to polar bear diet over a period of time spanning from 1991 to the early 2000s (Thiemann *et al.*, 2008a; McKinney *et al.*, 2009). Bearded seal prefer haul out sites located along ice floes and open leads, and are often observed in greater abundance on unconsolidated pack ice, rotten ice (dark to grey ice) and over shallow waters (Kingsley *et al.*, 1985; Kingsley & Stirling, 1991; Chambellant *et al.*, 2012a). Sea ice conditions throughout Hudson Bay have changed considerably over the past decade, with increased habitat fragmentation, reduced sea ice extent, and increased presence of both rotten and unconsolidated pack ice observed in recent years (Gagnon & Gough, 2005, 2006; Sahanatien & Derocher, 2012; Hochheim & Barber, 2014). Therefore, it is possible that sea ice conditions and increased fragmentation have created more favourable habitat for bearded seals. Unconsolidated sea ice is also preferred by walrus (Kiliaan & Stirling, 1978) which also increased in consumption over time, specifically in subadult bears (Fig. 3). Similar to bearded seal, walrus herds may become localized in areas with unconsolidated pack ice during years when sea ice is fragmented, creating scavenging opportunities for polar bears. Since information on the current distribution and abundance of polar bear prey in Hudson Bay remains limited, relationships between polar bear diet composition and prey are poorly understood. Future research on seal populations in this area may provide greater insight into polar bear foraging behaviour and their adaptations to a changing sea ice habitat.

### *Niche breadth, diet and body condition*

Variation in polar bear diet composition across sex and age class was also reflected in dietary niche breadth. Specifically, we found adult males to have the broadest dietary niche compared to females and younger bears (Table 1, Fig. 4), and niche breadth increased with body size. Larger bodied individuals of a species are often more dominant and can capture and handle larger bodied prey (Schoener, 1971; Morse, 1974). For example, Weise *et al*. (2010) found foraging behaviour among California sea lions (*Zalophus californianus*) to differ based on body size, as larger individuals successfully captured larger prey and were more efficient foragers. To allow for individuals of differing competitive abilities to coexist in similar habitats, subordinate individuals (likely to be females with dependents and subadults) may adopt some degree of foraging plasticity to minimize dietary overlap with dominant individuals (Morse, 1974). In our study, for example, adult and subadult females generally consumed fewer prey types relative to males (Table 1, Fig. 4), however, there was greater individual variation as some females consumed a broad range of prey. This suggests that although more limited in the types of prey they can capture, some subordinate individuals may broaden their dietary niche by adopting scavenging behaviour (Sciullo *et al.*, in press; Stirling and McEwan, 1975). Both body size and social dominance has been suggested to result in dietary and niche breadth differences in polar bears (Sciullo *et al*., in press; Thiemann *et al*., 2008, 2011), whereby large males may be able to exclude subordinates from foraging in high quality habitat (Stirling *et al.*, 1993; Pilfold *et al.*, 2014) and partition prey across polar bears of different age/sex groups (Stirling, 1974; Derocher & Stirling, 1990a).

Diet composition and niche breadth influenced body condition of polar bears differently depending on sex and reproductive status. Body condition (adipose tissue lipid content) increased with greater dietary niche breadth in adult males, but declined in females with dependents (Fig. 5). This suggests that females specializing on fewer prey types (narrow niche breadth) were able to amass greater lipid stores compared to females who consumed multiple prey types. Highly available prey have greater capture probability and therefore provide a more reliable caloric return (Drickamer *et al.*, 2002). Furthermore, predator species with mobile prey are more likely to forage on prey that are comparatively easier to capture instead of solely selecting for highest quality prey (Sih & Christensen, 2001). In our study, when proportional consumption of ringed seal and walrus increased, niche breadth declined in adult males, females with dependents and subadults (Table 2), suggesting specialization on these prey types. Ringed seal are the smallest marine mammal prey consumed by WH polar bears and their ubiquitous distribution allows for easy capture, particularly in the spring when weaned pups are abundantly available and constitute up to 50% fat by wet weight (Stirling & Archibald, 1977; Stirling & Øritsland, 1995; Stirling, 2002). Expending energy on easily captured prey therefore translates into greater accumulation of lipid stores necessary for survival during the ice-free season. Specialization on walrus, however, may be due to opportunistic foraging in small areas with large haul-outs that may result in a stampede event, increasing the likelihood of walrus mortality and providing scavenging opportunities for polar bears (Kochnev, 2005). In general, a greater niche breadth was associated with reduced body condition in females (Fig. 5), suggesting that scavenging behaviour is not an ideal foraging strategy and may be an adaptive response to either changes in prey availability or energetic state. Thus, although females may scavenge on multiple prey types providing some caloric value, this does not seemingly translate into improved body condition and fitness.

Fundamental differences in polar bears associated with age and sex likely play an important role in structuring foraging behaviour and consequently influence diet composition and niche breadth. Prey selection in polar bears is therefore structured based on body size and energetic demands that vary based on sex and reproductive status. Identifying the mechanisms underlying foraging behaviour and its role in diet, niche breadth and body condition, however, requires further study into the relationship between such intrinsic factors and environmental conditions. Understanding the influence of the environment on prey availability and predator behavioural response may provide better insight into the impacts of a changing environment on predator populations.

## Acknowledgements

We are very grateful to the Inuit hunters of Nunavut for the collection of fat samples from marine mammals harvested during annual subsistence hunts. We are thankful for the assistance with chromatographic analyses by S. Budge, C. Barry (Dalhousie University) and M. Galicia (York University), as well as S. Lang (Dalhousie University) for providing information regarding QFASA diet modelling. Thank you to the researchers, field assistants and helicopter personnel that assisted in the capture and handling of polar bears in western Hudson Bay throughout the years. This study was supported by the Natural Sciences and Engineering Research council (NSERC, Canada), Environment and Climate Change Canada, Fisheries and Oceans Canada, Nunavut Wildlife Management Board, Churchill Northern Studies Centre, Earth Rangers Foundation, Isdell Family Foundation, Manitoba Sustainable Development, Parks Canada Agency, Schad Foundation, Wildlife Media Inc., Northern Scientific Training Program (NSTP), and York University.

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# Figures and Tables

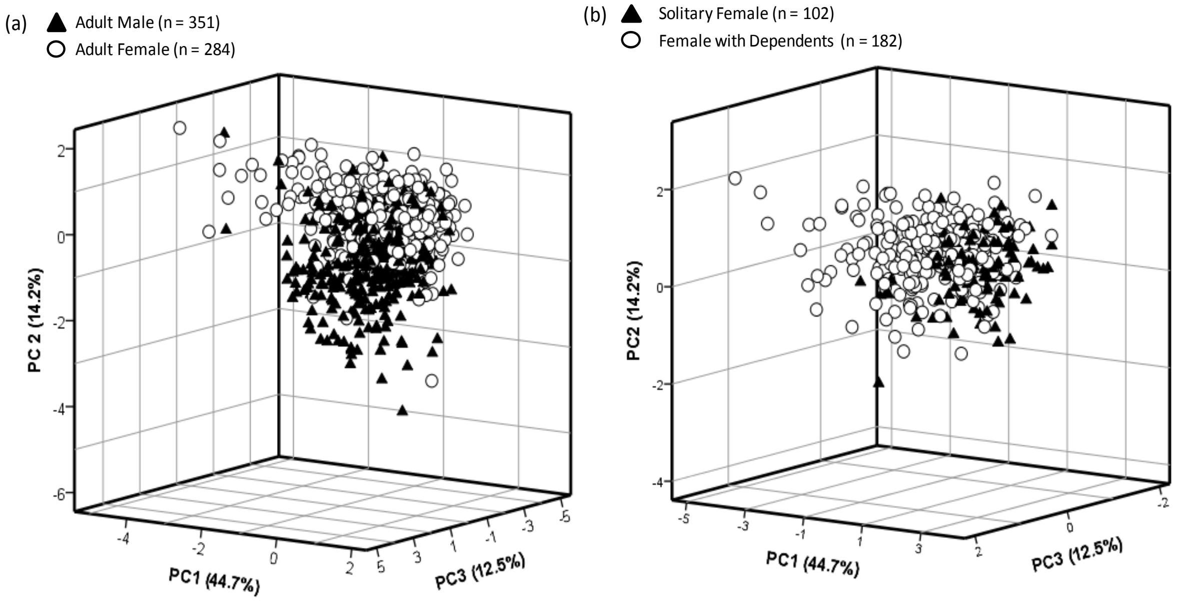

**Figure 1.** Variation in the fatty acid (FA) profiles of polar bears captured in western Hudson Bay in the fall, 2004 - 2014 based on principal component analysis (PC) of 38 dietary and extended dietary FA. For clarity, PC figures separated by: (a) sex (adult male and adult female) and (b) reproductive status (solitary adult female and females supporting dependent offspring). PCA score plot of PC1, PC2 and PC3 accounts for 71.4% of the total explained variance.

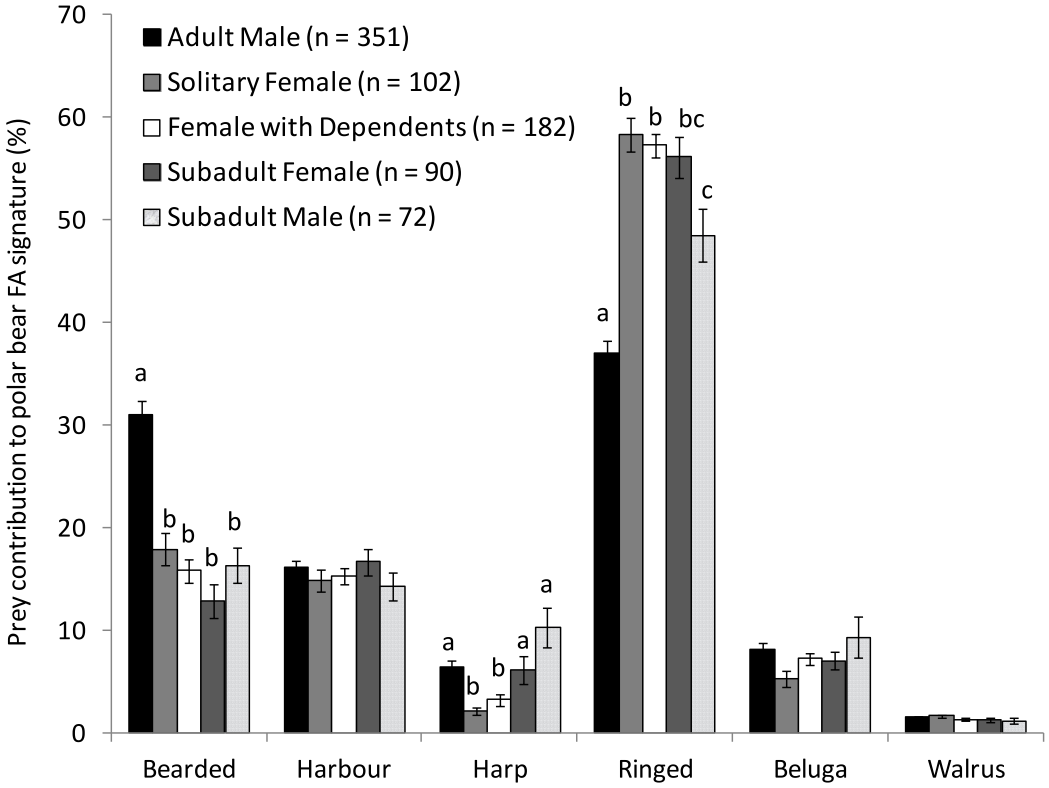

**Figure 2.** Diet composition of polar bears across age/sex group for individuals captured in western Hudson Bay in the fall, 2004-2014. Each prey species' biomass contribution to individual diet composition is represented as a mean ± SEM and sample size of each group denoted by (n). Different letters above bars denote significant differences in proportional consumption of prey types among age/sex groups. Prey types with no lettering indicate no significant differences among age/sex group in proportional consumption.

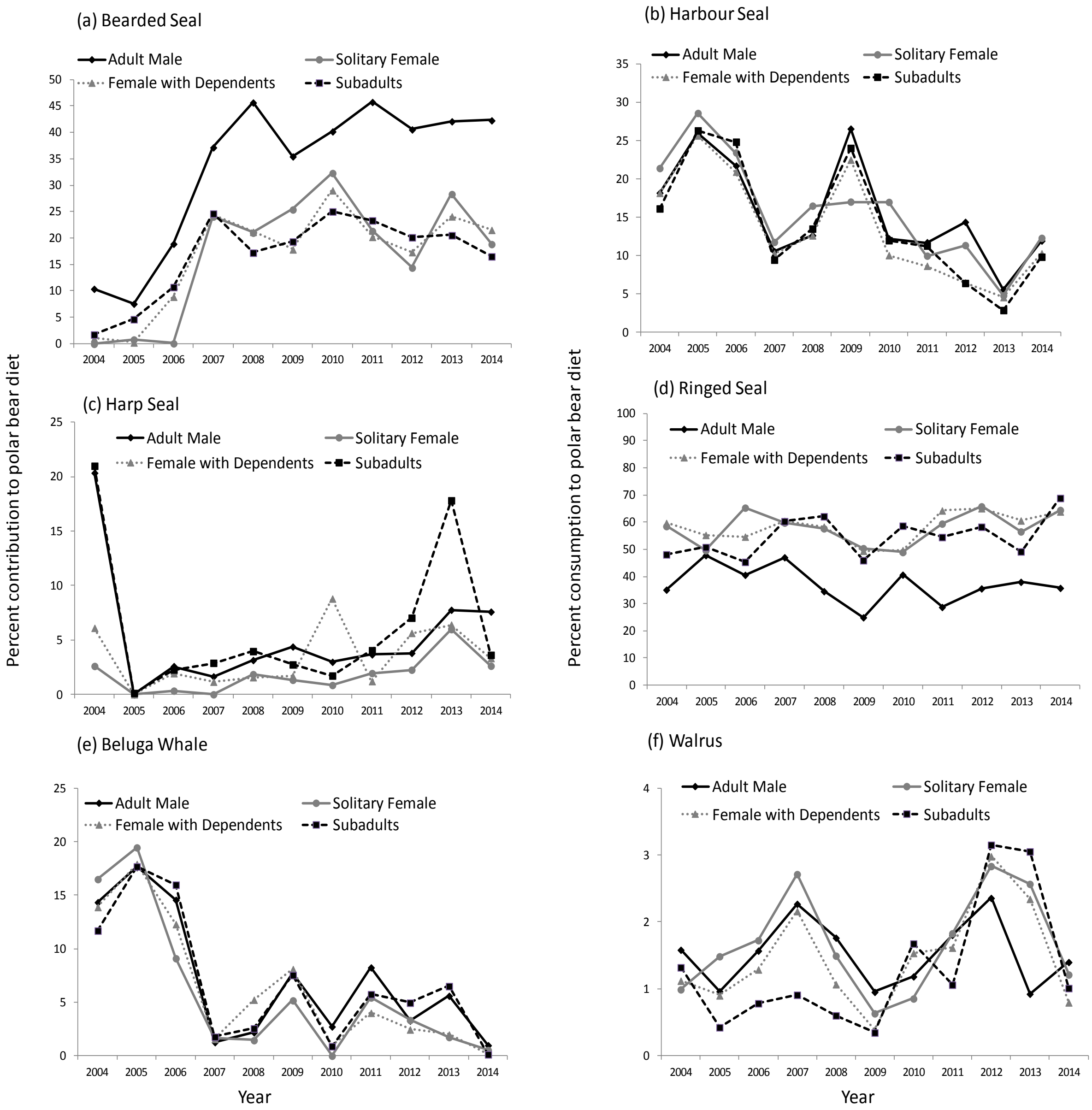

**Figure 3.** Temporal trends in diet composition of Western Hudson Bay polar bears, 2004-2014 as modelled by QFASA. Trends over time in individual prey species consumption are represented for adult male (n = 351), solitary adult females (n = 102), adult females supporting dependent offspring (n = 182) and subadults (n = 162). Each prey species' biomass contribution to diet composition is represented as a mean.

**Table 1.** Mean ± SEM values of estimated body mass (kg), adipose tissue lipid content (expressed as % wet weight) and dietary niche breadth for polar bears captured in western Hudson Bay in the fall, 2004-2014. Bears are separated based on age/sex group. Minimum and maximum individual observations of dietary niche breadth are indicated. Differing letters indicate significant differences (Mann-Whitney U Tests) in niche breadth across groups.

| Age & Sex Group | Mean Body Mass (kg) | Lipid Content (% Wet Wt) | Niche Breadth | Minimum - Maximum Niche Breadth |
|---|---|---|---|---|
| Adult Male | 395.18 ± 3.94 | 71.25 ± 0.57 | 2.46 ± 0.03[a] | 1.01 - 4.22 |
| Solitary Adult Female | 242.59 ± 5.30 | 79.47 ± 0.77 | 2.22 ± 0.04[b] | 1.35 - 3.22 |
| Female with Dependents | 204.81 ± 2.22 | 76.35 ± 0.67 | 2.31 ± 0.04[b] | 1.15 - 3.86 |
| Subadult Male | 227.16 ± 6.77 | 73.52 ± 1.23 | 2.53 ± 0.07[a] | 1.43 - 3.83 |
| Subadult Female | 169.00 ± 3.46 | 79.89 ± 0.84 | 2.26 ± 0.05[b] | 1.30 - 3.71 |

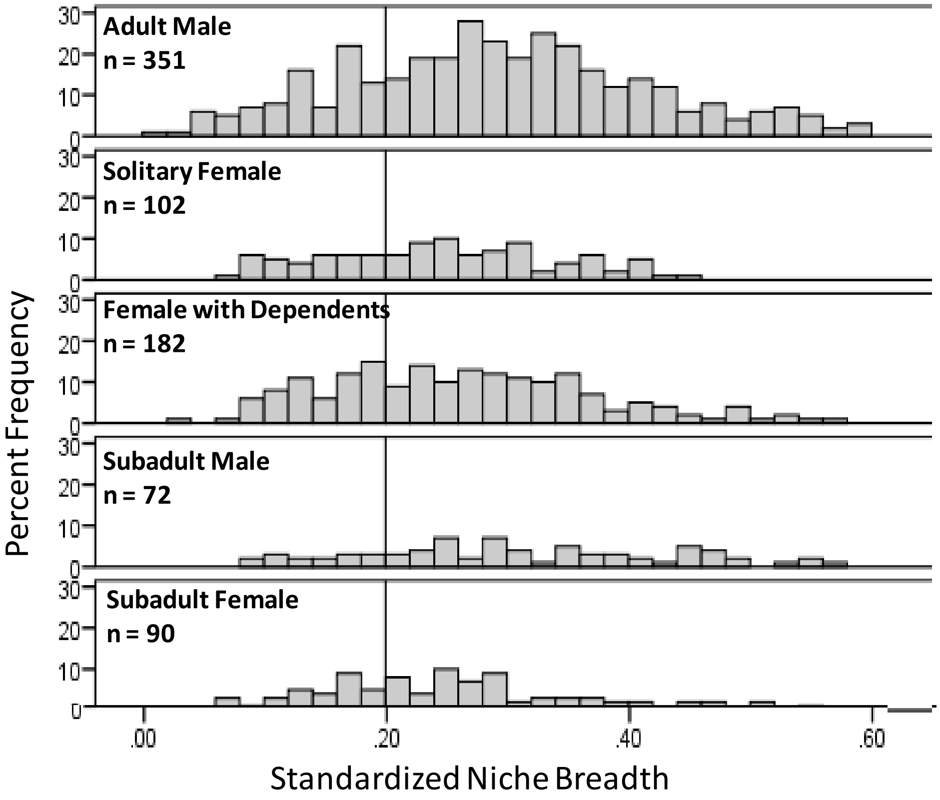

**Figure 4.** Percent frequency of occurrence in standardized dietary niche breadth of polar bears captured in western Hudson Bay in the fall 2004-2014 based on age/sex group.

**Table 2.** Spearman rank correlation coefficient ($r_s$) and *p*-values for niche breadth versus individual prey species consumption for polar bears captured in western Hudson Bay in the fall, 2004-2014 separated based on age/sex group. * represents significant negative correlations.

| | Adult Male<br>n = 351 | | Solitary Female<br>n = 102 | | Female with Dependents<br>n = 182 | | Subadult Male<br>n = 72 | | Subadult Female<br>n = 90 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | $r_s$ | *p* | $r_s$ | *p* | $r_s$ | *p* | $r_s$ | *p* | $r_s$ | *p* |
| Bearded Seal | -0.08 | 0.096 | 0.46 | <0.001 | 0.33 | <0.001 | 0.34 | 0.003 | 0.33 | 0.001 |
| Harbour Seal | 0.29 | <0.001 | 0.21 | 0.034 | 0.31 | <0.001 | 0.19 | 0.100 | 0.27 | 0.010 |
| Ringed Seal* | -0.11 | 0.028 | -0.93 | <0.001 | -0.91 | <0.001 | -0.75 | <0.001 | -0.86 | <0.001 |
| Walrus* | -0.21 | <0.001 | -0.16 | 0.101 | -0.26 | <0.001 | -0.27 | 0.021 | -0.22 | 0.036 |
| Beluga | 0.35 | <0.001 | 0.36 | <0.001 | 0.37 | <0.001 | 0.48 | <0.001 | 0.30 | 0.003 |
| Harp Seal | 0.04 | 0.360 | 0.06 | 0.501 | 0.09 | 0.210 | 0.27 | 0.022 | 0.18 | 0.076 |

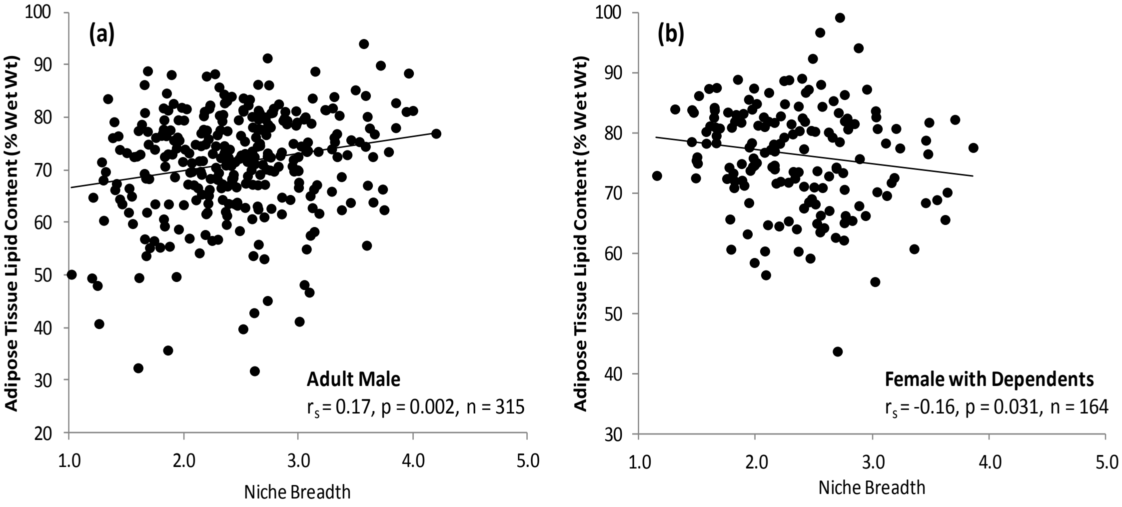

**Figure 5**. Relationship between adipose tissue lipid content (% wet weight) and niche breadth for (a) adult male polar bears and (b) females supporting dependent offspring captured in western Hudson Bay, fall 2004 - 2014

**Table 3.** Top regression models of relationship between adipose tissue lipid content and diet composition of bears captured in western Hudson Bay in the fall, 2004-2014. Model comparisons are based on Akaike's information criteria for small sample size ($AIC_c$) and selected based on $\Delta AIC_c$ (comparison against the full model with the lowest $AIC_c$, indicated below with * and $\Delta AIC_c$ = 0.00). k indicates number of parameters included in each respective model.

| Rank | Model | k | $AIC_c$ | $\Delta AIC_c$ | *P (model)* |
|---|---|---|---|---|---|
| *Adult Male (n = 315)* | | | | | |
| 1* | Bearded seal + Niche Breadth | 2 | 2342.63 | 0.00 | <0.001 |
| 2 | Bearded seal + Harbour seal + Niche Breadth | 3 | 2343.94 | 1.30 | <0.001 |
| *Solitary Adult Female (n = 85)* | | | | | |
| 1* | Niche Breadth | 1 | 578.37 | 0.00 | 0.10 |
| 2 | Bearded seal | 1 | 579.14 | 0.77 | 0.17 |
| 3 | Ringed seal | 1 | 579.78 | 0.81 | 0.17 |
| *Females with Dependents (n = 164)* | | | | | |
| 1* | Beluga whale + Niche Breadth | 2 | 1166.71 | 0.00 | 0.001 |
| 2 | Beluga whale + Ringed seal + Niche Breadth | 3 | 1167.82 | 1.10 | 0.001 |

## Supplementary Information

**Table S1.** Mean values of 38 extended dietary fatty acids used for FA signature comparisons and divided into major lipid classes (% mass of total FA ± SEM) from western Hudson Bay polar bear biopsy samples (collected in the fall, 2004 - 2014). **Bold** represents FA used in the QFASA model to estimate diet composition. Sample size of each group denoted by (n).

| **Fatty Acid** | **Adult Male** (n = 351) | | **Solitary Female** (n = 102) | | **Female with Dependents** (n = 182) | | **Subadult Male** (n = 72) | | **Subadult Female** (n = 90) | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Saturated Fat** | | | | | | | | | | |
| 14:0 | 3.51 | ± 0.03 | 3.53 | ± 0.03 | 3.46 | ± 0.03 | 3.79 | ± 0.07 | 3.65 | ±0.05 |
| 16:0 | 8.09 | ± 0.06 | 7.62 | ± 0.08 | 6.99 | ± 0.06 | 7.49 | ± 0.16 | 7.38 | ±0.09 |
| 17:0 | 0.23 | ± 0.00 | 0.19 | ± 0.00 | 0.18 | ± 0.00 | 0.20 | ± 0.01 | 0.17 | ±0.00 |
| **Monounsaturated Fat** | | | | | | | | | | |
| 16:1n-7 | 16.08 | ± 0.10 | 17.33 | ± 0.14 | 15.86 | ± 0.12 | 14.97 | ± 0.24 | 15.91 | ±0.17 |
| 18:1n-9 | 22.62 | ± 0.09 | 22.38 | ± 0.13 | 24.07 | ± 0.12 | 23.58 | ± 0.23 | 23.38 | ±0.15 |
| 18:1n-7 | 6.15 | ± 0.04 | 5.75 | ± 0.04 | 5.67 | ± 0.03 | 5.48 | ± 0.05 | 5.67 | ±0.04 |
| 20:1n-11 | 1.42 | ± 0.02 | 1.26 | ± 0.03 | 1.46 | ± 0.02 | 1.58 | ± 0.04 | 1.42 | ±0.03 |
| **20:1n-9** | 5.36 | ± 0.06 | 5.23 | ± 0.09 | 5.96 | ± 0.07 | 6.30 | ± 0.14 | 5.89 | ±0.11 |
| **20:1n-7** | 0.87 | ± 0.01 | 0.61 | ± 0.01 | 0.67 | ± 0.01 | 0.72 | ± 0.02 | 0.66 | ±0.01 |
| **22:1n-11** | 0.77 | ± 0.02 | 0.62 | ± 0.03 | 0.67 | ± 0.02 | 0.84 | ± 0.04 | 0.70 | ±0.02 |
| **22:1n-9** | 0.35 | ± 0.01 | 0.30 | ± 0.01 | 0.34 | ± 0.00 | 0.38 | ± 0.01 | 0.34 | ±0.01 |
| **22:1n-7** | 0.07 | ± 0.00 | 0.06 | ± 0.00 | 0.06 | ± 0.00 | 0.07 | ± 0.00 | 0.07 | ±0.00 |
| **Polyunsaturated Fat** | | | | | | | | | | |
| **16:2n-6** | 0.04 | ± 0.00 | 0.03 | ± 0.00 | 0.04 | ± 0.00 | 0.05 | ± 0.01 | 0.04 | ±0.00 |
| **16:2n-4** | 0.25 | ± 0.00 | 0.21 | ± 0.00 | 0.22 | ± 0.00 | 0.22 | ± 0.00 | 0.21 | ±0.01 |
| **16:3n-6** | 0.33 | ± 0.00 | 0.37 | ± 0.00 | 0.35 | ± 0.00 | 0.33 | ± 0.01 | 0.34 | ±0.00 |
| **16:3n-4** | 0.06 | ± 0.00 | 0.04 | ± 0.00 | 0.05 | ± 0.00 | 0.08 | ± 0.01 | 0.06 | ±0.01 |
| **16:4n-3** | 0.08 | ± 0.00 | 0.06 | ± 0.01 | 0.07 | ± 0.00 | 0.07 | ± 0.01 | 0.08 | ±0.01 |
| **16:4n-1** | 0.03 | ± 0.00 | 0.02 | ± 0.00 | 0.02 | ± 0.00 | 0.04 | ± 0.01 | 0.03 | ±0.00 |
| **18:2n-6** | 2.53 | ± 0.02 | 2.71 | ± 0.02 | 2.79 | ± 0.02 | 2.63 | ± 0.04 | 2.77 | ±0.03 |
| 18:2n-4 | 0.11 | ± 0.00 | 0.10 | ± 0.00 | 0.10 | ± 0.00 | 0.10 | ± 0.00 | 0.10 | ±0.00 |
| **18:3n-6** | 0.12 | ± 0.00 | 0.12 | ± 0.00 | 0.12 | ± 0.00 | 0.12 | ± 0.00 | 0.12 | ±0.00 |
| **18:3n-4** | 0.22 | ± 0.00 | 0.22 | ± 0.00 | 0.22 | ± 0.00 | 0.22 | ± 0.00 | 0.21 | ±0.00 |
| **18:3n-3** | 0.53 | ± 0.00 | 0.58 | ± 0.01 | 0.55 | ± 0.01 | 0.52 | ± 0.01 | 0.57 | ±0.01 |
| **18:3n-1** | 0.10 | ± 0.00 | 0.08 | ± 0.00 | 0.09 | ± 0.00 | 0.09 | ± 0.00 | 0.09 | ±0.00 |
| **18:4n-3** | 0.33 | ± 0.00 | 0.31 | ± 0.01 | 0.30 | ± 0.00 | 0.30 | ± 0.01 | 0.31 | ±0.01 |
| **18:4n-1** | 0.10 | ± 0.00 | 0.12 | ± 0.00 | 0.10 | ± 0.00 | 0.09 | ± 0.00 | 0.10 | ±0.00 |
| **20:2n-6** | 0.32 | ± 0.00 | 0.29 | ± 0.00 | 0.30 | ± 0.00 | 0.30 | ± 0.00 | 0.30 | ±0.00 |
| **20:3n-6** | 0.12 | ± 0.00 | 0.13 | ± 0.00 | 0.13 | ± 0.00 | 0.12 | ± 0.00 | 0.12 | ±0.00 |
| **20:4n-6** | 0.36 | ± 0.01 | 0.30 | ± 0.01 | 0.26 | ± 0.00 | 0.27 | ± 0.01 | 0.27 | ±0.01 |
| **20:3n-3** | 0.08 | ± 0.00 | 0.08 | ± 0.00 | 0.07 | ± 0.00 | 0.07 | ± 0.00 | 0.08 | ±0.00 |
| **20:4n-3** | 0.49 | ± 0.01 | 0.56 | ± 0.01 | 0.48 | ± 0.01 | 0.44 | ± 0.01 | 0.48 | ±0.01 |
| **20:5n-3** | 2.52 | ± 0.04 | 2.78 | ± 0.05 | 2.29 | ± 0.04 | 2.15 | ± 0.09 | 2.36 | ±0.06 |
| **21:5n-3** | 0.32 | ± 0.00 | 0.32 | ± 0.00 | 0.32 | ± 0.00 | 0.31 | ± 0.01 | 0.32 | ±0.00 |
| **22:4n-6** | 0.17 | ± 0.00 | 0.12 | ± 0.00 | 0.13 | ± 0.00 | 0.13 | ± 0.00 | 0.13 | ±0.00 |
| **22:5n-6** | 0.21 | ± 0.00 | 0.17 | ± 0.00 | 0.18 | ± 0.00 | 0.19 | ± 0.01 | 0.18 | ±0.00 |
| **22:4n-3** | 0.09 | ± 0.00 | 0.08 | ± 0.00 | 0.08 | ± 0.00 | 0.10 | ± 0.00 | 0.09 | ±0.00 |
| **22:5n-3** | 5.79 | ± 0.06 | 6.35 | ± 0.06 | 6.59 | ± 0.07 | 6.26 | ± 0.15 | 6.52 | ±0.09 |
| **22:6n-3** | 9.74 | ± 0.11 | 10.13 | ± 0.14 | 9.96 | ± 0.13 | 9.61 | ± 0.25 | 9.94 | ±0.16 |

**Table S2.** Model results using Akaike's Information Criterion ($AIC_c$) to predict adipose tissue lipid content based on proportional consumption of differing prey types and niche breadth in polar bears across age and reproductive status (adult male, solitary adult female, and females supporting dependents). Each model reports on number of parameters (*k*), Akaike's Information Criterion for small sample size ($AIC_c$), difference in *AIC* values ($\Delta AIC_c$), overall model *P* values (*P*), and Log Likelihood values (*LL*).

| Model Parameters | *k* | $AIC_c$ | $\Delta AIC_c$ | *P(model)* | *LL* |
|---|---|---|---|---|---|
| *Adult Male (n= 315)* | | | | | |
| Ringed seal | 1 | 2359.45 | 16.51 | 0.14 | -1176.68 |
| Bearded seal | 1 | 2349.59 | 6.96 | <0.01 | -1171.75 |
| Harbour seal | 1 | 2355.61 | 12.97 | 0.01 | -1174.76 |
| Harp seal | 1 | 2361.33 | 18.70 | 0.65 | -1177.63 |
| Beluga | 1 | 2359.62 | 16.99 | 0.16 | -1176.77 |
| Walrus | 1 | 2361.53 | 18.90 | 0.99 | -1177.73 |
| Niche Breadth | 1 | 2348.42 | 5.79 | <0.001 | -1171.17 |
| Bearded + Harbour + Niche Breadth | 3 | 2343.94 | 1.30 | <0.001 | -1166.87 |
| Bearded + Niche Breadth | 2 | 2342.63 | 0.00 | <0.001 | -1167.25 |
| *Solitary Adult Female (n = 85)* | | | | | |
| Ringed seal | 1 | 579.18 | 0.81 | 0.17 | -286.44 |
| Bearded seal | 1 | 579.14 | 0.77 | 0.17 | -286.42 |
| Harbour seal | 1 | 580.76 | 2.39 | 0.62 | -287.23 |
| Harp seal | 1 | 581.00 | 2.63 | 0.99 | -287.35 |
| Beluga whale | 1 | 580.56 | 2.19 | 0.50 | -287.13 |
| Walrus | 1 | 580.94 | 2.57 | 0.81 | -287.32 |
| Niche Breadth | 1 | 578.37 | 0.00 | 0.10 | -286.03 |
| *Females with Dependents (n = 164)* | | | | | |
| Ringed seal | 1 | 1175.62 | 8.91 | 0.05 | -584.73 |
| Bearded seal | 1 | 1170.31 | 3.59 | <0.01 | -582.08 |
| Harbour seal | 1 | 1178.96 | 12.24 | 0.61 | -586.40 |
| Harp seal | 1 | 1178.57 | 11.86 | 0.42 | -586.21 |
| Beluga whale | 1 | 1174.56 | 7.84 | 0.03 | -584.20 |
| Walrus | 1 | 1178.57 | 11.85 | 0.42 | -586.21 |
| Niche Breadth | 1 | 1175.45 | 8.73 | 0.05 | -584.65 |
| Bearded + Beluga + Ringed + Niche Breadth | 4 | 1169.89 | 3.18 | <0.01 | -578.68 |
| Beluga + Ringed + Niche Breadth | 3 | 1167.82 | 1.10 | <0.01 | -578.72 |
| Beluga + Niche Breadth | 2 | 1166.71 | 0.00 | <0.01 | -579.23 |

# CHAPTER V

# Conclusions & Future Research

## Body condition & environmental variability

Monitoring the body condition of mammals, particularly at-risk populations experiencing declines in abundance, is crucial for the early identification of potential factors that may be negatively affecting survival. Generally, body condition has been directly related to fitness, nutrition and overall health in an organism (Peig & Green, 2010). For many species, body condition can fluctuate in response to environmental heterogeneity (seasonally or inter-annually), energetic demands, and life history (Clutton-Brock *et al.*, 1987; Gittleman & Thompson, 1988; Molnár *et al.*, 2009).

One particular limitation that exists across a multitude of studies is selecting the most appropriate and effective metric of body condition. One important finding of this dissertation was that body condition indices used on free-ranging polar bears quantified energy stores differently when measured across the same individual. In Chapter 2, I found that morphometric based measures, including zygomatic skull width and storage energy, are unable to accurately quantify internal fat stores as they are likely biased by skeletal structure and morphology. In contrast, adipose tissue lipid content, bioelectrical impedance analysis and energy density followed similar patterns in body condition across age, sex and reproductive groups. Furthermore, selection of the most ideal body condition metric should be based on efficiency in the field (in response to environmental conditions) as well as specific research goals. For example, species that undergo a seasonal fasting period must utilize stored fat as energy to survive, therefore metrics that quantify energy mobilized during fasting periods (i.e., energy density) are likely to be the most informative measure of body condition in fasting mammals. Furthermore, monitoring declines in energy density over broad temporal scales can infer the likelihood of survival during environmental fluctuations. In Chapter 2, I also provided evidence that females supporting multiple dependent offspring have a lower body condition (less stored energy) compared to solitary females, and thus environmental variability may be more likely to negatively affect survival in family groups.

The Hudson Bay region has experienced considerable environmental change since the early 1990s, including increased surface air temperatures, lengthening of the open water season, reduced sea ice extent, greater sea ice fragmentation and poorer habitat quality (Sahanatien & Derocher, 2012; Hochheim & Barber, 2014). Past research has predicted that such changes could negatively influence polar bear body condition (Stirling *et al.*, 1999), however this was not previously quantified. This dissertation provided novel information identifying the decline in polar bear body condition in western Hudson Bay (WH) during the past decade. The findings of this study indicated that the timing of sea ice breakup and freeze-up influenced body condition across age and sex class. However, it is also likely that additional factors such as sea ice extent, thickness, and changes to consolidated ice or pack ice are also influencing polar bear body condition. Furthermore, successive seasonal declines in sea ice will not only reduce feeding time, but also exert stress on individuals, contributing to a reduced body condition that is likely to be intensified in senescent bears as well as females supporting offspring (Derocher *et al.*, 2004).

## Foraging behaviour & polar bear life history

Intraspecific variation in foraging behaviour may occur among individuals based on differences in life history, sex and energetic state. Although polar bear diet has been investigated in past studies, little was known regarding variation in diet composition among females and how energetic demands as well as intraspecific competition may function to structure foraging behaviour. One of the primary findings of this dissertation was that diet composition, and therefore foraging patterns, differ among females as a function of body size (i.e., differences in proportional consumption of large bodied prey types among adult and subadult females), as well as across reproductive state. In Chapter 3, I demonstrated that diet composition differs among solitary females and females supporting dependents, likely due to avoidance behaviour exhibited by family groups to reduce the probability of aggressive interactions by adult males. In this sense, females in family groups typically avoid areas of high productivity along open leads, as these regions are often monopolized by adult male bears (Stirling *et al.*, 1993). This was the first study to produce quantitative support that suggests solitary females forage in areas along the floe edge alongside adult males (Stirling *et al.*, 1993). I further provided such evidence in Chapter 4, in which diet composition of adult males is more similar to solitary females than females of other age or reproductive classes.

Differences in foraging behaviour and dietary niche breadth between sexes has been documented in other species as a function of sexual size dimorphism (Erlinge, 1979; Litvaitis *et al.*, 1986; Beck *et al.*, 2007; Weise *et al.*, 2010). In Chapter 4, I provided evidence that sexual size dimorphism plays a significant role in structuring diet and niche breadth in polar bears. A broad dietary niche in adult males positively influenced body condition as inferred from greater adipose tissue lipid content. In females supporting dependent offspring, however, consumption of a broader range of prey types was associated with reduced adipose tissue lipid content. The findings in Chapter 4 provided novel insight that suggest females supporting offspring and likely in an energy deficit state, may scavenge on multiple prey types that provides temporary sustenance but does not translate into greater energy stores in the long term.

Intrinsic factors as suggested above structure foraging behaviour, however, extrinsic factors such as availability of prey can also influence diet and behaviour. In this dissertation, I presented long term temporal trends in individual prey consumption across age and sex class. Specifically, my research was the first to show inverse-trends in consumption of ringed seal and harbour seal. Since both prey types are found in Hudson Bay, I suggest that temporary and sporadic periods of increased harbour seal consumption was likely due to local availability as a result of sea ice conditions that isolate harbour seal along the coast and therefore make them more accessible to polar bears. Furthermore, the inter-annual fluctuations in prey consumption I presented in both Chapter 3 and Chapter 4 provide additional evidence of scavenging behaviour on large bodied and less accessible prey types. A rapid and sporadic influx in beluga whale or walrus consumption in specific years imply the possibility of random events that result in a concentrated food source of either entrapment of individuals or carcasses. These results provide quantitative evidence to support the historical observations of polar bears in the High Arctic scavenging on large bodied prey types (Freeman, 1973; Heyland & Hay, 1976; Rugh & Shelden, 1993).

## Future Directions

My dissertation provided insights into the current shifts that are occurring in both polar bear body condition and diet composition as influenced by ongoing changes to the Arctic environment. Since this research spans a period of ten years, it provides great insight into the foraging behaviour of polar bears in one of the southernmost subpopulations. However, prey selection is often structured by habitat conditions and foraging location (Weimerskirch, 1998; Kie & Bowyer, 1999; Juarez & Marinho-Filho, 2002; Hierlihy *et al.*, 2013), therefore future research is needed in the form of telemetry studies that can identify migration patterns and foraging grounds of both male and female bears while on the sea ice. Combining quantitative diet data with location information will provide insight into optimal foraging habitat and evidence of resource and habitat partitioning among age and sex groups.

In addition to combining diet and location data for a broad scale analysis of population level foraging, it would also be interesting to investigate individual-level dietary shifts that may exist as polar bears develop from dependent offspring to subadult and into adulthood. In this sense, the high probability of recapture of polar bears in WH allows for a fine-scale investigation of phenotypic dietary plasticity that may exist in polar bears as they grow in age and body size. This can provide additional evidence of dietary shifts that develop as a function of both age (experience) and body size.

The results of this dissertation showed inter-annual fluctuations in prey consumption, and a particularly unique finding was the inverse trend in harbour seal and ringed seal consumption that followed similar patterns in abundance estimates obtained via aerial surveys. Although the trends in prey consumption I presented were similar to those based on survey data of ringed, bearded and harbour seal over a short time scale (Chambellant *et al.*, 2012a; Young *et al.*, 2015; Ferguson *et al.*, 2016) much of our knowledge regarding current seal distribution and abundance estimates remains limited. In order to better understand the possible influence of declining sea ice habitat on prey species in Hudson Bay, additional count data on prey are needed. This information could test the hypothesis that localized increases in prey availability in specific years directly results in the simultaneous temporary influx in consumption of particular prey types as observed through diet estimates.

## Conservation Implications

Current monitoring and research programs are underway for many of the 19 subpopulations of polar bears that exist throughout the circumpolar Arctic. Much of the High Arctic subpopulations, however, due to extreme environmental conditions, remain relatively unknown in terms of foraging behaviour and body condition. My research provides evidence that long term environmental changes occurring in Hudson Bay are influencing prey selection, length of foraging and fasting time, and consequently reducing overall fatness in bears. This is predicted to also occur in High Arctic subpopulations, thus this line of research provides an early warning indicator for impending changes that may occur across the entire Arctic. This research can assist in future improvements on management strategies and conservation efforts not only for WH, but for neighbouring subpopulations as well, since polar bears can span broad geographic distances while on the sea ice and share both similar habitat and food resources. The extent to which polar bears can exhibit phenotypic plasticity in their foraging behaviour and adapt to reduced sea ice in a shortened period of time remains largely unknown, however my research of WH polar bears provides an ideal opportunity to investigate the species response and possible behavioural adaptations to environmental change.

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Sciullo, L., Thiemann, G.W., Lunn, N.J. (2016). Comparative assessment of metrics for monitoring the body condition of polar bears in western Hudson Bay. *Journal of Zoology*. **300**: 45-58.

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