DIET CHARACTERIZATION OF HUDSON BAY RINGED SEALS IN A CHANGING SUB-ARCTIC MARINE ENVIRONMENT

By

Cassandra Daye Debets

A Thesis submitted to the Faculty of Graduate Studies of

The University of Manitoba

in partial fulfilment of the requirements of the degree of

DOCTOR OF PHILOSOPHY

Department of Biological Sciences

University of Manitoba

Winnipeg

Thesis Abstract

Rapid environmental change in the Arctic can influence food web structure and dynamics. Ice-obligate species, such as ringed seals (*Pusa hispida*), are particularly vulnerable to decreased sea ice extent. In this thesis, I examined the patterns and foraging plasticity of ringed seals in Hudson Bay, an ecosystem undergoing rapid ecological change, to make inferences on possible changes to the Arctic marine food web dynamics. To examine ringed seal diet, I used muscle and liver tissues from subsistence harvested seals, and vibrissae segments from live captured ringed seals. Specifically, I investigated spatial, temporal, and within-individual variation in the diet of ringed seal populations. I used long-term datasets from two Nunavut communities over the years of 2003 – 2017 to quantify the general increase in isotopic niche breadth for seals in western Hudson Bay and a decrease in eastern Hudson Bay, despite having similar diet proportions. Using chronological tissue sampling, I then revealed high variation among individuals rather than within individuals of seals in the same age and sex class, indicating that these generalist feeders are foraging with individualized strategies. Lastly, I compared ringed seal diet signatures with two other Hudson Bay phocid species and indicated that ringed seal diets do not generally overlap with harbour seals (*Phoca vitulina*). I then determined reliable estimates of sympagic and pelagic algal carbon sources to the diets of the three seal species and found that ringed seals have more pelagic algal content and less sympagic algal carbon in their diet compared to harbour seals and bearded seals (*Erignathus barbatus*). Overall, this thesis highlights the limits to foraging plasticity and spatio-temporal feeding patterns of ringed seals in a changing environment.

Acknowledgements

I gratefully acknowledge the learning opportunities I have been afforded while studying at the University of Manitoba located on original lands of Anishinaabeg, Cree, Oji-Cree, Dakota, and Dene peoples, and on the homeland of the Métis Nation. Additionally, I was afforded opportunities to learn on Treaty 5 territory, the territory of Nunavut, and Northwest Territories throughout my program, and will forever be grateful to the connections with the land and people I met.

I am especially grateful to the Inuit communities of Arviat and Sanikiluaq, Nunavut for their contributions to long-term monitoring projects. My deepest thanks to the hunters and trappers associations of these communities for coordination efforts. Thank you to all the community members, particularly, the late Frank Nutarasugnik (Arviat) who has provided samples during the subsistence hunts and have made research projects, like this, possible. I will always remember my Inuktitut lessons out on the land waiting to harvest seals with Frank and other community members. Thank you for the warm welcome and sharing your knowledge and your land with me.

Thank you, Dr. Steve Ferguson, for providing the opportunity to be involved in your research program and be part of the DFO scientific community. Thank you for your advice, inspiration for project ideas and especially for the many opportunities to visit northern communities. These visits deepened my understanding of the Arctic and are experiences I will always remember fondly. To my committee members, Dr. Gail Davoren, Dr. Stephen Petersen and Dr. Rick Baydack, thank you for being on this journey of discovery with me. The advice, support, and encouragement you provided never went unnoticed and I thank you my entire committee for shaping me into the biologist that I am. I also thank Dr. Ken Jeffries for being involved in my candidacy examination and reminding me that physiology is just as important as ecology, and also serving as chair of my defence. Thank you to my external reviewer, Dr. Ryan Norris for his thoughtful comments and discussion on dietary plasticity and hypothesis formation.

The success of this project would not have been possible without the logistical support of many people at the freshwater institute. Thank you to Blair Dunn and David Boguski for their support in these marine mammal research projects. Thank you to Brent Young, who was always so knowledgeable and welcoming when I would come seeking advice. To Tera Edkins, thank you for all your work in the stable isotope lab and for the days we spent in the freezers trying to locate the specific samples among the hundreds of sample boxes. Thank you to Bruno Rosenberg for running stable isotope samples. Thank you to Drs. Marianne Marcoux and Cortney Watt-Wheeler for opportunities to participate in field work and be part of the DFO community, and to Claire Hornby for the laughs and hugs in the field! I also thank Drs. Dominique Henri, Jenn Provencher and Magali Houde for inviting me to be part of the ringed seal educational workshops and letting me see how science extends beyond the walls of laboratory or field site. Thank you to Dr. David Yurkowski for the many stimulating conversations that got me thinking about next steps in my project. I thank Dr. Cory Matthews for his support and advice on stable isotope ecology and R coding. A special thank you to Dr. Gregory Thiemann, my master's supervisor, for his guidance and advice on Arctic science and my current doctoral thesis project.

Navigating graduate school can be daunting but is enjoyable with outstanding peers by your side. Thank you to all my fellow lab mates at FWI for helping me stay the course. I am especially grateful to Wesley Ogloff and Cody Carlyle, who both helped me troubleshoot seal problems and helped me better understand our study species. I am also particularly appreciative of Kasey Ryan and Kyle Lefort who have always been there for the ups and downs, your support and frienship has meant a lot to me. Thank you, Dr. Melissa Galicia, for your continued friendship since our student days in Greg's lab, I am grateful for all your support scientifically and personally. Thank you, Magnus Andreasen, for the many conversations in Svalbard about the Arctic, and reminding me to keep living life to the fullest. I am glad to have a lifelong friend from our short time coring sea ice under the midnight sun. To all the graduate students in the department and the BSGSA, thank you for making me laugh by sharing the triumphs of graduate school, and being there during our low days particularly during the once in a lifetime global pandemic.

I thank the incredible department of Biological Sciences. At some point or another along my way I have had conversations with just about all faculty members about science and in some cases, specifically my project. The support I have received from all members of this department has guided me through this process and the extra challenges our world faced. I particularly thank Drs. Jim Roth, Jillian Detwiller, Jay Treberg and Gail Davoren for the stimulating conversations in the stable isotope working group. I thank Dr. Jake Stout for his guidance in my critical thinking, writing, and sharing an overall excitement about cool science. I also thank Dr. Jane Waterman for her guidance of the program's milestone and for her advice in navigating a PhD and career. I would also like to thank Jane for all her encouragement in the completion of both my graduate programs. I also had tremendous support and probes from Dr. Gary Anderson to ensure that I would complete this PhD while also navigating the beginning of my academic teaching career. Thank you to Dr. Olwyn Friesen for your friendship and the many pep talks, I am glad to have such a strong female mentor. I also would like to thank Dr. Alex Quijida-Rodriguez for his encouragement and friendship that I know will extend well into our careers, there is no one else I would rather troubleshoot academia with. To the amazing office support staff for making sure paperwork, travel grants, stipends were all in order, so that grad school could be a little bit easier to manage, thank you! I am especially grateful to Dr. Kevin Scott for his unwavering encouragement and support, reminders of the bigger picture of science, and for being part of my PhD journey. Thank you, Kevin, for your mentorship, it allowed me to find my passion for teaching and scientific communication, and will be invaluable well into my academic teaching career in Biology.

I thank all my friends for their encouragement and support while I have been a 'forever student'. I thank my family, especially my parents Denise (Doyle) and Bob (Dale) for their love and kindness. I sincerely thank my dad for sharing his passion for polar bears and the Arctic with me Your encouragement for me to explore the north, it has been the most rewarding adventure.

Most importantly, my deepest and sincere thanks to my husband, Garrett. I could not have done this without your patience, constant support and belief that I could do it. At my lowest points, you were always reminding me of why I could do this, and what I hoped to accomplish. I appreciated all the bowls of grapes by the computer so I would eat! I will forever be grateful to have you by my side, thank you for encouraging me to do all that I have done, and will do in the future.

Table of Contents

List of Tables

List of Figures

Contribution of Authors

This thesis is organized as a "sandwich" or grouped-manuscript thesis with chapters 2, 3 and 4, in prepareation for published journal articles, all three chapters are awaiting publication and not yet published. Following are the titles of the prepared research articles, the manuscript review status at the time of submission of this thesis, the authors' contributions, and relevant chapters of the thesis:

1. Chapter 2 has content that is in preparation for a journal publication titled “Temporal and spatial stable isotope patterns in ringed seal (*Pusa hispida*) diet composition”
   Author contrubutions:
   Cassandra Debets (*Thesis author*): Conceptualization and project design, data collection and analysis, writing the original draft.
   Brent Young: Data Collection, sample preparation, project design
   Steve Fergusion: Conceptulization, funding accquirement, review and editing

2. Chapter 3 has content that is in preparation for a journal publication titled “High inter-individual diet variation in ringed seals (*Pusa hispida*) revealed using stable isotope ratios from chronological sections of vibrissae”
   Author contrubutions:
   Cassandra Debets (*Thesis author*): Conceptualization and project design, data collection and analysis, writing the original draft.
   Cory Matthews: Project design, revising and editing
   David Yurkowski: Project design
   Seth Newsome: Project design, sample analysis
   Gregory Thiemann: Project design, sample analysis
   Brent Young: Data Collection, sample preparation, project design
   Steve Fergusion: Conceptulization, funding accquirement, review and editing

3. Chapter 4 has content that is in preparation for a journal publication titled “Estimating dietary overlap between three phocid species using stable isotopes and sea ice carbon biomarkers”
   Author contrubutions:
   Cassandra Debets (*Thesis author*): Conceptualization and project design, data collection and analysis, writing the original draft.
   David Yurkowski: Project design
   Tom Brown: Project design, sample analysis
   Brent Young: Data Collection, sample preparation, project design
   Steve Fergusion: Conceptulization, funding accquirement, review and editing

Chapter 1: General Introduction

Food webs describe the ecological interactions within an ecosystem, which involve multiple trophic levels and relationships among species (Paine 1980). Energy is transferred from primary producers to consumers which are categorized into relatively discrete trophic levels. (Elton 1927; Lindeman 1942). The structure of the ecosystem comes from each individual species' niche that allows a particular species to survive in the ecosystem (Hutchison 1957). Moreover, ecosystem functioning stems from the individual species interactions within the foodweb, encompassing both abiotic and biotic components of the environment (Odum and Barrett 1971). Thus, a single species' foraging ecology can provide insights into the overall structure and functioning of the food web.

Investigating foraging ecology can involve estimation of diet composition and identifying animal movement patterns, both of which are crucial in understanding the costs and benefits of associated foraging decisions made by individuals (Bestley et al. 2015). Foraging behaviour can provide important insights into predator-prey interactions, diet, and habitat use influencing the structure and function of a community (Baum and Worm 2009). Furthermore, an organism's diet can reveal much about their biology including their energy requirements, habitat use, trophic level within the ecosystem and their impacts on community assemblages (Hairston et al. 1960; Vander Zanden and Rasmussen 1996). Higher trophic level consumers tend to be more mobile and need to acquire energy from multiple resources from spatially separated habitats (e.g. benthic vs. pelagic food chains) (Vander Zanden and Vadeboncoeur 2002; Gellner and McCann 2012).

Optimal foraging theory suggests that individuals will use strategies to maximize the net energy intake; however, this will vary based on age, sex, and body size (Sih and Christensen 2001).

Within age classes dietary specialization of conspecifics has been observed across multiple taxa (Woo et al. 2008; Thiemann et al. 2011; Matich and Heithaus 2015; Yurkowski et al. 2016). Diet specialization is defined by an individual having a narrower niche breath compared to the population's niche (Sih and Christensen 2001; Newsome et al. 2015). Top predators are found at the highest trophic level of a food chain; their preference in prey species can thus influence population abundance and exert strong top-down effects. A better understanding of the foraging behaviour of predators and their diet specialization, in combination with prey distribution and environmental drivers, can ultimately aid in assessing population dynamics to improve conservation and management strategies (Baum and Worm 2009; Thiemann et al. 2011).

Anthropogenic climate change is a prominent issue affecting global biodiversity, leading to dire predictions for species persistence and biodiversity. Understanding how species respond to both climate change and habitat loss is crucial for biological conservation. Species inhabiting the Arctic are of large concern as they face significant climate change-induced habitat modifications (Burek et al. 2008; Laidre et al. 2008; 2015; Moore and Huntington 2008). The Arctic is warming faster than any other ecosystem on the planet (IPCC, 2021; Rantanen et al. 2022). Increases in atmospheric temperatures have led to increased temperatures in the Arctic Ocean and consequently decreased sea ice extent and thickness (Comiso 2003; Gagnon and Gough 2005). Sea ice as measured by summer minimum has been observed to be decreasing at a rate of between 9.4 – 13.6% per decade since 1979 when monitoring of sea ice via Satellites began (IPCC, 2014). Hudson Bay, the southern extent of the Arctic, has experience a loss of 1.5% sea ice habitat per year over the past three decades (Sahanatien and Derocher 2012). Sea ice models indicate a continued disappearance of winter sea ice cover in the coming decades (Stroeve et al. 2007; Castro

de la Guardia et al. 2013; Overland and Wang 2013). The loss of sea ice has the potential to have large impact global climate. The changes in sea ice phenology can be a direct abiotic stress to organisms that depend on the sea ice at any life stage for foraging, reproducing and habitat (Post et al. 2013; Ogloff et al. 2022). Decrease in sea ice extent can also be attributed to changing food-web dynamics and interspecies interactions (Bartley et al. 2019; Yurkowski et al. 2020). Indeed, seabird diets have switched from being dominated by Arctic cod (*Boreogadus saida*) to a more temperate species, capelin (*Mallotus villosus*; Provencher et al. 2012).

The Arctic is unlike other biomes in that it is a region of seasonal extremes (sea ice extent, day length, resource abundance, and prey availability) (Arrigo 2014; Leu et al. 2015). Therefore, Arctic fauna must be well adapted to these extremes (Falk-Petersen et al. 2000; Laidre et al. 2008; 2015). In addition, the timing and composition of sea ice algae and phytoplankton primary production has changed in various parts of the Arctic (Ji et al. 2013; Lewis et al. 2020). Ongoing changes in sea ice phenology are affecting life history traits and behavioural ecology of many marine mammal species. The survival of Arctic marine mammals is contingent on the sea ice and they are sensitive to any alterations to their habitat caused by climate change (Laidre et al. 2008). The reduction in sea ice has been empirically linked to polar bear (*Ursus maritimus*) body condition, recruitment and survival in several areas of the Arctic (Regher et al. 2007; Rode et al. 2014). In Hudson Bay, polar bear body condition has declined over a 30-year period (Scuillo et al. 2016) and with an increasing on-shore period could mean up to 48% of adult polar bears not having the energy budget to survive a fasting period of 180 days (Molnar et al. 2010; 2014). The sea ice is an integral component to Arctic marine food webs. Changes in the Arctic marine food web has

been intrinsically linked to the reduction of sea ice extent through climate change (Smetacek and Nicol 2005; Blumn and Gardinger 2008).

Ringed seals (*Pusa hispida*) are a small pinniped species with a circumpolar distribution inhabiting the Arctic and sub-Arctic similar to other pinnipeds, such as bearded seals (*Erignathus barbatus*) (Smith and Hammill 1981; Laidre et al. 2008). Ringed seals are an ice-associated species and are sensitive to climate change and increased variability in sea ice habitat largely because their life history has been shaped by sea ice dynamics (McLaren 1958; Laidre et al. 2008). Their primary habitat is sea ice which they can inhabit year-round due to their ability to create and maintain breathing holes in the thick land-fast ice with anterior flipper claws (McLaren 1958). This preference for land-fast and snow-covered ice is largely for their subnivean birthing lairs to wean pups (Smith and Stirling 1975; Smith and Hammill 1981), although the presence of birth lairs on drifting pack ice has been observed (Finley et al. 1983). These birth lairs are extremely important for the species, as they provide protection for young naïve pups to possible polar bear predation and shelter from the elements (Ferguson et al. 2005; Iacozza and Ferguson 2014). Females will give birth to a single pup in the late spring inside the birth lairs where the pups will remain until weaned (McLaren 1958; Lydersen and Smith 1989). With their presence in a variety of Arctic and sub-Arctic habitats, ringed seals make an excellent model species to study temporal trophic relationships. Thus, understanding ringed seal foraging ecology in Hudson Bay and the possible responses to changing sea ice regimes may provide a better understanding of how this sub-Arctic marine food web is being affected by global climate change.

Hudson Bay is a shallow (mean depth 150 m) inland sea connected to the Arctic Ocean through Foxe Basin and the Atlantic ocean through the Hudson Straight (Prinsenberg 1986).

There is seasonal sea-ice coverage, with ice typically forming along the northwestern coast in early November (Jones and Anderson 1994; Hochheim and Barber 2010). The eastern region of Hudson Bay, including James bay are the last to freeze up and will be the first areas to undergo the spring melt in late May (Hochheim et al. 2011). Hudson Bay receives a high volume of riverine input from western and northeastern Canada, representing 20% of total runoff to the Arctic Ocean, annually (Déry and Wood 2004). There are many dynamic forces including wind, cyclconic currents and input from river systems that creates differences in sea ice formation and thickness within Hudson Bay (Saucier et al., 2004; Hochheim and Barber 2014). For instance, there is a large persistent Polynya in northwestern Hudson Bay, and thicker ice in eastern Hudson Bay with ridges (Saucier et al. 2004; Kirillov et al. 2020). Significant negative sea ice concentration trends have been documented in Hudson Bay where breakup was occurring 0.3-1.25 days/year earlier from 1971 – 2003 (Gough et al. 2004; Gagnon and Gough 2005; Stroeve et al. 2024). Moreover, the trends of sea ice decline between the western and eastern portions of Hudson Bay are asymmetrical, with the eastern region not significantly impacted by warming temperatures (Gagnon and Gough 2005); However, further spatial data and sea ice models continue to show spatial differences in sea ice decline but also negative trends, of up to 30 days for both areas of Hudson Bay (Hochheim et al. 2011; Kirillov et al. 2020).

Many ringed seal diet studies across the Arctic and focused in Hudson Bay have relied on stomach content analyses (Dehn et al. 2007; Chambellant et al. 2013). Using stomach contents is limited to a narrow temporal scale of what the individual had recently ingested. It can provide evidence for prey types that are commonly ingested and overlook rarer prey types that may contribute to the diet (Hyslop 1980). Thus, stomach content analysis does not provide insights into

long term diet trends, however, stomach contents have been useful in describing which prey types should be considered and included in dietary modelling. As a result of the limitations of stomach content, more recent investigations of diet have relied on chemical signatures, such as those using stable isotopes to determine patterns of prey intake (Young and Ferguson 2013). Both Carbon and Nitrogen stable isotope biomarkers can be used to reconstruct the diets of individuals, populations and be used to assess spatial-temporal differences in diet (Young and Ferguson 2013; Yurkowski et al. 2016).

Stable isotopes can be used to infer trophic position (Nitrogen; Zhao et al. 2004) and foraging location (e.g. benthic, pelagic, off-shore; Petersen and Fry 1987; Das et al. 2004). Stable isotope analysis can be useful to determine foraging of different individuals, groups, and overall variable temporal scales. Stable isotopes are more useful than stomach content analyses because all prey consumed within a few months' time are incorporated into the tissues, rather than only the most recent prey consumed in stomach content analyses (Hyslop 1980). Conversely, stomach content analysis does allow for detetction of rare prey types, and does allow for biomass and frequency of occurrence to be calculated (Hyslop 1980; Polito et al. 2011). In addition to stable isotope ratios, highly branched isoprenoids (HBIs) are lipids synthesized by sympagic, the sea ice habitat, diatoms that are incorporated predictability into predators diet (Belt et al. 2012; Brown et al. 2014). This biomarker in combination with stable isotopes can provide insights into where a predator foraged (Brown et al. 2014; 2018).

Ringed seals at the southern limits of their range, have been documented to have increased cortisol, decreased body condition (Ferguson et al. 2017; Ferguson et al. 2020; Reimer et al. 2019; Ogloff et al. 2022) and changes in their foraging behaviour (Hamilton et al. 2015). However, the

diet composition inferred from patterns of stable isotope ecology of ringed seals in Hudson Bay has not been thoroughly investigated. The overall objective of this thesis is to investigate the temporal and spatial trends of the ringed seal's isotopic and dietary niche to gain a better understanding into ringed seal ecology and their role in the Arctic marine food web. Specifically, in Chapter 2, I investigate the foraging patterns of ringed seal populations in Hudson Bay from 2003 – 2017. With an overall focus of understanding temporal and spatial variation in isotopic and dietary markers in ringed seals in Hudson Bay, the first experimental chapter focuses on patterns of dietary niche breath and specifically investigates ringed seal stable isotope signatures to measure changes in isotopic breadth from 2003 – 2017 from two communities (Arviat and Sanikiluaq). Using stable isotope ratios of two tissues (muscle and liver) allows for the investigation of possible isotopic and dietary shifts among ringed seal age classes.

In Chapter 3, I assess intra-individual foraging consistency and variation of individuals within a population using chronological diet estimation from vibrissae segments of live captured ringed seals from Sanikiluaq, Nunavut. In Chapter 4, I quantify the dietary niche breadth and overlap of ringed seals with bearded and harbour seals in Hudson Bay using stable isotope and highly branched isoprenoids. Finally, in Chapter 5, I discuss the significance of the findings for ringed seal ecology and our understanding of the Hudson Bay marine ecosystem. This thesis will help to identify ringed seal dietary shifts in the southern extent of their range during a period of rapid environment change.

Literature Cited

Arrigo, K. R. (2014). Sea ice ecosystems. *Annual review of marine science*, *6*, 439-467.

Bartley, T. J., McCann, K. S., Bieg, C., Cazelles, K., Granados, M., Guzzo, M. M., ... & McMeans, B. C. (2019). Food web rewiring in a changing world. *Nature Ecology & Evolution*, *3*(3), 345-354.

Baum, J. K., & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology*, *78*(4), 699-714.

Belt, S. T., Brown, T. A., Rodriguez, A. N., Sanz, P. C., Tonkin, A., & Ingle, R. (2012). A reproducible method for the extraction, identification and quantification of the Arctic Sea ice proxy IP 25 from marine sediments. *Analytical methods*, *4*(3), 705-713.

Brown, T. A., Belt, S. T., Tatarek, A., & Mundy, C. J. (2014). Source identification of the Arctic sea ice proxy IP25*, Nature Communications*, 5, 4197.

Brown, T. A., Galicia, M. P., Thiemann, G. W., Belt, S. T., Yurkowski, D. J., & Dyck, M. G. (2018). High contributions of sea ice derived carbon in polar bear (*Ursus maritimus*) tissue. *PloS one*, *13*(1), e0191631.

Bestley, S., Jonsen, I. D., Hindell, M. A., Harcourt, R. G., & Gales, N. J. (2015). Taking animal tracking to new depths: synthesizing horizontal–vertical movement relationships for four marine predators. *Ecology*, *96*(2), 417-427.

Burek, K. A., Gulland, F. M., & O'Hara, T. M. (2008). Effects of climate change on Arctic marine mammal health. *Ecological Applications*, *18*(sp2), S126-S134.

Castro de la Guardia, L., Derocher, A. E., Myers, P. G., Terwisscha van Scheltinga, A. D., & Lunn, N. J. (2013). Future sea ice conditions in Western Hudson Bay and consequences for polar bears in the 21st century. *Global Change Biology*, *19*(9), 2675-2687.

Chambellant, M., Stirling, I., & Ferguson, S. H. (2013). Temporal variation in western Hudson Bay ringed seal *Phoca hispida* diet in relation to environment. *Marine Ecology Progress Series*, *481*, 269-287.

Comiso, J. C. (2003). Warming trends in the Arctic from clear sky satellite observations. *Journal of Climate*, *16*(21), 3498-3510.

Das, K., Holsbeek, L., Browning, J., Siebert, U., Birkun Jr, A., & Bouquegneau, J. M. (2004). Trace metal and stable isotope measurements (δ13C and δ15N) in the harbour porpoise *Phocoena phocoena relicta* from the Black Sea. *Environmental Pollution*, *131*(2), 197-204.

Dehn, L. A., Sheffield, G. G., Follmann, E. H., Duffy, L. K., Thomas, D. L., & O'Hara, T. M. (2007). Feeding ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as determined by stomach contents and stable isotope analysis. *Polar Biology*, *30*, 167-181.

Elton, C. S. (1927). The nature and origin of soil-polygons in Spitsbergen. *Quarterly Journal of the Geological Society*, *83*(1-5), 163-NP.

Ferguson, S. H., Stirling, I., & McLoughlin, P. (2005). Climate change and ringed seal (*Phoca hispida*) recruitment in western Hudson Bay. *Marine Mammal Science*, *21*(1), 121-135.

Ferguson, S. H., Young, B. G., Yurkowski, D. J., Anderson, R., Willing, C., & Nielsen, O. (2017). Demographic, ecological, and physiological responses of ringed seals to an abrupt decline in sea ice availability. *PeerJ*, *5*, e2957.

Ferguson, S. H., Yurkowski, D. J., Young, B. G., Fisk, A. T., Muir, D. C., Zhu, X., & Thiemann, G. W. (2020). Comparing temporal patterns in body condition of ringed seals living within their core geographic range with those living at the edge. *Ecography*, *43*(10), 1521-1535.

Finley, K. J., Miller, G. W., Davi, R. A., & Koski, W. R. (1983). A distinctive large breeding population of ringed seals (*Phoca hispida*) inhabiting the Baffin Bay pack ice. *Arctic*, 162-173.

Gagnon, A. S., & Gough, W. A. (2005). Trends in the dates of ice freeze-up and breakup over Hudson Bay, Canada. *Arctic*, 370-382.

Gough, W. A., Cornwell, A. R., & Tsuji, L. J. (2004). Trends in seasonal sea ice duration in southwestern Hudson Bay. *Arctic*, 299-305.

Gellner, G., & McCann, K. (2012). Reconciling the omnivory-stability debate. *The American Naturalist*, *179*(1), 22-37.

Hairston, N. G., Smith, F. E., & Slobodkin, L. B. (1960). Community structure, population control, and competition. *The American Naturalist*, *94*(879), 421-425.

Hamilton, C. D., Lydersen, C., Ims, R. A., & Kovacs, K. M. (2015). Predictions replaced by facts: a keystone species' behavioural responses to declining Arctic sea-ice. *Biology Letters*, 11(11), 20150803.

Hochheim, K. P., & Barber, D. G. (2010). Atmospheric forcing of sea ice in Hudson Bay during the fall period, 1980–2005. Journal of Geophysical Research: Oceans, 115(C5).

Hochheim, K. P., & Barber, D. G. (2014). An update on the ice climatology of the Hudson Bay system. Arctic, antarctic, and alpine research, 46(1), 66-83.

Hochheim, K. P., Lukovich, J. V., & Barber, D. G. (2011). Atmospheric forcing of sea ice in Hudson Bay during the spring period, 1980–2005. Journal of Marine Systems, 88(3), 476-487.

Hutchinson, G. E. (1957). Concluding remarks: Cold Spring Harbor symposium. *Quantitative Biology*, *22*, 415-427.

Hyslop, E. J. (1980). Stomach contents analysis—a review of methods and their application. *Journal of Fish Biology*, *17*(4), 411-429.

Iacozza, J., & Ferguson, S. H. (2014). Spatio-temporal variability of snow over sea ice in western Hudson Bay, with reference to ringed seal pups survival. *Polar biology*, *37*, 817-832.

IPCC, 2021: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA,

Ji, R., Jin, M., & Varpe, Ø. (2013). Sea ice phenology and timing of primary production pulses in the Arctic Ocean. *Global Change Biology*, *19*(3), 734-741.

Jones, E. P., & Anderson, L. G. (1994). Northern Hudson Bay and Foxe Basin: water masses, circulation and productivity. *Atmosphere-Ocean*, *32*(2), 361-374.

Kirillov, S., Babb, D., Dmitrenko, I., Landy, J., Lukovich, J., Ehn, J., ... & Stroeve, J. (2020). Atmospheric forcing drives the winter sea ice thickness asymmetry of Hudson Bay. *Journal of Geophysical Research: Oceans*, *125*(2), e2019JC015756.

Laidre, K. L., Stern, H., Kovacs, K. M., Lowry, L., Moore, S. E., Regehr, E. V., ... & Ugarte, F. (2015). Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conservation Biology*, *29*(3), 724-737.

Laidre, K. L., Stirling, I., Lowry, L. F., Wiig, Ø., Heide-Jørgensen, M. P., & Ferguson, S. H. (2008). Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. *Ecological Applications*, *18*(sp2), S97-S125.

Lindeman, R. L. (1942). The trophic-dynamic aspect of ecology. *Ecology*, *23*(4), 399-417.

Leu, E., Mundy, C. J., Assmy, P., Campbell, K., Gabrielsen, T. M., Gosselin, M., ... & Gradinger, R. (2015). Arctic spring awakening–Steering principles behind the phenology of vernal ice algal blooms. *Progress in Oceanography*, *139*, 151-170.

Lewis, K. M., Van Dijken, G. L., & Arrigo, K. R. (2020). Changes in phytoplankton concentration now drive increased Arctic Ocean primary production. *Science*, *369*(6500), 198-202.

Lydersen, C., & Smith, T. G. (1989). Avian predation on ringed seal *Phoca hispida* pups. *Polar Biology*, *9*, 489-490.

Matich, P., & Heithaus, M. R. (2015). Individual variation in ontogenetic niche shifts in habitat use and movement patterns of a large estuarine predator (*Carcharhinus leucas*). *Oecologia*, *178*(2), 347-359.

McLaren, I. A. (1958). The biology of the ringed seal *(Phoca hispida)* in the eastern Canadian Arctic (Vol. 118). Ottawa: Fisheries Research Board of Canada.

Moore, S. E., & Huntington, H. P. (2008). Arctic marine mammals and climate change: impacts and resilience. *Ecological Applications*, *18*(sp2), S157-S165.

Newsome, S. D., Clementz, M. T., & Koch, P. L. (2010). Using stable isotope biogeochemistry to study marine mammal ecology. *Marine Mammal Science*, *26*(3), 509-572.

Newsome, S. D., Garbe, H. M., Wilson, E. C., & Gehrt, S. D. (2015). Individual variation in anthropogenic resource use in an urban carnivore. *Oecologia*, *178*(1), 115-128.

Odum, E. P., & Barrett, G. W. (1971). *Fundamentals of ecology* (Vol. 3, p. 5). Philadelphia:Saunders.

Ogloff, W. R., Anderson, R. A., Yurkowski, D. J., Debets, C. D., Anderson, W. G., & Ferguson, S. H. (2022). Spatiotemporal variation of ringed seal blubber cortisol levels in the Canadian Arctic. *Journal of Mammalogy*,103(5), 1208-1220.

Overland, J. E., & Wang, M. (2013). When will the summer Arctic be nearly sea ice free? *Geophysical Research Letters*, *40*(10), 2097-2101.

Paine,R.T.(1980). Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology*, *49*(3), 667-685.

Peterson, B. J., & Fry, B. (1987). Stable isotopes in ecosystem studies. *Annual review of ecology and systematics*, *18*(1), 293-320.

Polito M.J., Trivelpiece W.Z., Karnovsky N.J., Ng E., Patterson W.P., & Emslie S.D. (2011). Integrating stomach content and stable isotope analyses to quantify the diets of pygoscelid penguins. *PLoS One*, 6(10), e26642.

Post, E., Bhatt, U. S., Bitz, C. M., Brodie, J. F., Fulton, T. L., Hebblewhite, M., ... & Walker, D. A. (2013). Ecological consequences of sea-ice decline. *Science*, *341*(6145), 519-524.

Prinsenberg, S. J. (1986). The circulation pattern and current structure of Hudson Bay. *Elsevier oceanography series*, *44*, 187-204.

Provencher, J. F., Gaston, A. J., Hara, P. O., & Gilchrist, H. G. (2012). Seabird diet indicates changing Arctic marine communities in eastern Canada. *Marine Ecology Progress*

Series, *454*, 171-182.

Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., ... & Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment*, *3*(1), 168.

Reimer, J. R., Caswell, H., Derocher, A. E., & Lewis, M. A. (2019). Ringed seal demography in a changing climate. *Ecological Applications*, *29*(3), e01855.

Saucier, F. J., Senneville, S., Prinsenberg, S., Roy, F., Smith, G., Gachon, P., ... & Laprise, R. (2004). Modelling the sea ice-ocean seasonal cycle in Hudson Bay, Foxe Basin and Hudson Strait, Canada. *Climate Dynamics*, *23*, 303-326.

Sahanatien, V., & Derocher, A. E. (2012). Monitoring sea ice habitat fragmentation for polar bear conservation. *Animal Conservation*, *15*(4), 397-406.

Sih, A., & Christensen, B. (2001). Optimal diet theory: when does it work, and when and why does it fail? *Animal Behaviour*, *61*(2), 379-390.

Smith, T.G., & Hammill, M. O. (1981). Ecology of the ringed seal, *Phoca hispida*, in its fast ice breeding habitat. *Canadian Journal of Zoology*. *59*(6): 966-981.

Stroeve, J., Holland, M. M., Meier, W., Scambos, T., & Serreze, M. (2007). Arctic sea ice decline: Faster than Forecast. *Geophysical Research Letters*, *34*(9).

Thiemann, G. W., Iverson, S. J., Stirling, I., & Obbard, M. E. (2011). Individual patterns of prey selection and dietary specialization in an Arctic marine carnivore. *Oikos*, *120*(10), 1469-1478.

Vander Zanden, M. J., & Rasmussen, J. B. (1996). A trophic position model of pelagic food webs: impact on contaminant bioaccumulation in lake trout. *Ecological Monographs*, *66*(4), 451-477.

Vander Zanden, M. J., & Vadeboncoeur, Y. (2002). Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology*, *83*(8), 2152-2161.

Woo. J., Elliott, K. H., Davidson, M., Gaston, A. J., & Davoren, G. K. (2008). Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. *Journal of Animal Ecology*, 77(6), 1082-1091.

Young, B. G., & Ferguson, S. H. (2013). Seasons of the ringed seal: pelagic open-water hyperphagy, benthic feeding over winter and spring fasting during molt. *Wildlife Research*, *40*(1), 52-60.

Yurkowski, D.J., Richardson, E.S., Lunn, N.J., Muir, D.C., Johnson, A.C., Derocher, A.E., Ehrman, A.D., Houde, M., Young, B.G., Debets, C.D. Sciullo, L., Thiemann, G. & Ferguson, S. H.(2020). Contrasting temporal patterns of mercury, niche dynamics, and body fat indices of polar bears and ringed seals in a melting icescape. *Environmental Science & Technology*, 54(5), pp.2780-2789.

Yurkowski, D. J., Ferguson, S., Choy, E. S., Loseto, L. L., Brown, T. M., Muir, D. C., ... & Fisk, A. T. (2016). Latitudinal variation in ecological opportunity and intraspecific competition indicates differences in niche variability and diet specialization of Arctic marine predators. *Ecology and Evolution*, 6(6), 1666-1678.

Zhao, Q., Jorgensen, S. E., & Nielsen, S. N. (2004). Application of nitrogen isotopes as indicators of food sources in an agricultural catchment. *Environmental Pollution, 129*(1), 63-71.

Chapter 2: Temporal and spatial stable isotope patterns in ringed seal (*Pusa hispida*) diet composition

Abstract

Arctic ecosystem dynamics are becoming more temperate due to sea ice loss caused by global climate change. Understanding the shifts in these dynamics can be gained through investigations of predator dietary changes, which can fluctuate with prey availability. To assess the variation in the Hudson Bay ecosystem, I examined temporal and spatial trends in ringed seal (*Pusa hispida*) $\delta^{13}C$ and $\delta^{15}N$ in muscle and liver tissues, as dietary markers, from 2003 – 2017. Adult ringed seals also consumed the highest proportion of sand lance and capelin, whereas pups and juveniles had more invertebrate contributions to the diet. I also found contrasting patterns in niche breadth over time in each community. I found that adult ringed seals from Arviat had the narrowest niche breadth (0.68 ‰²), and was broader in Sanikiluaq (2.06‰²). The expansion of the niche suggests possible diversification of prey types by the seals. Using MixSIAR, I was able to estimate dietary proportions which revealed a dependence on forage fish species for seals from both regions, particularly sand lance (*Ammodytes* spp.) and capelin (*Mallotus villosus*). Diet of seals in Arviat were dominated by sand lance, whereas diet of seals in Sanikiluaq revealed a more balanced proportion between capelin and sand lance, and to a lesser extent other different prey types. Overall, ringed seals in Hudson Bay demonstrate flexible foraging strategies with varied diet proportions in the two regions across three periods; However, it remains difficult to assess foraging plasticity and efficiency with limited information of prey species abundance and distribution in this area. Characterizing the diet of these ecological and cultural significant species is essential in understanding the ecosystem dynamics of Hudson Bay.

Keywords: Hudson Bay, niche breadth, stable isotopes, diet proportions, ringed seal

Introduction

All species have a specific set of physiological and physical requirements to survive, grow and reproduce (Hutchison 1957). Optimal foraging theory predicts that an individual will consume prey that optimize net energy gain (MacArthur and Pianka 1966). When community assemblages flucuate due to species distributional changes, a predator may exhibit adaptative foraging strategies to compensate for loss of preferred (high energy) prey to lower quality or more abundant prey types. Changing environmental conditions can cause species-specific distributional shifts that alter the structure and function of ecosystems (Pecl et al. 2017). Specifically, food web interactions can be altered by species range expansions (Martin and Valentine 2022).With increasing temperatures, many species have shifted their distributions towards the poles (Parmesan et al. 1999; Araújo et al. 2004; Parmesan 2006). In particular, the Arctic is warming at a faster rate than the global mean (Post et al. 2009, IPCC 2021), altering food web dynamics (Van Der Putten et al. 2010, Galicia et al. 2021). Ongoing climate change is resulting in continued sea ice decline, particularly in seasonal sea ice regimes (Comiso 2003; Overland and Wang 2013), leading to changes in community assemblages (Yurkowski et al. 2018).

Ecological niches are dynamic, resulting from species distribution shifts and resource availability (Wiens et al. 2009; Thuiller 2024). Species may expand their niche as a response to a changing environment, which can increase their resilience to abiotic and biotic factors including environmental changes, and species assemblages within a community. Community dynamics can be influenced by many factors. For instance, resource availability such as species available in an region may constrict predator ranges closer to the poles (Laidre et al. 2008; Ferguson et al. 2020). Further perturbations to community assemblages may come from increased prevalence of seasonal

migrant species in the Arctic and have the potential for increased competition with endemic species (Laidre et al. 2008). Indeed, within the Arctic marine food web, boreal generalist species such as marine forage fish have experienced pronounced distributional shifts due to climate change (Wassmann et al. 2011; Kortsch et al. 2015; Florko et al. 2021). The range expansions could favour species associated with temperate marine environments. Changes to community assemblages in association with warming temperatures have been documented in marine food webs across the Arctic (Gradinger and Bluhm 2020; Pecuchet et al. 2020). For instance, temperate fish species such as capelin (*Mallotus villosus)* and sand lance (*Ammodytes* spp.) ranges have expanded into sub-Arctic waters as sea ice extent has declined in both coverage and duration and many populations are thriving in these waters (McNicholl et al. 2018; Pedro et al. 2020). Moreover, Arctic cod (*Boreogadua saida*) an endemic Arctic species, has decreased in abundance of predator diets in lower latitudes and observed northward shifts of these fish species have caused dietary shifts in marine predators, including belugas (*Delphinapterus leucas*) and seabirds (Watt et al. 2016 and Gaston and Elliott 2014, respectively).

The niche expansion hypothesis predicts that species will use possible ecological opportunity by broadening their niche within-individuals or among individuals in the population and may limit some interspecific competition (Costa et al. 2008). The broadening of a niche, or niche expansion, may also be indictative of changes within the community assemblage by providing increased ecological opportunity (Sjödin et al. 2018). The variation of a population's niche could change overall niche position and/or width (Van Valen 1965; Bolnick et al. 2003). Indeed, Polar bears (*Ursus maritimus*) in southern areas of their range have expanded their niche and are consuming an increased proportion of land-based foods (Johnson et al. 2019; Yurkowski

et al. 2020; Galicia et al. 2021). In addition, Yurkowski et al. (2016) found that four Arctic marine species' dietary niche changed, specifically ringed seals shifted their diet to increased forage fish proportion, altering their niche position and exhibiting flexible foraging behaviour. By contrast, ringed seals have been documented to travel further to the sea-ice edge to consume high energy prey, Arctic cod, in the Barents Sea (Hamilton et al. 2015). When not following the distribution of preferred, caloric-rich prey, predators may exhibit dietary shifts to temperate species, (Chambellant et al. 2013), and possible niche constriction (Yurkowski et al. 2020).

Ringed seals are an abundant Arctic mesopredator that are the primary prey of polar bears, and a key link of energy transfer from lower trophic levels to the apex predator (Laidre et al. 2008; Thiemann et al. 2008). Ringed seals feed extensively in the open water period when prey is more abundant compared to the winter months, when ringed seals mobilize energy reserves in their blubber layer (Young and Ferguson 2013; Yurkowski et al. 2016; Ogloff et al. 2022). Ringed seals are generalist consumers that feed opportunistically and have been shown to have ontogenetic shifts from invertebrate and low trophic fish in juvenile diets towards high trophic level fish in the diets of adults (Lowry et al. 1980; Young and Ferugson 2010; Yurkowski et al. 2016). Historically, Arctic cod was a dominant prey type consumed by ringed seals throughout the Arctic (Lowry et al. 1980; Smith 1987; Wathne et al. 2000). In Hudson Bay, stomach content analysis has shown that sand lance was the most dominant prey type, and to a lesser exent, Arctic cod and capelin in harvested ringed seal stomachs between 1991 and 2006 (Chambellant et al. 2013). Stable isotope (Young and Ferguson 2013; 2014) and fatty acid composition analyses (Thiemann et al. 2007; Young and Ferguson 2013) have previously been used to reflect seasonal and spatial differences in ringed seal isotope ratios in Hudson Bay. To date, ringed seal diet has not been quantitatively

estimated with use of stable isotope ratios. With their wide distribution and presence in a variety of Arctic and sub-Arctic habitats, the ringed seal makes an excellent model species to study temporal trophic relationships. Thus, an understanding of changes in ringed seal diet composition over the past three decades in association with changing sea ice regimes may provide a better understanding of how environmental change is affecting this vital part of the sub-Arctic marine food web.

Stable isotope biomarkers can be used to investigate the niche breadth and diet composition of predators (Ben-David and Flaherty 2012). In marine systems $\delta^{13}C$ values reflect primary production and where the individuals are foraging (pelagic vs. benthic; Petersen and Fry 1987). $\delta^{15}N$ values increase trophically (DeNiro and Epstein 1981). Stable isotope ratios have been used to infer dietary patterns of polar bears (Johnson et al. 2019; Yurkowski et al. 2020) and have been used to qualitatively describe spatial patterns in isotope ratios of ringed seals (Young and Ferguson 2014) in this study area. Temporal changes to isotopic ratios may allow for monitoring of ecosystem changes that may be influenced by climate change. To date, there has not been examination or estimation of dietary proportions that may explain the expanding niche breadth described by Yurkowski et al. (2020).

I used $\delta^{15}N$ and $\delta^{13}C$ from two tissues (liver and muscle) of ringed seals in two regions of Hudson Bay to investigate (1) within-ringed seal population dietary differences related to age and (2) ringed seal dietary changes over time from samples collected in 2003 – 2017. In this investigation I tested the hypothesis that ringed seals show dietary flexibility by quantifying dietary niche breadth and prey type proportions. I predicted that ringed seal niche breath would broaden in more recent years in all age classes to include a higher proportion of new prey species that have

migrated into this sub-Arctic marine ecosystem and are now thriving due to suitable conditions in these waters..

Methods

Sample Collection

Ringed seals were harvested in Arviat and Sanikiluaq, Nunavut. These locations are in a marine environment with a seasonal sea ice regime, where the open water period is from July – November and complete ice coverage during the winter (Laidre et al. 2015). Inuit hunters collected muscle and liver tissue samples from individuals that were harvested during subsistence harvests from September to November in 2003 – 2017. Sex was recorded during tissue collection and age was determined from counts of cementum annuli from the lower right canine at the Matson's Laboratory LLC (Missoula, MT, USA) (Stewart et al. 1996, Young and Ferguson 2014). I used age estimates to classify seals as pups (< 1 year of age), juveniles (1 – 4 years), or adults (≥ 5 years; Stewart 1996; Quakenbush et al. 2011, de la Vega et al. 2021).

Overall, 387 muscle samples and 323 liver samples were collected from ringed seals of all age classes in Arviat. In Sanikiluaq, 238 muscle samples and 90 liver samples were collected (see Table 2.1 for breakdown of sample sizes by community and year). The two tissue types used for stable isotope analysis represent different time period, due to tissue turn-over rates (Hobson and Welch 1992; Vander Zanden et al. 2015). Liver represents a shorter turnover period, one to two months, compared to muscle, approximately four months (Vander Zanden et al. 2015). Liver and muscle from the seals harvested for this study respresent consumptions during the open water period, when seals are known to forage extensively (Young and Ferguson 2013).

Potential seal prey species, included fish and invertebrate species, were collected from communities throughout Hudson Bay between 2004 – 2007 (Elliott and Gaston 2008; Chambellant et al. 2013). While acknowledging that the stable isotope ratios of the prey items likely vary seasonally, annually and spatially between regions, we compiled all prey samples together, assuming the overall shift would be minimal. I grouped samples based on collection year into three periods: 2003 – 2007, 2008 – 2012, and 2013 – 2017, to increase sample size in all age class categories allowing for an investigation of changes over time.

Laboratory analysis

I measured stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) of ringed seal muscle and liver at the Freshwater Institute, Fisheries and Oceans Canada (Winnipeg, MB, Canada). I subsampled ~ 5 g of tissue that was freeze dried for 48 hours and then homogenized using a mortar and pestle. Lipids were extracted using a 2:1 chloroform: methanol solvent following a modified method from Bligh and Dyer (1959) and ~ 400 µg of tissue was weighed into tin capsules. The use of chemical lipid extraction may influence the ratios of nitrogen isotopes in the tissue samples; however, many studies, including those of marine mammals, have found the effects to be minimal (Ingram et al. 2007; Yurkowski et al. 2015). Lipids are extracted as they are known to be more deplected in $\delta^{13}C$ compared to proteins (Post et al. 2007). Samples were then combusted to measure $\delta^{13}C$ and $\delta^{15}N$ using a continuous flow isotope ratio mass spectrometer (Delta V Plus; Thermo Scientific) interfaced with an elemental analyzer (ECS 4010; Costech Instruments) and connected via a Conflo IV interface (Thermo Scientific).

Muscle and liver isotope ratios are expressed in per mil (‰) deviation from the standard, the Vienna Pee Dee Belemnite for carbon, and atmospheric nitrogen for nitrogen, in delta (δ) notation using the equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

Where X refers to ^{13}C or ^{15}N, and R refers to the ratio of heavy to light isotopes ratios of ^{13}C:^{12}C or ^{15}N:^{14}N. Both precision and accuracy were assessed using replicates of standard reference material (USGS 40 and USGS41a) spaced throughout runs and was determined to be ≤ 0.28‰ for $\delta^{13}C$ and ≤ 0.16‰ for $\delta^{15}N$. Every tenth seal sample was run in duplicate resulting in standard deviations ranging from 0.01-0.66‰ for $\delta^{13}C$ and 0.0-0.70‰ for $\delta^{15}N$. Carbon to Nitrogen ratios (C:N) were inspected and there was likely no added variation in $\delta^{13}C$ due to higher lipid content as all samples were less than 3.51 (Post et al. 2007).

Data analysis

The isotopic niche breath of each age class in each of the three periods for both communities was calculated using Stable Isotope Bayesian Ellipses in R (SIBER; Jackson et al. 2011) separately using muscle and liver tissues. To reflect the population level niche breadth, I used the 95% prediction ellipse, which encompasses 95% of data (Jackson et al. 2011; Yurkowski et al. 2016). The ellipse area was calculated using a Bayesian technique using 10^5 iterations with a burn in of 100,000 and thinned by 10 with two chains and 95% credible interval (Jackson et al. 2011, Yurkowski et al. 2016).

The R package Bayesian isotope mixing model MixSIAR (Stock and Semmens 2013) was used with uninformed priorts, to quantitatively estimate the relative contribution of prey types to the seal diet for each muscle and liver sample. To account for trophic discrimination, species-specific trophic discrimination factors estimated from harp seals (*Pagophilus groenlandicus*) by Hobson et al. (1996) were used, as no ringed seal specific discrimination factors are available for these two tissue types. Thus I incorporated the following discrimination factors into the model, muscle δ^{15}N = 2.4, δ^{13}C = 1.3; liver δ^{15}N = 3.1, δ^{13}C = 0.6 with an arbitrary standard deviation of 0.2 being used for each discrimination factor. All models were run with three Markov Chain Monte Carlo chains of 100,000 iterations, 50,000 burn-in, and thinning of 50. Gelman-Rubin and Geweke diagnostic tests were used to examine chain convergence.

To determine diet proportion, prey types were clumped together when their isotopic ratios could not be independently distinguished for a total of five possible prey types for the model. The groups included in this study followed the prey groups used by Yurkowski et al. (2016) to investigate ringed seal niches in Chesterfield Inlet, Nunavut. I used prey samples from previously collected and published data on species that have previously been found in ringed seal stomach contents (Chambellant et al. 2013). The prey type groups I used were *Themisto libellula* (mean ± SD of 7 individuals: δ^{15}N= 8.4 ± 0.3‰, δ^{13}C = -23.0 ± 0.2‰), capelin (mean ± SD of 46 individuals: δ^{15}N= 13.7 ± 0.8‰, δ^{13}C = -19.8 ± 1.1‰), sand lance (mean ± SD of 47 individuals : δ^{15}N= 12.7 ± 1.4‰, δ^{13}C = -21.0 ± 1.2‰), *Gammarus sp.* (mean ± SD of 4 individuals: δ^{15}N= 9.7 ± 0.3‰, δ^{13}C = -18.1 ± 0.6‰), and cod+sculpin (mean ± SD of 61 individuals : δ^{15}N= 14.9 ± 0.7‰, δ^{13}C = -19.2 ± 0.6‰). Where cod+sculpin represented samples of primarily Greenland cod (*Gadus ogac*), Arctic cod and sculpin (*Cottoidea sp*.), that had overlapping isotope ratios not

significantly different. Analysis was limited to these groupings to assist in model performance (Phillips et al. 2014). Prey samples were homogenized and prepared for stable isotope analysis with methods used for seals samples. All prey samples were lipid extracted following the modified Blight & Byer (1959) method using a chloroform:methonal solvent with a 2:1 ratio, a complete detail of the modified lipid extraction is outlined in Logan et al. (2008).

I tested the underlying parametic assumptions, and found a near normal distribution and and homogeneity of varirance, thus I used three-factor ANOVAs to determine whether there were significant differences in $\delta^{15}N$ and $\delta^{13}C$ values among age classes, periods, and regions. I used Tukey post hoc tests when significant differences were detected. The significance of statistical tests was assessed at $\alpha = 0.05$ and analyses were conducted in JMP Pro 16 (SAS Institute Inc 2021) and R version 3.4.4 (R Core Team 2021).

Results

There were differences in ringed seal stable isotope ratios in muscle and liver among regions and age classes (Table 2.2). Values of $\delta^{13}C$ in muscle differed significantly by age class (3-factor ANOVA, $F_{1, 384} = 19.49$, $p < 0.001$) where adults were the least depleted in carbon (-19.58 ‰; Table 2.2) than juveniles ($p < 0.001$) but subadults and pups did not differ significantly ($p = 0.12$) when periods and regions were combined.. There were no significant interactions between age, period and region (region:period:age $F_{4,384} = 2.90$, $p = 0.06$; period:age $F_{4,384} = 0.28$, $p = 0.76$). There were significant differences in $\delta^{13}C$ between communites ($F_{1, 384} = 24.49$, $p < 0.001$), where seals from Sanikiluaq were less depleted compated to seals in Arviat (Table 2.2).

There were significant interactions between region and period ($F_{4,384} = 4.11$, $p = 0.02$) where adults were less depleted in carbon in 2012-2017 compared to 2003- 2007 in Sanikiluaq ($p = 0.02$). Values of $\delta^{13}C$ in liver were not significacntly different by age class in (3-factor ANOVA, $F_{2, 384} = 9.41$, $p= 0.53$), and ranged from -19.94 to -20.64‰ in Arviat, the least depleated values found in pups compared to adults with the most depleated values (Table 2.3). In Sankiluaq, the carbon isotope ratios ranged from -19.02 to 20.12‰, with both the least and most depleted values observed in pups (Table 2.3) Values of $\delta^{13}C$ in liver were significantly different by region (3-way ANOVA, $F_{2, 384} = 55.65$, $p < 0.001$; Table 2.3). Adults in Sanikiluaq had the least depletion in their $\delta^{13}C$ liver values compared to those in Arviat ($p=0.01$, Table 2.3) and there was a significant interaction between period and region in the model (region:period $F_{4,384} =15.56$, $p< 0.001$). Subsequent Tukey tests revealed signicant differences between periods 2003-2007 and 2013 –2017 ($p < 0.001$) and 2008 – 2012 and 2013 – 2017 ($p <0.001$).

Values of $\delta^{15}N$ in muscle were significantly different by age class (3-factor ANOVA, $F_{2, 384} = 39.05$, $p<0.0001$). Adult muscle had significantly higher $\delta^{15}N$ values compared juveniles ($p <0.001$) and pups ($p=0.01$) and juveniles were higher than pups ($p=0.01$; Table 2.2). Values of $\delta^{15}N$ in liver were significantly higher for adults compared to juveniles ($p=0.03$) and pups ($p=0.01$), but not between juveniles and adults ($p = 0.23$) and pups and junveniles ($p = 0.3$; Table 2.3). There were no significant difference in the values of $\delta^{15}N$ in muscle between periods (3-factor ANOVA, $F_{2, 384} = 1.48$, $p=0.2246$; Table 2.2), although there were significant difference in $\delta^{15}N$ in liver (3-factor ANOVA, $F_{2, 384} = 3.62$, $p=0.03$; Table 2.3). In both tissues, $\delta^{15}N$ the interaction between region and period was significant (muscle 3-factor ANOVA, $F_{2, 384} = 3.62$, $p=0.03$; Table

2.3). $\delta^{15}N$ in liver tissues increased over the time period from 15.40 to 16.2 ‰, with only 2003 – 2007 being significantly different from 2013 – 2017 ($p = 0.01$).

Isotopic Niche Breadth

Isotopic niche breadth varied among age classes and periods (Table 2.2 and 2.3). The isotopic niche breadth was largest for all age classes in Arviat for both muscle and liver, with the largest niche breadth measured for pups in 2003 – 2007 (Table 2.2; Figure 2.2 and 2.3). Age classes occupy similar isotopic niche space, with adults having less depleted carbon and higher nitrogen in both muscle (Figure 2.2) and liver (Figure 2.3). The lowest isotopic niche breadth was in the recent time-period (2013 – 2017) for all age classes in Arviat. Indeed, the adult niche breadth was three times narrower in the recent time period compared to 2003 – 2007. The niche breadth for pups was also decreased by nearly half over the study period from 3.97 to 2.39 ‰^{2}; Table 2.2). In liver, the same patterns were observed, where Arviat seals of all age classes had their niche breadth narrowed over the study period (Table 2.3). In Sanikiluaq, the opposite trend was observed where instead the niche breadth of all age classes using either tissue type increased over the study periods (Table 2.2 and Table 2.3). Sanikiluaq adults had the broadest niche in 2013 – 2017 measured from liver compared to other age-classes (Table 2.3). However, when measuring niche breadth using muscle tissue, juveniles experience a narrowing of their niche from 3.06 to 0.88‰^{2} (Table 2.2)**.**

Diet Estimations

Sand lance comprised the majority of the diet, followed by capelin and *Themisto* for all age classes in both study locations across all three periods in muscle samples (Figure 2.4). In liver samples, capelin represented a higher proportion of the diet for Sankiluaq seals across all age classes and periods (Figure 2.5). However, in Arviat, sand lance comprised the greatest proportion of seal diets. There was minimal (<10%) benthic prey types in the diets of Arviat seals when estimating diet from liver (Figure 2.5), and Sankiluaq seals when estimating diet from muscle tissues (Figure 2.4). The greatest contribution of benthic prey proportions was estimated for juveniles in 2007 – 2011 using muscle tissues from Arviat seals, and in Sanikiluaq pups from 2012 – 2017 using liver tissue.

Discussion

Shifting community dynamics in the Hudson Bay marine ecosystem was reflected in the isotope ratios and niche breadth of ringed seals, as I demonstrate with the 15 years of dietary analysis of ringed seal populations in Arviat and Sanikiluaq. Specifically, in Figures 2.2 and 2.3, the shift of niche ellipse in isotopic space was observed, and contrasting patterns of niche broadening and narrowing was documented between communities. The results of this study support previous description of Hudson Bay as a a heterogenous marine environment (Pedro et al. 2020, Florko et al. 2023). These results are the first to estimate dietary proportions of Hudson Bay ringed seals using stable isotope biomarkers. Here, seals were found to consume primarily forage fish (sand lance and capelin), which have been previously shown to have high occurrence in ringed seal diets from stomach content analysis (Chambellant et al. 2013). I also found congruent patterns with previously reported SI ontogenetic foraging patterns in ringed seals (Yurkowski et al. 2016),

where adults were more likely to consume more pelagic forage fish than juveniles. Finally, I found that niche breadth of seals had increased from 2003 – 2017 in Sanikiluaq for most age classes using both tissue types, except for juvenile muscle, but this age class had decreased niche breadth during the same time- period in Arviat.

Adult seals had the narrowest niche breadth of 0.68 ‰² in Arviat, during the 2013 – 2017 period, dissimilar to the observations of adult seals in Sanikiluaq, where the broadest niche breadth, 2.06 ‰², was recorded during the 2003 – 2007 period. Adult and juvenile seals in Arviat in the recent period have a niche breadth three to four times narrower, respectively, compared to 2003 – 2007 in the same region. The narrow niche breadth could reflect changes in the prey base within this marine system. For instance, shifts in prey stable isotope values may have caused corresponding changes in those of their predator (Post et al. 2007). Since I only used prey samples from a single time point to estimate the diet, I am unable to differentiate whether there has been a baseline shift or if prey stable isotope values are converging with those of other prey species due to similarities in their diet. Alternatively, seals with narrower niche breadths could be using a specialist strategy where all individuals are consistently consuming similar prey types (Bolnick et al. 2003). Ringed seals have been known to specialize on Arctic cod (Yurkowski et al. 2016), which are a fish that have retreated to areas in high Arctic where there is longer sea ice coverage (Steiner et al. 2019). Ringed seals dive longer and swim farther in areas where there is sea ice loss, likely in search for this prey type (Hamilton et al. 2015) and thus would exhibit a narrower niche. The narrower niche may reflect lower variety of prey types that provide energetic returns (Bolnick et al. 2003). Using stable isotope analysis Young and Ferguson (2014) found amphiopods contributing to the diet of ringed seals in Hudson Bay following the predominance of sand lance.

Similarly, Chambellent et al. (2013) used stomach content analysis which also revealed limited Arctic cod consumption in Hudson Bay ringed seals.

Conversely, a strategy that is adaptative to the changing prey availabilities would result in a broader niche breadth as seals in that population are likely using a generalist foraging strategy that allows the individuals to alter their behaviour (Bolnick et al. 2003). The adult ringed seals in Sanikiluaq have broadened their niche breadth from 1.42 ‰² to 2.06 ‰², which may suggest a more plastic diet. The niche breadth patterns observed in this study reveal that Hudson Bay ringed seals have varied dietary consumption based on the carbon and nitrogen isotopic niche; However, this study has not included prey distribution and abundance data and I am not be able to suggest predator foraging choices, but rather heterogeneity in the marine environment that ringed seals are likely foraging in, reflected in varying diet istope ratios and estimated diet compositions. Previous analysis of ringed seal niche breadth from western Hudson Bay, Chesterfield Inlet, revealed similar niche widths between 1 - 2 ‰² for adults and subadults using muscle and liver, and dietary estimates found sand lance, capelin and Arctic cod the main species during 1999 – 2011 (Yurkowski et al. 2016). Ongoing borealization of sub-Arctic waters provides ringed seals opportunity to consume a wider variation of prey types (Bengtsson et al. 2020) and we would expect an increasing niche width. Additionally, there are contrasting niche patterns to those observed here, where ringed seal niche size remained relatively consistent over the same study period (Yurkowski et al. 2020). A possible explanation to the difference observed in this study and by Yurkowski et al. (2020) could be due to the dietary markers used to estimated niche width. Additionally, the samples sizes and age classes used between the studies were somewhat different, with a greater proportion of younger seals used in Yurkowski et al. (2020) compared to this study.

The isotope ratios and niche breadth of ringed seals estimated here is in accordance with dietary studies of seals in other Canadian Arctic regions (Yurkowski et al. 2016; Kunisch et al. 2021; Ross et al. 2022). Ringed seal diets have been documented to vary regionally, and both intra- and interannually (Thiemann et al. 2007; Young and Ferguson 2013; Ross et al. 2022). I found significant variation in ringed seal isotope ratios, further documenting the dietary changes of this species. Seals in Sanikiluaq align with patterns documented in higher latitudes (Yurkowski et al. 2016). For instance, seals are thought to be increasing their dietary niche in areas where temperate species are thriving (Kunisch et al. 2021), a strategy that has been observed by other predators that are experiencing species distributional shifts (Pecuchet et al. 2020). The niche expansion hypothesis is not supported with our data from Arviat, as I have documented a reduction in the niche breadth and similar estimated diet proportions over our study period. Seals in this southern area of their range are also responding to environmental changes which have been correlated with negative body condition trends, where increased open water periods result in a thinner blubber layer in ringed seals (Ferguson et al. 2020). The observed decline in the seals' condition, which is linked to an extended open water period, may suggest that the seals are either foraging on prey that fails to sufficiently offset their foraging costs or are expending excessive energy on high-yield but demanding prey. This situation implies a limitation in their foraging adaptability or plasticity.

Adult ringed seals had the highest $\delta^{15}N$ and least depleted $\delta^{13}C$ values compared to other age classes (Table 2.2). Given that nitrogen reflects trophic levels (DeNiro and Epstein 1981) it is not surprising that adults, who may have more experience developing their foraging strategy can capitalize on higher energy content prey types (Hamilton et al. 2015. Ogloff et al. 2021). Adult seals are also more likely to spend more time diving and have the capabilities to have longer dives

to reach deeper depths and therefore their $\delta^{13}C$ isotope ratio may reflect benthic contributions to their diet (Crawford et al. 2012; Ogloff et al. 2021). For instance, *Themisto libellula* are a pelagic invertebrate that are often close to the surface (Wathne et al. 2000) and juvenile ringed seals in large open water areas were observed to have shallow mean daily dive depths of 25.4 m which were more pelagic than adults (Ogloff et al. 2021). The lower $\delta^{13}C$ isotope ratio observed here in juuvenile ringed seal diet estimations demonstrates increased consumption of pelagic soures in both one month (liver) and longer term (muscle) time intervals in both regions compared to adults. Adult ringed seals in this study had higher proportion of benthic prey, and higher trophic level benthic fish compared to juveniles and pups. Seals that travel closer to shore, exhibit deeper dives and resident behaviour across the Canadian Arctic including seals tagged in Hudson Bay (Yurkowski et al. 2016) are likely consuming benthic prey. Dietary marker analysis alone, such as in this study, cannot verify foraging behaviour but can infer likely habitat use for foraging.

Limitations to this study include the lack of prey distribution and abundance data for the area which limit my capabilities to determine if foraging shifts are occuring. An understanding of what prey are available, and their abundance can give us better insight into prey preference of ringed seals in this southern part of their range. The patterns of ringed seal niche breadth in Hudson Bay during our study period reflect that ringed seals have varying foraging strategies at the population level in a responsive manner to a changing environment. Understanding ringed seal isotope ratios can help us better understand shifts in the food web and dynamics of apex predators, such as polar bears, that rely on this ice-associated species. Climate-induced environmental effects are predicted to continue to influence species distribution, altering this food web, and research studies that can link various trophic levels together with a combination of dietary markers will

provide a more refined understandings of the complex interactions in the food web structure. Ringed seal isotope values can be a useful tool for capturing these shifts in Arctic marine food web dynamics to better understand entire ecosystem changes.

This study examined the dietary composition changes in ringed seal diets using stable isotope analysis. I investigated the dietary patterns and niche breadth of ringed seals over a 15-year period in two locations within Hudson Bay, revealing significant variations in isotopic signatures and niche breadths among age classes and over time. These findings shed light on the flexlible responses of ringed seals to shifting environmental conditions and associated influences on prey abundances and distributions. Further research integrating prey distribution and abundance data are crucial for a comprehensive understanding of predator-prey interactions and ecosystem resilience in the Arctic marine environment.

Literature Cited

Araújo, M. B., Alagador, D., Cabeza, M., Nogués-Bravo, D., & Thuiller, W. (2011). Climate change threatens European conservation areas. *Ecology Letters*, 14(5), 484-492.

Ben-David, M., & Flaherty, E. A. (2012). Stable isotopes in mammalian research: a beginner's guide. *Journal of Mammalogy*, 93(2), 312-328.

Bengtsson, O., Lydersen, C., Kovacs, K. M., & Lindstrøm, U. (2020). Ringed seal (*Pusa hispida*) diet on the west coast of Spitsbergen, Svalbard, Norway: during a time of ecosystem change. *Polar Biology*, *43*, 773-788.

Bligh, E. G., & Dyer, W. J. (1959). A rapid method of total lipid extraction and purification. *Canadian Journal of Biochemistry and Physiology*, 37(8), 911-917.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A, Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, 161,1–28.

Chambellant, M., Stirling, I., & Ferguson, S. H. (2013). Temporal variation in western Hudson Bay ringed seal *Phoca hispida* diet in relation to environment. *Marine Ecology Progress Series*, 481, 269-287.

Comiso, J. C. (2003). Large-scale characteristics and variability of the global sea ice cover. Sea ice: an introduction to its physics, chemistry, biology and geology, 112-142.

Costa, G. C., Mesquita, D. O., Colli, G. R., & Vitt, L. J. (2008). Niche expansion and the niche variation hypothesis: does the degree of individual variation increase in depauperate assemblages?. *The American Naturalist*, *172*(6), 868-877.

Crawford, J. A., Frost, K. J., Quakenbush, L. T., & Whiting, A. (2012). Different habitat use strategies by subadult and adult ringed seals (Phoca hispida) in the Bering and Chukchi seas. *Polar Biology*, *35*(2), 241-255.

Das, K., Holsbeek, L., Browning, J., Siebert, U., Birkun, A., & Bouquegneau, J. M. (2004). Trace metal and stable isotope measurements (δ 13 C and δ 15 N) in the harbour porpoise *Phocoena phocoena relicta* from the Black Sea. Environmental Pollution, 131(2), 197-204.

De la Vega, C., Mahaffey, C., Yurkowski, D. J., Norman, L., Simpson, E., Smout, S., ... & Jeffreys, R. M. (2021). Biomarkers in ringed seals reveal recent onset of borealization in the high-compared to the mid-latitude Canadian Arctic. *Frontiers in Marine Science*, *8*, 700687.

DeNiro, M. J., & Epstein, S. (1977). Mechanism of carbon isotope fractionation associated with lipid synthesis. S*cience*, 197(4300), 261-263.

Elliott, K. H., & Gaston, A. J. (2008). Mass-length relationships and energy content of fishes and invertebrates delivered to nestling thick-billed murres *Uria lomvia* in the Canadian Arctic, 1981-2007. *Marine Ornithology*, *36*, 25-34.

Ferguson, S. H., Yurkowski, D. J., Young, B. G., Fisk, A. T., Muir, D. C., Zhu, X., & Thiemann, G. W. (2020). Comparing temporal patterns in body condition of ringed seals living within their core geographic range with those living at the edge. *Ecography*, *43*(10), 1521-1535.

Florko, K. R., Ross, T. R., Ferguson, S. H., Northrup, J. M., Obbard, M. E., Thiemann, G. W., ... & Auger-Méthé, M. (2023). The dynamic interaction between predator and prey drives mesopredator movement and foraging ecology. *BioRxiv*, 2023-04.

Florko, K. R., Tai, T. C., Cheung, W. W., Ferguson, S. H., Sumaila, U. R., Yurkowski, D. J., & Auger-Méthé, M. (2021). Predicting how climate change threatens the prey base of Arctic marine predators. *Ecology Letters*, *24*(12), 2563-2575.

Gaston, J., & Elliott, K.H. (2014). Seabird diet changes in northern Hudson Bay, 1981-2013, reflect the availability of schooling prey. *Marine Ecology Progress Series* , 513, 211-223.

Galicia, M. P., Thiemann, G. W., Dyck, M. G., & Ferguson, S. H. (2021). Polar bear diet composition reveals spatiotemporal distribution of Arctic marine mammals across Nunavut, Canada. *Ecological Indicators*, *132*, 108245.

Gradinger, R., & Bluhm, B. A. (2020). First analysis of an Arctic sea ice meiofauna food web based on abundance, biomass and stable isotope ratios. *Marine Ecology Progress Series*, *634*, 29-43.

Hamilton, C. D., Lydersen, C., Ims, R. A., & Kovacs, K. M. (2015). Predictions replaced by facts: a keystone species' behavioural responses to declining arctic sea-ice. *Biology Letters*, 11(11), 20150803.

Hobson, K. A., Schell, D. M., Renouf, D., & Noseworthy, E. (1996). Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. *Canadian Journal of Fisheries and Aquatic Sciences,* 53(3), 528-533.

Hobson, K. A., & Welch, H. E. (1992). Determination of trophic relationships within a high Arctic marine food web using δ 13 C and δ 15 N analysis. *Marine Ecology Progress Series*, 9-18.

Hutchinson, G. E. (1957). Cold spring harbor symposium on quantitative biology. *Concluding remarks*, 22, 415-427.

Ingram, T., Matthews, B., Harrod, C., Stephens, T., Grey, J., Markel, R., & Mazumder, A. (2007). Lipid extraction has little effect on the δ15N of aquatic consumers. *Limnology and Oceanography: Methods*, *5*(10), 338-342.

IPCC, 2021: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y.

Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA,

Jackson, A.L., Inger, R., Parnell, A.C., & Bearhop, S. (2011). Comparing isotopic width niches among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, *80* (3), 595-602.

Johnson, A. C., Hobson, K. A., Lunn, N. J., McGeachy, D., Richardson, E. S., & Derocher, A. E. (2019). Temporal and intra-population patterns in polar bear foraging ecology in western Hudson Bay. *Marine Ecology Progress Series*, *619*, 187-199.

Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A. V., & Aschan, M. (2015). Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1814), 20151546.

Kunisch, E. H., Graeve, M., Gradinger, R., Haug, T., Kovacs, K. M., Lydersen, C., ... & Bluhm, B. A. (2021). Ice-algal carbon supports harp and ringed seal diets in the European Arctic: evidence from fatty acid and stable isotope markers. *Marine Ecology Progress Series*, *675*, 181-197.

Laidre, K. L., Stirling, I., Lowry, L. F., Wiig, Ø., Heide-Jørgensen, M. P., & Ferguson, S. H. (2008). Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. *Ecological Applications*, 18(sp2).

Laidre, K. L., Stern, H., Kovacs, K. M., Lowry, L., Moore, S. E., Regehr, E. V., ... & Born, E. W. (2015). Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conservation Biology*, 29(3), 724-737.

Logan, J. M., Jardine, T. D., Miller, T. J., Bunn, S. E., Cunjak, R. A., & Lutcavage, M. E. (2008). Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. *Journal of Animal Ecology*, 838-846.

Lowry, L. F., Frost, K. J., & Burns, J. J. (1980). Trophic relationships among ice-inhabiting phocid seals and functionally related marine mammals in the Chukchi Sea. Alaska Department of Fish and Game.

MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, 100(916), 603-609.

Martin, C. W., & Valentine, J. F. (2022). Climate-induced expansion of consumers in seagrass ecosystems: lessons from invasion ecology. *Frontiers in Marine Science*, *9*, 867173.

McNicholl, D. G., Davoren, G. K., Majewski, A. R., & Reist, J. D. (2018). Isotopic niche overlap between co-occurring capelin (*Mallotus villosus*) and polar cod (*Boreogadus saida*) and the effect of lipid extraction on stable isotope ratios. *Polar Biology*, *41*, 423-432.

Ogloff, W. R., Anderson, R. A., Yurkowski, D. J., Debets, C. D., Anderson, W. G., & Ferguson, S. H. (2022). Spatiotemporal variation of ringed seal blubber cortisol levels in the Canadian Arctic. *Journal of Mammalogy*, *103*(5), 1208-1220.

Ogloff, W. R., Ferguson, S. H., Fisk, A. T., Marcoux, M., Hussey, N. E., Jaworenko, A., & Yurkowski, D. J. (2021). Long-distance movements and associated diving behaviour of ringed seals (*Pusa hispida*) in the eastern Canadian Arctic. *Arctic Science*, *7*(2), 494-511.

Overland, J. E., & Wang, M. (2013). When will the summer Arctic be nearly sea ice free? Geophysical Research Letters, 40(10), 2097-2101.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.*, *37*, 637-669.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., ... & Warren, M. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, *399*(6736), 579-583.

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., ... & Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332), eaai9214.

Peterson, B. J., & Fry, B. (1987). Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics*, 18(1), 293-320.

Pecuchet, L., Blanchet, M. A., Frainer, A., Husson, B., Jørgensen, L. L., Kortsch, S., & Primicerio, R. (2020). Novel feeding interactions amplify the impact of species redistribution on an Arctic food web. *Global Change Biology*, *26*(9), 4894-4906.

Pedro, S., Fisk, A. T., Ferguson, S. H., Hussey, N. E., Kessel, S. T., & McKinney, M. A. (2020). Broad feeding niches of capelin and sand lance may overlap those of polar cod and other native fish in the eastern Canadian Arctic. *Polar Biology*, *43*, 1707-1724.

Phillips, D. L., Inger, R., Bearhop, S., Jackson, A. L., Moore, J. W., Parnell, A. C., ... & Ward, E. J. (2014). Best practices for use of stable isotope mixing models in food-web studies. *Canadian Journal of Zoology*, *92*(10), 823-835.

Post, D. M., Layman, C. A., Arrington, D. A., Takimoto, G., Quattrochi, J., & Montana, C. G. (2007). Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*, *152*, 179-189.

Quakenbush, L., Citta, J., & Crawford, J. (2011). Biology of the ringed seal (*Phoca hispida*) in Alaska, 1960–2010. *Final Report to: National Marine Fisheries Service*.

Ross, T. R., Thiemann, G. W., Young, B. G., & Ferguson, S. H. (2022). Complementary diet analyses reveal intraspecific and temporal variation in ringed seal (*Pusa hispida*) foraging in the Canadian high arctic. *Polar Biology*, *45*(3), 465-480.

Sjödin, H., Ripa, J., & Lundberg, P. (2018). Principles of niche expansion. *Proceedings of the Royal Society B*, *285*(1893), 20182603.

Steiner, N. S., Cheung, W. W., Cisneros-Montemayor, A. M., Drost, H., Hayashida, H., Hoover, C., ... & VanderZwaag, D. L. (2019). Impacts of the changing ocean-sea ice system on the key forage fish Arctic cod (*Boreogadus saida*) and subsistence fisheries in the western Canadian Arctic—Evaluating linked climate, ecosystem and economic (CEE) models. *Frontiers in Marine Science*, *6*, 179.

Stewart, R. E., Stewart, B. E., Stirling, I., & Street, E. (1996). Counts of growth layer groups in cementum and dentine in ringed seals (*Phoca hispida*). *Marine Mammal Science*, *12*(3), 383-401.

Stock, B. C., & B. X. Semmens. (2013). MixSIAR User Manual. Version 3.1. https://github.com/brianstock/MixSIAR

Thiemann, G. W., Iverson, S. J., & Stirling, I. (2007). Variability in the blubber fatty acid composition of ringed seals (*Phoca hispida*) across the Canadian Arctic. Marine Mammal Science, 23(2), 241-261.

Thiemann, G. W., Iverson, S. J., & Stirling, I. (2008). Polar bear diets and arctic marine food webs: insights from fatty acid analysis. *Ecological Monographs*, 78(4), 591-613.

Thuiller, W. (2024). Ecological niche modeling. Current Biology, 34 (6), R225-229.Vander Zanden, M. J., Clayton, M. K., Moody, E. K., Solomon, C. T., & Weidel, B. C. (2015). Stable isotope turnover and half-life in animal tissues: a literature synthesis. *PloS one*, *10*(1), e0116182.

Vander Zanden, H. B., Tucker, A. D., Hart, K. M., Lamont, M. M., Fujisaki, I., Addison, D. S., ... & Bjorndal, K. A. (2015). Determining origin in a migratory marine vertebrate: a novel

method to integrate stable isotopes and satellite tracking. *Ecological Applications*, *25*(2), 320-335.

Van der Putten, W. H., Macel, M., & Visser, M. E. (2010). Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1549), 2025-2034.

Van Valen, L. (1965). Morphological variation and width of ecological niche. *The American Naturalist*, 99(908), 377-390.

Wassmann, P., Duarte, C. M., Agusti, S., & Sejr, M. K. (2011). Footprints of climate change in the Arctic marine ecosystem. *Global change biology*, *17*(2), 1235-1249.

Wathne, J.A, Haug, T., & Lydersen, C. (2000). Prey preference and niche overlap of ringed seals *Phoca hispida* and harp seals *P.groenlandica* in the Barents Sea. *Marine Ecology Progress Series*, 194, 233-239.

Watt, C. A., Orr, J., & Ferguson, S. H. (2016). A shift in foraging behaviour of beluga whales Delphinapterus leucas from the threatened Cumberland Sound population may reflect a changing Arctic food web. *Endangered Species Research*, *31*, 259-270.

Wiens, J. A., Stralberg, D., Jongsomjit, D., Howell, C. A., & Snyder, M. A. (2009). Niches, models, and climate change: assessing the assumptions and uncertainties. *Proceedings of the National Academy of Sciences*, *106*(supplement_2), 19729-19736.

Young, B. G., Loseto, L. L., & Ferguson, S. H. (2010). Diet differences among age classes of Arctic seals: evidence from stable isotope and mercury biomarkers. *Polar Biology*, 33(2), 153-162.

Young, B. G., & Ferguson, S. H. (2013). Seasons of the ringed seal: pelagic open-water hyperphagy, benthic feeding over winter and spring fasting during molt. *Wildlife Research*, 40(1), 52-60.

Young, B.G., & Ferguson, S.H. (2014). Using stable isotopes to understand changes in ringed seal foraging ecology as a response to a warming environment, *Marine Mammal Science*, 30(2), 706-725.

Yurkowski, D. J., Ferguson, S. H., Semeniuk, C. A., Brown, T. M., Muir, D. C., & Fisk, A. T. (2016). Spatial and temporal variation of an ice-adapted predator's feeding ecology in a changing Arctic marine ecosystem. *Oecologia*, 180(3), 631-644.

Yurkowski, D. J., Hussey, N. E., Ferguson, S. H., & Fisk, A. T. (2018). A temporal shift in trophic diversity among a predator assemblage in a warming Arctic. *Royal Society Open Science*, *5*(10), 180259.

Yurkowski, D. J., Hussey, N. E., Semeniuk, C., Ferguson, S. H., & Fisk, A. T. (2015). Effects of lipid extraction and the utility of lipid normalization models on δ13C and δ15N values in Arctic marine mammal tissues. *Polar Biology*, 38(2), 131-143.

Yurkowski, D. J., Richardson, E. S., Lunn, N. J., Muir, D. C., Johnson, A. C., Derocher, A. E., Ehrman, A.D., House, M., Young, B.G., Debets, C.D., Scuillo, L., Thiemann, G.W., & Ferguson, S. H. (2020). Contrasting temporal patterns of mercury, niche dynamics, and body fat indices of polar bears and ringed seals in a melting icescape. *Environmental Science & Technology*, *54*(5), 2780-2789.

Tables

Table 2.1. The number of ringed seal samples from each age class (Adult [> 5 years], Juvenile [1 – 4 years], Pups [< 1 year of age]). Samples were collected from 2003 – 2017 in two regions of Hudson Bay, Arviat (west) and Sanikiluaq (east), by community Inuit harvesters.

	Pups			Juveniles			Adults		
	2003 - 2007	**2008 - 2012**	**2013 – 2017**	**2003 - 2007**	**2008 - 2012**	**2013 – 2017**	**2003 - 2007**	**2008 - 2012**	**2013 – 2017**
Muscle									
Arviat	46	44	24	47	36	19	48	76	47
Sanikiluaq	54	27	7	43	18	9	36	22	22
Liver									
Arviat	50	23	24	52	14	20	45	47	48
Sanikiluaq	2	9	9	5	12	10	4	17	22

Table 2.2. Stable isotope ratio ($\delta^{13}C$ and $\delta^{15}N$, mean ± SE) and isotopic niche breadth, mode of Bayesian ellipse areas and (95% credible intervals) from ringed seal muscle tissues sampled in Arviat and Sanikiluaq, Nunavut during fall 2003 – 2017.

Age	Time period	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)		Niche breadth (‰²)	
		Arviat	Sanikiluaq	Arviat	Sanikiluaq	Arviat	Sanikiluaq
Pups	2003 – 2007	-20.13 (0.14)	-20.17 (0.09)	12.75 (0.24)	14.48 (0.12)	3.97 (2.98 – 5.37)	1.60 (1.22 – 2.10)
	2008 – 2012	-20.57 (0.11)	-19.78 (0.15)	15.14 (0.18)	14.54 (0.19)	2.05 (1.54 – 2.82)	1.72 (1.19 – 2.59)
	2013 – 2017	-20.49 (0.20)	-20.54 (0.30)	15.83 (0.22)	14.60 (0.31)	2.39 (1.59 – 3.66)	1.82 (0.81 – 4.88)
Juvenile	2003 – 2007	-20.34 (0.12)	-20.05 (0.11)	15.72 (0.17)	14.89 (0.09)	2.68 (2.02 – 3.63)	3.06 (1.63 – 6.25)
	2008 – 2012	-20.60 (0.10)	-20.07 (0.11)	15.72 (0.08)	14.37 (0.16)	0.75 (0.55 – 1.06)	1.24 (0.92 – 1.70)
	2013 – 2017	-20.62 (0.18)	-19.86 (0.44)	16.26 (0.11)	14.84 (0.34)	0.71 (0.45 – 1.15)	0.88 (0.56 – 1.47)
Adult	2003 – 2007	-19.96 (0.11)	-19.51 (0.10)	15.73 (0.15)	14.76 (0.13)	2.25 (1.68 – 3.04)	1.42 (1.03 – 2.01)
	2008 – 2012	-20.22 (0.07)	-19.84 (0.15)	15.83 (0.22)	14.40 (0.19)	1.02 (0.81 – 1.29)	1.68 (1.09 – 2.67)
	2013 – 2017	-20.37 (0.08)	-19.45 (0.15)	16.30 (0.07)	15.72 (0.25)	0.68 (0.51 – 0.92)	2.06 (1.38 – 3.22)

Table 2.3. Stable isotope ratio ($\delta^{13}C$ and $\delta^{15}N$, mean ± SE) and isotopic niche breadth (mode of Bayesian ellipse areas and 95% credible intervals) from liver of ringed seals sampled in Arviat and Sanikiluaq, Nunavut during fall 2003 – 2017.

Age	Time period	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)		Niche breadth (‰²)	
		Arviat	Sanikiluaq	Arviat	Sanikiluaq	Arviat	Sanikiluaq
Pups	2003 – 2007	-19.94 (0.13)	-19.02	15.32 (0.20)	15.6	3.71 (2.80 – 4.93)	-
	2008 – 2012	-20.46 (0.09)	-20.10 (0.24)	16.21 (0.10)	15.10 (0.20)	0.63 (0.42 – 0.97)	0.25 (0.18 – 0.49)
	2013 – 2017	-20.44 (0.21)	-20.12 (0.11)	16.32 (0.15)	15.03 (0.17)	1.51 (1.02 – 2.33)	0.71 (0.54 – 0.91)
Juvenile	2003 – 2007	-20.32 (0.10)	-19.44 (0.14)	15.26 (0.29)	15.23 (0.12)	3.14 (2.40 – 4.19)	0.67 (0.55 – 1.01)
	2008 – 2012	-20.27 (0.18)	-19.65 (0.18)	16.41 (0.12)	15.35 (0.17)	0.79 (0.47 – 1.41)	1.18 (0.98 – 1.91)
	2013 – 2017	-20.81 (0.10)	-19.67 (0.32)	16.41 (0.10)	15.40 (0.19)	0.72 (0.45 – 1.14)	1.33 (1.01– 1.63)
Adult	2003 – 2007	-20.19 (0.11)	-19.41 (0.19)	15.75 (0.21)	15.76 (0.16)	3.09 (2.32 – 4.20)	1.56 (1.14 – 1.91)
	2008 – 2012	-20.23 (0.10)	-19.84 (0.14)	16.67 (0.08)	15.29 (0.14)	1.03 (0.78 – 1.39)	1.24 (1.09 – 1.56)
	2013 – 2017	-20.64 (0.21)	-19.27 (0.17)	16.48 (0.07)	16.13 (0.29)	0.68 (0.51 – 0.91)	2.78 (1.79 – 3.22)

Figures

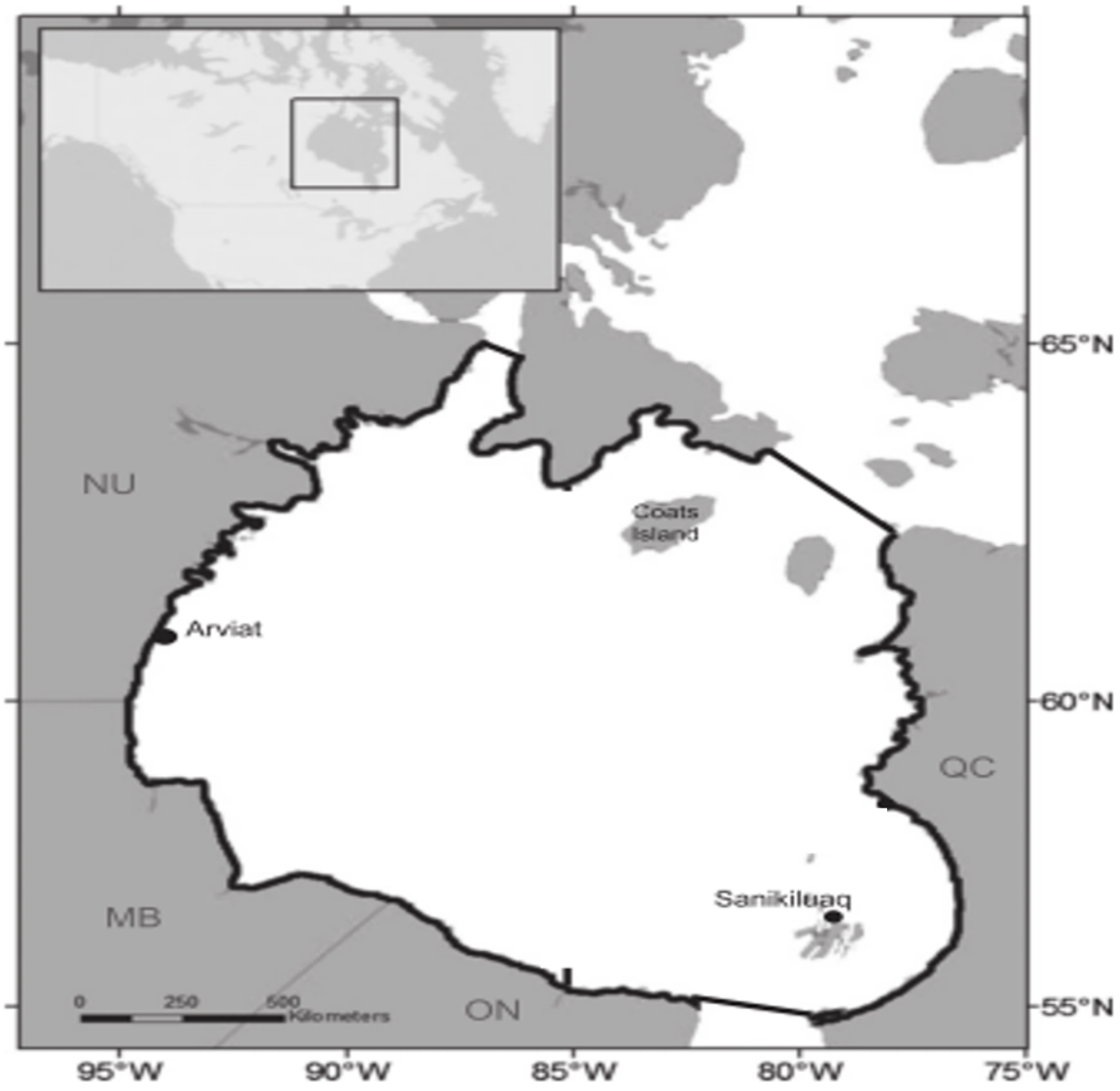

Figure 2.1. Hudson Bay study area with Arviat and Sanikiluaq identified where seal samples were collected in the fall from 2003 – 2017. Modified from Young and Ferguson (2014).

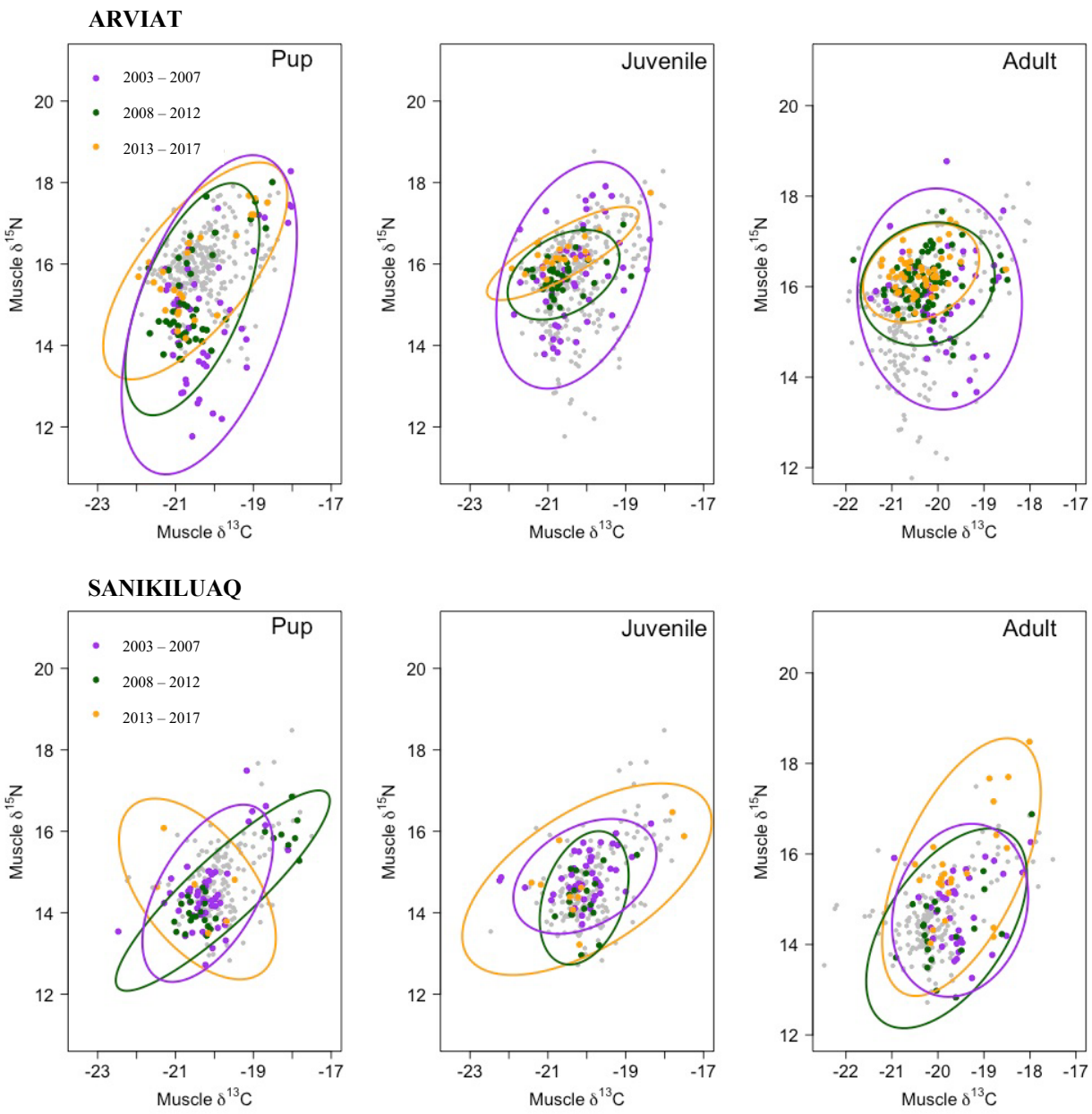

Figure 2.2. Isotopic niche biplot of δ13C and δ15N for ringed seal muscle sampled in Arviat (top row) and Sanikiluaq (bottom row) from 2003 – 2017 separated by age class and periods. Purple represents 2003 = 2007, green represents 2008 – 2012 and yellow represent 2013 – 2017. Gray dots represent the entire population of ringed seals.

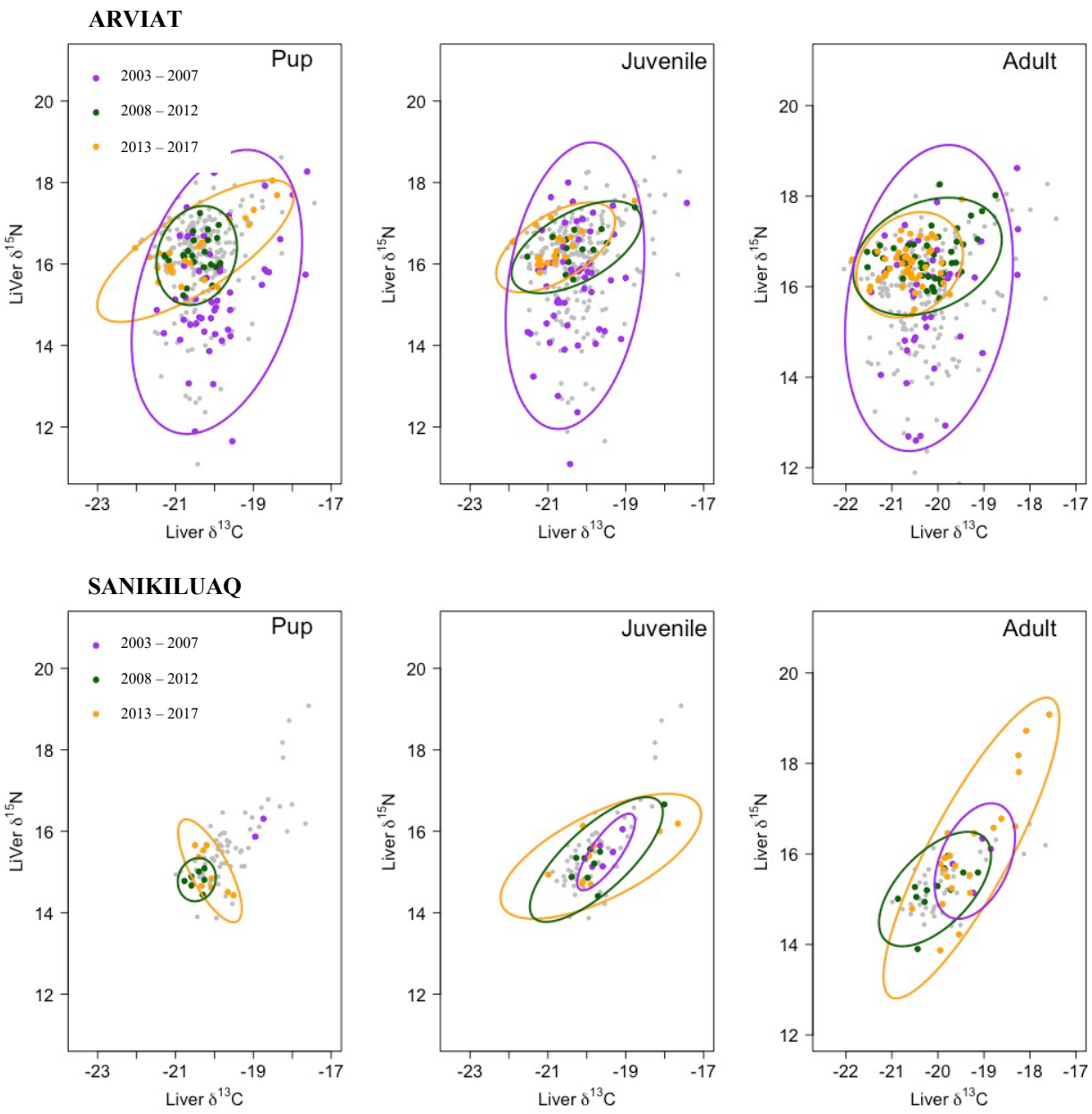

Figure 2.3. Isotopic niche biplot of δ13C and δ15N for ringed seal liver sampled in Arviat (top row) and Sanikiluaq (bottom row) from 2003 – 2017 separated by age class and periods. Purple represents 2003 = 2007, green represents 2008 – 2012 and yellow represent 2013 – 2017. Gray dots represent the entire population of ringed seals.

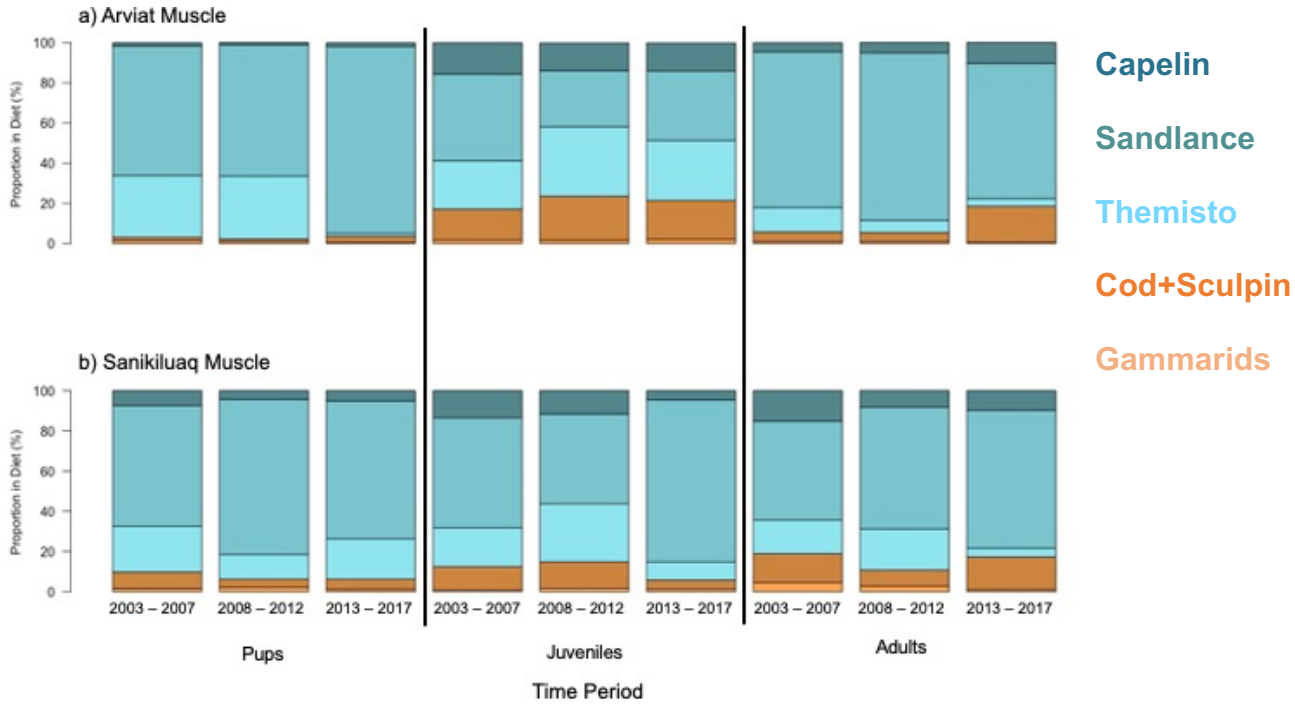

Figure 2.4. Mean estimate diet proportions (%) of muscle MixSIAR prey portions of ringed seal age classes sampled in Arviat (a) and Sanikiluaq (b) from 2003 – 2017.

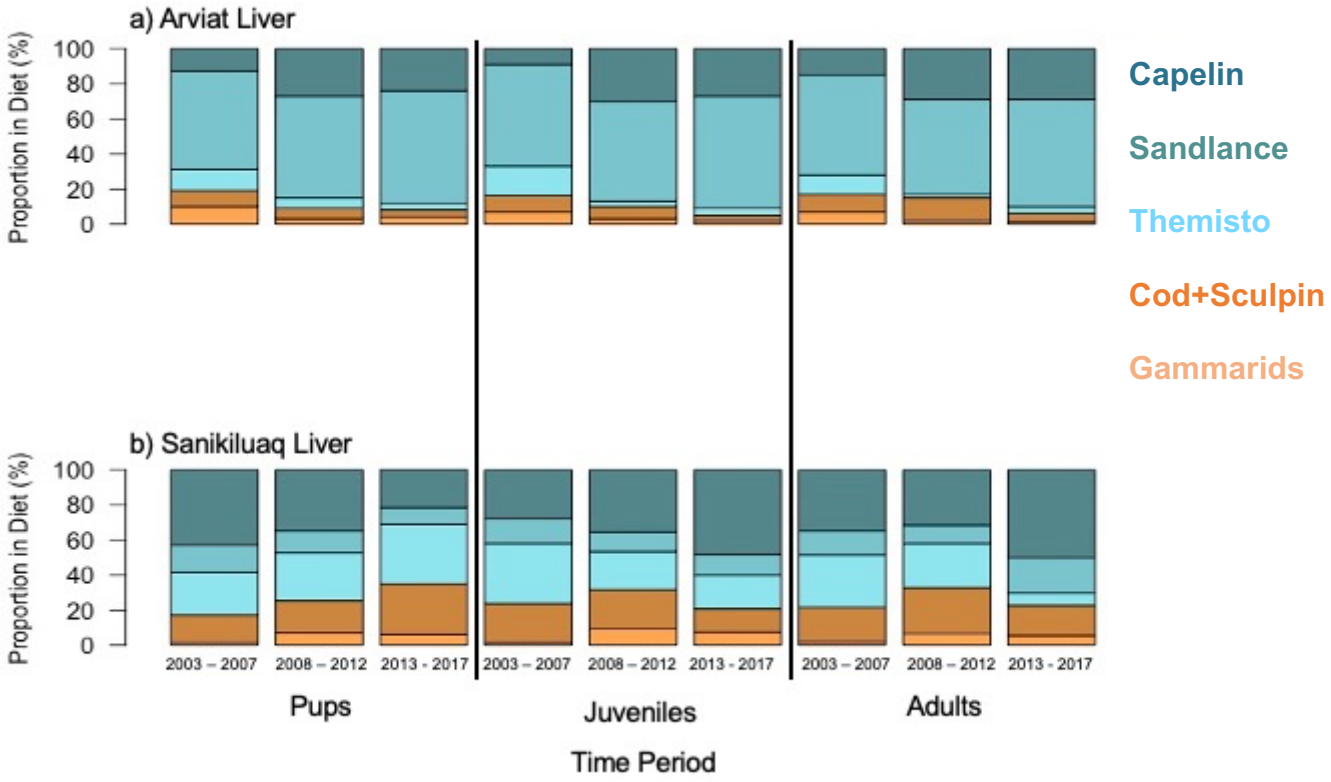

Figure 2.5. Mean estimate diet proportions (%) of liver MixSIAR prey portions of ringed seal age classes sampled in Arviat (a) and Sanikiluaq (b) from 2003 – 2017.

Connecting Statement

The previous chapter provides population level insights into the dietary patterns of ringed seals in Hudson Bay and supports the hypothesis that ringed seals are a generalist foraging species that has high flexibility. The next chapter investigates intrapopulation patterns; that is, are individuals within the population all generalists? Alternately, do foraging patterns of individuals display a degree of individual specialization and dietary plasticity? Conducting stable isotope analyses on a tissue that grows chronologically allows for examination of the consistency of diet measures within and between individuals of the same age and sex class.

Chapter 3: High inter-individual diet variation in ringed seals (*Pusa hispida*) revealed using stable isotope ratios from chronological sections of vibrissae

Abstract

Understanding the niche variation within populations is required to assess whether a population is comprised of individual specialists consuming different prey types or individual generalists. I examined inter-individual niche variation using chronological vibrissae in 42 ringed seals (*Pusa hispida*) sampled during 2006-2010 from Sanikiluaq, Nunavut, Canada. Samples were analyzed to examine the effects of age, sex and individual on diet specialization using carbon and nitrogen stable isotope ratios. I determined that total niche width was broader among adult seals compared to juveniles. Notably, the between-individual component explained more variance (88%) in the total niche width, indicating a high degree of individual specialization. Pups primarily consumed invertebrate prey (56%), whereas adults consumed less than 40% invertebrates and predominantly targeted forage fish species (69%). Adult male seals consumed the highest proportion of cod+sculpin (18%) compared to the other age classes. Diets for all seals combined showed high proportion of Themisto (29%) and sand lance (17%). Adult females had the highest proportion (32%) of sand lance in their diet , 15% higher than all seals combined and other age classes. The high intra-individual consistency observed in dietary proportions suggests consistent foraging strategies that differ from those of other conspecifics. These findings hold particular significance in the context of predicted sea-ice decline in Hudson Bay, providing a valuable reference point for future climate-mediate ringed seal foraging studies.

Keywords: diet consistency, individual specialization, stable isotopes, ringed seal, vibrissae

Introduction

Optimal foraging theory suggests that individuals will use strategies to maximize their net energy intake; however, this will vary based on age, sex, and body size (Sih and Christensen 2001). Inividuals within a population may specialize on specific resources, leading to variability in dietary consumption among individuals within a population (Van Valen 1965). Within populations, individuals consume a narrow portion of resources compared to the population which exists to minimize intraspecific competition resulting in the population niche variation (Van Valen 1965; Roughgarden 1972). When great variation exists between individuals represented by a low within individual component it suggests that individual predators are using different proportions of resources within the populations' niche (WIC; Bolnick et al. 2005; Newsome et al. 2015). Within age classes, dietary specialization of conspecifics has been observed across multiple taxa (Bolnick et al. 2002; Woo et al. 2008; Thiemann et al. 2011; Matich and Heithaus 2015; Yurkowski et al. 2016). A population could either be specialist, where all the individuals are feeding on a single and same prey type (i.e., have a narrow total niche breadth), or a generalist population (i.e. wide total niche breadth; Bolnick et al. 2003; Bearhop et al. 2004). Within generalist populations, individuals could either be consuming a wide variety of prey taxa and, thus, also have a wide individual niche breadth (high WIC), or each individual could be partitioning the population niche by consuming differing proportions of prey taxa compared to other conspecifics, resulting in a wide population niche breadth but narrow individual niche breadths (Van Valen 1965, Bolnick et al. 2003, Svanback and Bolnick 2005).

Consumers have complex life cycles where ontogenetic diet shifts and differences between sexes and ages have been documented (Polis 1984; Werner and Gilliam 1984). Demographic

differences within a species explain a large portion of the variability in a consumer's use of resources (Rudolf and Rasmussen 2013). The age structure (e.g., pups, juvenile, and adult age classes) in a generalist predator population influences food web and ecosystem structure (Rudolf and Lafferty 2011). Most predators shift from generalists as subadults to specialists as adults (Werner and Gilliam 1984). Ontogenetic generalist consumers are more resilient and are more likely to survive dramatic changes in available prey types, whereas an ontogenetic specialist consumer population may be more sensitive to the removal of a prey species which can potentially result in extirpation of individuals (Bolnick et al. 2003; Rudolf and Lafferty 2011).

Predators are likely to encounter a variety of prey types that they will either consume or continue to search for other prey types (MacArthur and Pianka 1966; Araujo et al. 2011). An individual's dietary niche will be dependent on choices made while foraging and ultimately, their foraging opportunities (Bolnick et al. 2003). Foraging opportunities will vary as resources within ecosystems become available or limited within the year in response to environmental conditions. Consumers can modify their behaviour and resource use in relation to these environmental conditions (Polis and Strong 1996). Flucuations of high and low energy resource availabilities persist in a diversity of ecosystems ranging from Arctic marine to terrestrial communities (Rooney and McCann 2012; McMeans et al. 2013). Both intra- and inter-annual variation in a predator's dietary composition may reflect changes in feeding preferences, biology, or environmental conditions resulting in altered prey availability, quantity, or quality. Thus, resource variability, habitat coupling, and the dynamics of an entire food web can change seasonally due to consumers switching to a more abundant resource during productive periods and will influence the niche variation within a population (McMeans et al. 2013).

Ringed seals have been previously described as a generalist consumer that may switch their diet and foraging habits in relation to season and prey availability (Thiemann et al. 2007; Chambellant et al. 2012; Young and Ferguson 2013). Historically, Arctic cod (*Boreogadus saida*) were dominant prey types in many Arctic areas (Lowry et al. 1980; Smith 1987; Wathne et al. 2000). It is thought that in Hudson Bay, Arctic cod have shifted northwards as depicted in seabird diets (Gaston and Elliott 2014). In Hudson Bay, analysis of seal stomach contents has shown that sand lance (*Ammodyotes spp*.) were the most dominant prey type, while Arctic cod and capelin (*Mallotus villous)* were also important prey types in harvested ringed seal stomachs between 1991 and 2006 (Chambellant et al. 2013). Patterns in stable isotope ratios (Young and Ferguson 2013; 2014) and fatty acid composition (Thiemann et al. 2006; Young and Ferguson 2013) have been used to reflect seasonal and spatial differences in ringed seal biomarkers in Hudson Bay. There have been documented diet composition differences between age-classes and geographic locations (Hobson et al. 1996; Thiemann et al. 2007; Young et al. 2010). Recently, Yurkowski et al. (2016b) highlighted total ringed seal niche breadth decreased with latitude, possibly because there was more ecological opportunity in the southern extent of the ringed seals range. With their wide distribution and presence in a variety of Arctic and sub-Arctic habitats, understanding diet shifts in ringed seals can help elucidate energy transfer within the Arctic marine food web. Thus, chronological estimations of ringed seal diet composition in Hudson Bay can provide quantified insights into the foraging strategies of this predator species in a heterogeneous marine environment dealing with resource fluctuations captured in the stable isotope ratios in the predator's tissues.

Biomarkers, such as stable isotope ratios of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$), have provided long-term characterization of the feeding ecology of ringed seals (Young and Ferguson

2013). The timeframe that stable isotope ratios reflect is tissue-dependent (Hobson et al. 1996). Inert tissues, such as vibrissae provide an opportunity to chronologically sample the tissue to provide a timeline of diet composition becaused these keratinised tissues document the stable isotope ratio for individuals at the time of growth and are inert once grown (Cherel et al. 2009; Newsome et al. 2010). This timeline allows for intra-individual diet comparisons and reveal if individual ringed seal diet composition is consistent or variable over time. The growth rates of phocid seal vibrissae are unclear, but approximately 2 mm/week for harbour seals (Greaves et al. 2004; Zhao and Schell 2004; Stegall et al. 2007; Tyrrell et al. 2013). Thus, vibrissae length up to 76 mm can represent up to 40 weeks and can be used to determine intra-individual dietary variation. Lowther et al. (2017) suggested that vibrissae grow and shed variably, meaning an individual can retain the same vibrissae for longer than a year, and that there is no complete turnover of vibrissaes during the spring molt period, making vibrissae a useful tissue for examining diet consistency as they are grown sequently (Cherel et al. 2009).

The purpose of this study is to determine the degree of individual specialization in ringed seal diet compostion using stable isotope (SI) ratios of carbon and nitrogen in chronologically sampled vibrissae in eastern Hudson Bay. To test the niche variation hypothesis, I predicted that ringed seals would exhibit inter-individual diet composition, a high between individual variation component, as generalist predators foraging in a heterogeneous marine environment. I predicted that ringed seal vibrissae SI ratios will show low within-individual diet variation within age-classes, indicating diet consistency. I also predicted that there would be differences in the degree of ringed seal individual specialization and diet consistency among age classes, with juveniles have a more plastic diet compared to adults that could be more specialized.

Methods

Field Collection

Field work was conducted in the open water period (July – October) of 2006 – 2010 around Sanikiliuaq, Belcher Islands, Nunavut, Canada (79.23 W, 56.53 N). Seals were live captured using monofilament nets (28 cm mesh size) in shallow water, and manually restrained for morphometric measurements (body mass, length, girth), tissue collection (vibrissae), and fitted with satellite transmitter (Luque et al. 2014). During processing, a single vibrissae from each individual was plucked, including the follicle, and stored in a whirl-pak bag for laboratory analysis. The seals were visually assessed for sex, and age was determined by counting the number of alternating light and dark claw annuli (McLaren 1958). Individual ringed seals were then grouped into age class categories following sexual maturity: adults ≥6 years of age, juveniles 1–5 years of age, and pups aged 0 (McLaren 1958). The handling time was typically less than 25 minutes and occurred near the capture location. Handling was approved and conducted under the Fisheries and Oceans Animal Care Protocol (FWI-ACC-2005-001, 3007-008, 2008-003, 2009-003, 2010-006) and DFO Licence to Fish for Scientific Purposes (S-05/06 to 09/10-1006-NU).

Based on previous ringed seal stomach content analyses in Hudson Bay, potential prey items included pelagic and benthic primary consumers and zooplanktivores, such as *Mysis sp*., gammrids, *Themisto libellul*a, arctic cod, capelin, sand lance, squid (*Gonatus sp.,*) and sculpin (*Cottoidea sp.,* Chamebellant 2012; Chambellant et al. 2013). Prey items were collected via nets and parental prey deliveries to seabird chicks (June–September) in Sanikiluaq and Coats Island, Nunavut by local hunters, and by stomach contents used in Provencher et al. (2012). I used stable isotope ratios of prey types for ringed seal diet estimation that were previously used in seabird diet

investigations (Provencher et al. 2012). Prey samples were freeze dried for 48 h and ground with a motor and pestle. All prey samples were lipid extracted following the modified Blight & Byer (1959) method using a chloroform:methonal solvent with a 2:1 ratio. A complete detail of the modified lipid extraction is outlined in Logan et al. (2008). Approximately 0.5 mg of the powdered prey sample was sealed into tin boats for stable isotope analysis.

Lab Analysis

To quantify carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in vibrissae, vibrissae were rinsed once with a 2:1 chloroform:methanol solution to remove surface contaminants. Cleaned vibrissae were then subsampled into 2 mm segments using nail clippers and sealed into tin boats for isotopic analysis. Carbon and nitrogen isotope ratios were determined using a mass spectrometer system, where seal vibrissae carbon and nitrogen isotope ratios were determined using a Carlo Erba elemental analyzer (NC 2500; Carlo Erba, Milan, Italy) interfaced with a Finnegan Delta Plus XL mass spectrometer (Carnegie Institution of Washington); and prey samples were combusted using a continuous flow isotope ratio mass spectrometer (Delta V Plus; Thermo Scientific) interfaced with an elemental analyzer (ECS 4010; Costech Instruments) and connected via a Conflo IV interface (Thermo Scientific). Stable isotope ratios are in delta (δ) notation using the equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

Where X refers to $\delta^{13}C$ or $\delta^{15}N$, and R refers to the ratio of heavy to light isotopes ratios of ^{13}C:^{12}C or ^{15}N:^{14}N. Both precision and accuracy were assessed using replicates of standard reference material (USGS 40 and USGS41a) spaced throughout runs and was determined to be $\leq 0.28‰$ for $\delta^{13}C$ and $\leq 0.16‰$ for $\delta^{15}N$. Every tenth seal liver sample was run in duplicate resulting in standard

deviations ranging from 0.01-0.66‰ for $\delta^{13}C$ and 0.0-0.70‰ for $\delta^{15}N$. Carbon to Nitrogen ratios (C:N) were inspected and there was likely no added variation in $\delta^{13}C$ due to higher lipid content as all samples were less than 3.51 (Post et al. 2007). The standards used were Vienna-Pee Dee Belemnite limestone (V-PDB) for carbon and atmospheric N_2 for nitrogen.

Statistical Analyses

To test the effects of four explanatory variables: age, sex, year, size (length) with individual seal ID, seal, being a random effect. I ran general linear mixed effect models on both $\delta^{13}C$ and $\delta^{15}N$ separately. The first model included all seals and both age and sex were determined to be important explanatory variables. Therefore, I conducted separate analyses by age classes and sex (e.g. adult females, juvenile females, adult males, juvenile males) with individual ID as a random effect in the models. I used Akaike Information criterion to determine model rank and select the optimal model. All models were assessed for normality and heteroscedasticity of residuals using normal quantile-quantile plots and residual fitted value plots, respectively. For each age/sex class and stable isotope ratio, the most optimal model was selected and then used in mixed-model variance component analysis in the random effect (seal ID, 'seal') term to estimate the variability in total niche breadth that was explained by intercept variability (intra-individual variability) and residual variability (inter-individual variability;Roughgarden 1972). The variance components for carbon and nitrogen were summed, as were residual components to calculate total niche breadth (Newsome et al. 2009).

Diet Modeling

The Bayesian isotope mixing model MixSIAR (Stock and Semmens 2016) was used to quantitatively estimate the relative contribution of prey types in the diet for each vibrissae segment, and then averaged for comparison between individuals. To determine diet proportion, prey types were clumped together when their isotopic ratios could not be independently distinguished for a total of six possible prey types (seperating out benthic and pelagic prey and low and high trophic levels) for the model. The prey type groups I used were *Themisto libellula* (mean ± SD of 7 individuals: δ^{15}N= 8.4 ± 0.3‰, δ^{13}C = -23.0 ± 0.2‰), capelin (mean ± SD of 46 individuals: δ^{15}N= 13.7 ± 0.8‰, δ^{13}C = -19.8 ± 1.1‰), sand lance (mean ± SD of 47 individuals : δ^{15}N= 12.7 ± 1.4‰, δ^{13}C = -21.0 ± 1.2‰), *Gammarus* sp. (mean ± SD of 4 individuals: δ^{15}N= 9.7 ± 0.3‰, δ^{13}C = -18.1 ± 0.6‰), squid species (mean ± SD of 12 individuals: δ^{15}N= 11.1 ± 0.4‰, δ^{13}C = -19.3 ± 0.5‰), and cod+sculpin (mean ± SD of 61 individuals : δ^{15}N= 14.9 ± 0.7‰, δ^{13}C = -19.2 ± 0.6‰), where cod+sculpin represented samples of primarily Greenland cod (*Gadus ogac*), arctic cod and sculpin, that had overlapping isotope ratios not significantly different. Analysis was limited to these groupings to assist in model performance (Phillips et al. 2014). The groups included in this study follow prey groups used by Yurkowski et al. (2016b) to investigate ringed seal niches in Chesterfield Inlet, Nunavut.

To account for trophic discrimination, species-specific trophic discrimination factors from harp seal vibrissae measured in Hobson et al. (1996) were used for both carbon (-3.2±0.6 ‰) and nitrogen (-2.8±0.3 ‰). I used uninformative priors in all our models as they had improved convergence. Models were run with three Markov Chain Monte Carlo chains of 100,000 iterations,

50,000 burn-in, and thinning of 50. The mean of the posterior distribution was used as the most likely proportion of each prey types, which was also calculated in the model output. Gelman-Rubin and Geweke diagnostic tests were used to examine chain convergence. All statistical analyses were performed in R v 3.2.2 (R Development Core Team 2015).

Results

The number of vibrissae segments analyzed for each individual ringed seal varied between 11 and 39, depending on the total vibrissae length, for a total of 1145 analyzed samples (Table 3.1). There were no significant correlations between vibrissae length and age class ($r = 0.156$, $p = 0.2$), sex ($r = 0.122$, $p = 0.3$) or body length ($r = 0.204$, $p = 0.2$). There was a narrow range of carbon $\delta^{13}C$, from -18.8 to -15.8‰, of all vibrissae isotopic values (Table 3.1, Figure 3.1). However, individual vibrissaes varied more for $\delta^{15}N$, ranging from 12.1 to 17.1‰ , $\delta^{15}N$ increased from 13.5‰ to 14.6‰ between pups and juvenile age classes, and up to 15.73‰ in the adult male age class indicating an approximate 1‰ between each age group (Table 3.1, Figure 3.1).

Isotope ratios of ages, sexes, and individuals

Vibrassiae $\delta^{13}C$ values differed between age classes and within each age class, individual $\delta^{13}C$ values differed significantly between sexes ($F_{7,164} = 32.1$, $p = 0.001$). Mean $\delta^{13}C$ values were mostly explained by individual seal ID, but models with only seal ID were not always the best model (Table 3.3). The most inter-individual variation of carbon was observed in the adult age classes (Figure 3.1, Table 3.4). For example, within the adult male group, $\delta^{13}C$ varied within and between individuals, where the maximum value was -14.7‰ and the minimum value was -19.2‰, a range of 4.5‰.

Mean δ^{15}N values differed with age class, sex, year, and individual seal ID (Table 3.2). Within all groups, individual seal ID explained most of the variation leading to a large between individual component (Table 3.4); However, year also had a significant effect for adult females in the optimal model (Table 3.2). For juveniles, individual body length also explained some of the inter-individual variation in nitrogen for females (Table 3.2). Adult males had the highest mean δ^{15}N values and pups had the lowest (Figure 3.1). Within individual vibrissae isotope ratio variation was largest in adult males (Table 3.4), but was also high in adult females. For instance, within one adult female the δ^{15}N ranged from 10.7 to 14.0‰, and among all females δ^{15}N ranged from 10.7 to 17.2‰. The total range between individuals was largest in females, which ranged 6.5‰, adult males 5.3‰, 5.2‰ in juvenile males and 2.4‰ in pups.

Results from the mixed-model variance component analysis revealed that group total between individual variability accounted for more that 85% of the total niche breadth variation in ringed seals of all age/sex groups (Table 3.4). The same pattern was observed for δ^{15}N, and when considering both isotope ratios together to determine the total population niche breadth, the between individual component explained most of the variation. Total intercept variation, a measure of the variation of all samples, for juveniles was similar compared to adults (86% compared to 88% respectively). However, pups had the lowest inter-individual (58%) but this was still greater than intra-individual variation measures (Table 3.4).

Diet composition

Most diet varitaion that was observed with isotopic ratios was explained by inter-individual component of the total trophic niche breadth (Table 3.4), and varied among individuals within the

same age class and sex (Figure 3.2). After trophic fractionation correction, the increase in δ^{15}N values for adult ringed seals reflects a shift in diet from pelagic invertebrates (39 ±11%) for pups to (17± 3%) for adults (Table 3.5; Figure 3.2). Similar to how δ^{13}C varied among age classes, diet also varied by age class and also sex. For females, the composition of diet consisting of *Themisto* decreased, and sand lance increased from the juvenile to adult age class. For males, the diet composition progressed from invertebrates (gammarids) to predominately fish (capelin) (Table 3.5; Figure 3.2).

Discussion

The inter-individual variation explained most of the variation found in the total niche breadth of all age classes. Total niche breadth increased with age and was consistently larger in males compared to females; δ^{15}N largely contributed to this increase and is reflective in the higher proportion of fish in adult diets versus juveniles and pups. The niche variation hypothesis is supported with the inter-individual variation observed with these ringed seals suggesting that this generalist population is comprised of individuals that exhibit disctinct diets from conspecifics (Bolnick et al. 2003).

The high degree of inter-individual variation recorded here further supports the trend of ringed seal populations at low latitudes compared to high Arctic latitudes having increased individual dietary specialization (Yurkowski et al. 2016b). Ringed seal diet in Hudson Bay has been examined using both stomach contents (Chambellant et al. 2013) and stable isotopes (Yurkowski et al. 2016b) and show a greater diversity of prey, compared to higher latitudes. Ringed seals, as generalist predators in Hudson Bay, likely have greater inter-individual variation

at the lower latitudes because of high prey diversity available as evident in seal stomach contents (Chambellant et al. 2013). There has been an increase in prey diversity and abundance, particularly forage fish species, capelin and sand lance, in Hudson Bay due to warmer conditions (Tittensor et al. 2010; Wassmann et al. 2011). Altered trophic dynamics with the increase of northward expansions of subarctic and temperate fish affects not only marine mammals but seabird diets (Provencher et al. 2012), thus changing the overall ecosystem structure.

Total niche breadth determined in this study for this southern population of ringed seals is broader compared to populations in northern latitudes, as observed between a region of comparable latitude (Chesterfield Inlet, Nunavut) and a higher latitude region, where ringed seals specialize on arctic cod (Yurkowski et al. 2016a; 2016b). Ringed seals in southern Hudson Bay are therefore considered generalist predators consuming primarily sand lance and also a temperate species, capelin, and to some extent pelagic invertebrates (Chambellant et al. 2013; this study). The most notable ontogenetic pattern seen is the diet switch from marine invertebrates to forage fish between pups, juveniles, and adult seals (Table 3.5). Interestingly, the percentages of capelin and sand lance remained fairly consistent across most age/sex groups, but were higher in adult female. In contrast, *Themisto* was more prevalent in juveniles and pups. Adult diets showed a shift toward a higher proportion of shanny+squid and cod+sculpin rather than to forage fish (Figure 3,1;3.2), indicating a greater benthic influence in the diet.

The proportions of diet represented here with a tissue that grows quickly and inert once grown enables an estimation of of prey types seals were foraging on during the open water period in some of the vibrissae segements. Capelin contributions in the diet are reported here in higher proportions than in Chapter 2 of this thesis, likely due to the fact that the diet estimates for a

segment of this tissue represent one week of diet. Considering the seals were captured near the end of August, many vibrissae segments would represent June – August. The general home range and habitat use of these animals previously showed that seals remained along the eastern shore of Hudson Bay, primarily in the northeastern area (Luque et al. 2014). The higher relative consumption of capelin and sand lance compared to Arctic cod may be an explanation to the document decrease in ringed seals condition (Ogloff et al. 2022). The higher proportion of sand lance and capelin in the diet may not be the leading cause to the decline in body condition, as limited differences in nutritional quality were observed between the three fish species (Pedro et al. 2019) and might suggest that there are no particular prey preferences among ringed seals. Prey are not uniformly distributed throughout the water column, and therefore individual foraging locations (e.g., diving benthically vs. pelagically) may explain some of the isotopic niche variation among seals in our study (Luque et al. 2014). Although there is a lack of evidence for prey preference, ringed seals have been observed to exhibit varying dive strategies and movement tracks in the high Canadian Arctic (Ogloff et al. 2021) and within Hudson Bay (Luque et al, 2014). Foraging location can most often explain differences in individual dietary composition, as prey are often distributed in patches in the heterogeneous marine environment. The movements and foraging behaviour determined through state-space models of the seals used in this study has previously been published (Luque et al. 2014; Fig. 7, Florko et al. 2023), and except for two individual juvenile females, all seals remained in eastern Hudson Bay. Thus, the distinct individual isotope ratios seen in the adult female group are not reflective of distinct foraging locations, but rather partitioning of isotopic niche available to individuals. Other records of marine predators highlight variability in vibrissae isotope ratios between individuals, and is correlated with dive

behaviour (Chilvers 2019). For instance, New Zealand sea lion (*Phocarctos hookeri)* individuals showed consistency in individual repeated isotope ratios but individuals had differing dive patterns (Chilvers 2019). There is limited potential for competition for these resources from other predators, such as bearded seals, as bearded seals are known to primarily feed on benthic food sources (Finley et al. 1983; Crawford et al. 2015), although the effect of interspecific competition cannot be resolved here.

The higher inter-individual variation contributed more to the wider trophic niche breadth than intra-indvidual variation of all age and sex class groups in this study. Similar results were found in other marine mammal species, including elephant seals (*Mirounga angustirostris*) (Hückstädt et al. 2012), sea otters (*Enhydra lutris*) (Newsome et al. 2015), subantarctic fur seals (*Arctocephalus tropicalis*) (Kernaleguen et al. 2012; 2015), and sea lions (Chilvers 2019). Previous individual specialization studies that elucidate high among-individual variation have attributed individual placisity in diet to a diversity of prey sources available (Woo et al. 2008; Newsome et al. 2015; Chilvers 2019). The high degree of inter-individual variation (~88% in all age groups, except pups [59%]) is one of the highest degree of individual specialization that has been observed in wild populations within age and sex classes compared to other marine predators (Kernalegiuen et al. 2012; 2015; Newsome et al. 2015; Chilver 2019).

Using vibrissae stable isotopes allows for research questions regarding intra-individual dietary consistency and potential seasonal diet composition to be investigated. Using closely related pinniped species, growth rates of ringed seal vibrissae can be estimated but little is known about moulting and continuous growth patterns of vibrissae of phocids compared to constant rate, non-shredded vibrissae reported in otariids (Lowther et al. 2017). Ringed seal diets in Hudson Bay

do vary seasonally (Chambellant 2012; Young and Ferguson 2013), but I caution interpreting any seasonal trends directly from these results as the exact date for each vibrissae segment is not known. If the mean growth rate of vibrissae is 2 mm/week, after adjusting for date of capture many of our individuals did show a characteristic oscillation in $\delta^{15}N$ around April –May, the typical timing of the moult in ringed seals at low latitudes (Holst et al. 1999; Young et al. 2015). The likelihood of the variable growth of vibrissae does limit the seasonal interpretations of isotopic ratios but does allow for chronological sampling to assess dietary consistency. Particularly, only one adult male showed strong specialization on a single prey resource, where the diet was consistently >85% Cod + Sculpin (Figure 3.1), whereas all other individuals had a more varied diet with contributions from all included isotopic prey groups (Figure 3.1, Figure 3.2).

In conclusion, this study investigated the individual specialization and temporal consistency of ringed seals using vibrissae isotopic ratios. I found a high degree of individual specialization. Using Bayesian mixing models further supported the individual foraging strategies and ontogenetic shift from consuming mainly pelagic invertebrates to pelagic forage fish. Changing sea ice conditions could be benefiting seals in two ways – increased prey diversity (niche expansion) and reduced predation pressure (limited polar bear access). Thus, increased population size may not need to partition resources to support an increased population of ringed seals (Ferguson et al 2020), it would depend on whether prey are limited (Bolnick et al. 2011). The high degree of between individual variation and broader population total niche breadth recorded here could support the hypothesis of instraspecific competition occurring if prey types are limited (Svanback and Bolnick 2005). These data serve as a baseline for quantified diet estimations that

could be useful in determining diet shifts seasonally and inter-annually. This research confirms that individuals are consistent in their diet.

Literature Cited

Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation. *Ecology Letters*, *14*(9), 948-958.

Bearhop, S., Adams, C. E., Waldron, S., Fuller, R. A., & MacLeod, H. (2004). Determining trophic niche breadth: a novel approach using stable isotope analysis. *Journal of Animal Ecology*, 73(5), 1007-1012.

Bligh, E. G., & Dyer, W. J. (1959). A rapid method of total lipid extraction and purification. *Canadian Journal of Biochemistry and Physiology*, 37(8), 911-917.

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., & Rudolf, V. H. W. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution*, 26,183–192.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A, Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, 161,1–28.

Bolnick, D. I., Yang, L. H., Fordyce, J. A., Davis, J. M., & Svanbäck, R. (2002). Measuring individual-level resource specialization. *Ecology*, *83*(10), 2936-2941.

Chambellant, M., Stirling, I., & Ferguson, S. H. (2013). Temporal variation in western Hudson Bay ringed seal *Phoca hispida* diet in relation to environment. *Marine Ecology Progress Series*, 481, 269-287.

Chambellant, M., Stirling, I., Gough, W. A., & Ferguson, S. H. (2012). Temporal variations in Hudson Bay ringed seal (*Phoca hispida*) life-history parameters in relation to environment. *Journal of Mammalogy*, 93(1), 267-281.

Cherel, Y., Kernaléguen, L., Richard, P., & Guinet, C. (2009). Whisker isotopic signature depicts migration patterns and multi-year intra-and inter-individual foraging strategies in fur seals. *Biology Letters*, *5*(6), 830-832.

Chilvers, B. L. (2019). Whisker stable isotope values indicate long-term foraging strategies for female New Zealand sea lions. *Endangered Species Research*, *38*, 55-66.

Crawford, J. A., Quakenbush, L. T., & Citta, J. J. (2015). A comparison of ringed and bearded seal diet, condition and productivity between historical (1975–1984) and recent (2003–2012) periods in the Alaskan Bering and Chukchi seas. *Progress in Oceanography*, 136, 133-150.

Ferguson, S. H., Yurkowski, D. J., Young, B. G., Fisk, A. T., Muir, D. C., Zhu, X., & Thiemann, G. W. (2020). Comparing temporal patterns in body condition of ringed seals living within their core geographic range with those living at the edge. *Ecography*, *43*(10), 1521-1535.

Finley, K. J., Miller, G. W., Davi, R. A., & Koski, W. R. (1983). A distinctive large breeding population of ringed seals (*Phoca hispida*) inhabiting the Baffin Bay pack ice. *Arctic*,162-173.

Florko, K. R., Shuert, C. R., Cheung, W. W., Ferguson, S. H., Jonsen, I. D., Rosen, D. A., ... & Auger-Méthé, M. (2023). Linking movement and dive data to prey distribution models: new insights in foraging behaviour and potential pitfalls of movement analyses. *Movement Ecology*, *11*(1), 17.

Greaves, D. K., Hammill, M. O., Eddington, J. D., Pettipas, D., & Schreer, J. F. (2004). Growth rate and shedding of vibrissae in the gray seal, *Halichoerus grypus*: a cautionary note for stable isotope diet analysis. *Marine Mammal Science*, *20*(2), 296-304.

Hobson, K. A., Schell, D. M., Renouf, D., & Noseworthy, E. (1996). Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. *Canadian Journal of Fisheries and Aquatic Sciences*, 53(3), 528-533.

Hückstädt, L. A., Koch, P. L., McDonald, B. I., Goebel, M. E., Crocker, D. E., & Costa, D. P. (2012). Stable isotope analyses reveal individual variability in the trophic ecology of a top marine predator, the southern elephant seal. *Oecologia*, *169*, 395-406.

Holst, M., Stirling, I., & Hobson, K.A. (1999). Diet of ringed seals (*Phoca hispida*) on the east and west side of the North Water Polynya, Northern Baffin Bay. Marine Mammal Science, 17, 888-908.

Kernaléguen, L., Arnould, J. P., Guinet, C., & Cherel, Y. (2015). Determinants of individual foraging specialization in large marine vertebrates, the Antarctic and subantarctic fur seals. *Journal of Animal Ecology*, *84*(4), 1081-1091.

Kernaleguen, L., Cazelles, B., Arnould, J. P., Richard, P., Guinet, C., & Cherel, Y. (2012). Long-term species, sexual and individual variations in foraging strategies of fur seals revealed by stable isotopes in whiskers. *PloS one*, *7*(3), e32916.

Logan, J. M., Jardine, T. D., Miller, T. J., Bunn, S. E., Cunjak, R. A., & Lutcavage, M. E. (2008). Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. *Journal of Animal Ecology*, 838-846.

Lowther, A. D., Fisk, A., Kovacs, K. M., & Lydersen, C. (2017). Interdecadal changes in the marine food web along the west Spitsbergen coast detected in the stable isotope composition of ringed seal (*Pusa hispida*) whiskers. *Polar Biology*, *40*, 2027-2033.

Luque, S. P., Ferguson, S. H., & Breed, G. A. (2014). Spatial behaviour of a keystone Arctic marine predator and implications of climate warming in Hudson Bay. *Journal of Experimental Marine Biology and Ecology*, *461*, 504-515.

MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, 100(916), 603-609.

Matich, P., & Heithaus, M. R. (2015). Individual variation in ontogenetic niche shifts in habitat use and movement patterns of a large estuarine predator (*Carcharhinus leucas*). *Oecologia*, 178(2), 347-359.

McLaren, I. A. (1958). The biology of the ringed seal (*Phoca hispida*) in the eastern Canadian Arctic (No. 118). Fisheries Research Board of Canada.

McMeans, B. C., Rooney, N., Arts, M. T., & Fisk, A. T. (2013). Food web structure of a coastal Arctic marine ecosystem and implications for stability. *Marine Ecology Progress Series*, 482, 17-28.

Newsome, S. D., Bentall, G. B., Tinker, M. T., Oftedal, O. T., Ralls, K., Estes, J. A., & Fogel, M. L. (2010). Variation in δ13C and δ15N diet–vibrissae trophic discrimination factors in a wild population of California sea otters. *Ecological Applications*, *20*(6), 1744-1752.

Newsome, S. D., Tinker, M. T., Gill, V. A., Hoyt, Z. N., Doroff, A., Nichol, L., & Bodkin, J. L. (2015). The interaction of intraspecific competition and habitat on individual diet specialization: a near range-wide examination of sea otters. *Oecologia*, 178(1), 45-59.

Newsome, S. D., Tinker, M. T., Monson, D. H., Oftedal, O. T., Ralls, K., Staedler, M. M., ... & Estes, J. A. (2009). Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis). Ecology*, *90*(4), 961-974.

Ogloff, W. R., Anderson, R. A., Yurkowski, D. J., Debets, C. D., Anderson, W. G., & Ferguson, S. H. (2022). Spatiotemporal variation of ringed seal blubber cortisol levels in the Canadian Arctic. *Journal of Mammalogy*, *103*(5), 1208-1220.

Ogloff, W. R., Ferguson, S. H., Fisk, A. T., Marcoux, M., Hussey, N. E., Jaworenko, A., & Yurkowski, D. J. (2021). Long-distance movements and associated diving behaviour of ringed seals (*Pusa hispida*) in the eastern Canadian Arctic. *Arctic Science*, *7*(2), 494-511.

Pedro, S., Fisk, A. T., Ferguson, S. H., Hussey, N. E., Kessel, S. T., & McKinney, M. A. (2019). Limited effects of changing prey fish communities on food quality for aquatic predators in the eastern Canadian Arctic in terms of essential fatty acids, methylmercury and selenium. *Chemosphere*, *214*, 855-865.

Phillips, D. L., Inger, R., Bearhop, S., Jackson, A. L., Moore, J. W., Parnell, A. C., ... & Ward, E. J. (2014). Best practices for use of stable isotope mixing models in food-web studies. *Canadian Journal of Zoology*, *92*(10), 823-835.

Polis, G. A. (1984). Age structure component of niche breadth and intraspecific resource partitioning: can age groups function as ecological species? *The American Naturalist*, 123(4), 541-564

Post, D. M., Layman, C. A., Arrington, D. A., Takimoto, G., Quattrochi, J., & Montana, C. G. (2007). Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*, *152*, 179-189.

Provencher, J. F., Gaston, A. J., Hara, P. O., & Gilchrist, H. G. (2012). Seabird diet indicates changing Arctic marine communities in eastern Canada. *Marine Ecology Progress Series*, 454, 171-182.

Rooney, N., & McCann, K. S. (2012). Integrating food web diversity, structure and stability. *Trends in Ecology and Evolution*, 27(1), 40-46.

Roughgarden, J. (1972). Evolution of niche width. *The American Naturalist*, *106*(952), 683-718.

Rudolf, V. H. W., & Lafferty, K. D. (2011). Stage structure alters how complexity affects stability of ecological networks. *Ecology letters*, 14(1), 75-79.

Rudolf, V. H., & Rasmussen, N. L. (2013). Ontogenetic functional diversity: size structure of a keystone predator drives functioning of a complex ecosystem. *Ecology*, 94(5), 1046-1056.

Semmens, B., Brian, C., Ward, E., Moore, J., Parnell, A., Jackson, A. L., & Inger, R. (2015). MixSIAR: A Bayesian stable isotope mixing model for characterizing intrapopulation niche variation.

Sih, A., & Christensen, B. (2001). Optimal diet theory: when does it work, and when and why does it fail? *Animal Behaviour*, 61(2), 379-390.

Stegall, V. K., Farley, S. D., Rea, L. D., Pitcher, K. W., Rye, R. O., Kester, C. L., & Bern, C. R. (2008). Discrimination of carbon and nitrogen isotopes from milk to serum and vibrissae in Alaska Steller sea lions (*Eumetopias jubatus*). *Canadian Journal of Zoology*, 86(1), 17-23.

Stock, B. C., & Semmens, B. X. (2016). Unifying error structures in commonly used biotracer mixing models. *Ecology*, *97*(10), 2562-2569.

Svanbäck, R., & Bolnick, D. I. (2005). Intraspecific competition affects the strength of individual specialization: an optimal diet theory method. *Evolutionary Ecology Research*, 7(7), 993-1012.

Thiemann, G. W., Iverson, S. J., & Stirling, I. (2007). Variability in the blubber fatty acid composition of ringed seals (*Phoca hispida*) across the Canadian Arctic. *Marine Mammal Science*, 23(2), 241-261.

Thiemann, G. W., Iverson, S. J., Stirling, I., & Obbard, M. E. (2011). Individual patterns of prey selection and dietary specialization in an Arctic marine carnivore. *Oikos*, 120(10), 1469-1478.

Tittensor, D. P., Mora, C., Jetz, W., Lotze, H. K., Ricard, D., Berghe, E. V., & Worm, B. (2010). Global patterns and predictors of marine biodiversity across taxa. *Nature*, *466*(7310), 1098-1101.

Tyrrell, L. P., Newsome, S. D., Fogel, M. L., Viens, M., Bowden, R., & Murray, M. J. (2013). Vibrissae growth rates and trophic discrimination factors in captive southern sea otters (*Enhydra lutris nereis*). *Journal of Mammalogy*, 94(2), 331-338.

Van Valen, L. (1965). Morphological variation and width of ecological niche. *The American Naturalist*, 99(908), 377-390.

Wassmann, P., Duarte, C. M., Agusti, S., & Sejr, M. K. (2011). Footprints of climate change in the Arctic marine ecosystem. *Global change biology*, *17*(2), 1235-1249.

Werner, E. E., & Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*, *15*(1), 393-425.

Zhao, L., & Schell, D. M. (2004). Stable isotope ratios in harbor seal *Phoca vitulina* vibrissae: effects of growth patterns on ecological records. *Marine Ecology Progress Series*, *281*, 267-273.

Tables

Table 3.1. Identification, morphometry, and mean isotope ratios of carbon and nitrogen for 42 ringed seal vibrissae, seals were captured around the Belcher Islands in 2006 -2010.

Group	ID	Capture Date	Mass (kg)	Length (cm)	Girth (cm)	No. of 2 mm vibrissae Segments	δ 13C	SD	δ 15N	SD
Adult Female	ARSQ-2006-0521	06-09-10	95	121.5	123	*11*	-16.6	0.4	16.2	0.2
	ARSQ-2006-0525	06-09-13	55	105	108	*26*	-18.1	0.2	15.7	1.3
	ARSQ-2008-0769	08-09-01	73	129	113	*32*	-17.3	0.2	16.1	0.5
	ARSQ-2008-0783	08-09-01	57	112	107	*30*	-17.8	0.3	15.3	0.8
	ARSQ-2010-0906	10-10-16	59	104	98.5	*32*	-18.3	0.3	12.2	0.8
	ARSQ-2010-0909	10-10-19	53	118	104.5	*30*	-18.2	0.4	12.7	1.0
	ARSQ-2010-0962	10-08-21	43	98	98.5	*29*	-18.6	0.2	14.0	0.7
	ARSQ-2010-0969	10-08-22	37	99.5	90.5	*29*	-18.3	0.3	14.2	0.5
Average			**59**	**111**	**105**	**27**	**-17.9**	**0.28**	**14.54**	**0.72**
Adult Male	ARSQ-2007-0639	07-09-14	67.5	122	115.5	*31*	-17.7	0.2	15.8	0.6
	ARSQ-2008-0767	08-08-30	69	120	120	*39*	-16.7	0.4	17.1	0.7
	ARSQ-2008-0778	08-09-02	73.5	135	117	*33*	-17.8	0.3	16.2	0.5
	ARSQ-2009-0898	09-08-08	37.5	95	97	*28*	-18.5	0.5	13.9	0.5
	ARSQ-2009-0899	09-07-31	60	101.5	104.5	*32*	-15.8	0.7	15.1	0.6
	ARSQ-2009-0905	09-08-09	47	113	98	*28*	-15.8	0.2	17.5	0.2
	ARSQ-2009-0908	09-08-10	54	121	101	*35*	-17.4	0.3	16.1	0.3
	ARSQ-2010-0975	10-08-21	74	118	118	*32*	-18.4	0.4	14.1	0.4
Average			**60**	**116**	**109**	**32**	**-17.3**	**0.38**	**15.73**	**0.48**
Juvenile Female	ARSQ-2006-0528	06-09-14	40	97	97	*28*	-18.1	0.2	13.6	0.7
	ARSQ-2007-0635	07-09-09	49.5	118.5	101	*24*	-17.2	0.2	16.1	0.4
	ARSQ-2007-0642	07-09-17	27	89	79	*18*	-18.3	0.3	15.1	0.4
	ARSQ-2009-0900	09-07-31	31	90.5	90	*27*	-17.5	0.4	13.2	0.9
	ARSQ-2009-0904	09-08-10	33	103	82	*24*	-18.0	0.2	13.4	0.6
	ARSQ-2010-0963	10-08-22	40	99	102	*31*	-16.5	0.6	15.3	1.4
	ARSQ-2010-0966	10-10-18	51	112	102	*29*	-17.8	0.2	14.9	1.1
	ARSQ-2010-0967	10-10-16	55	112	107.5	*29*	-18.2	0.2	14.7	0.8
	ARSQ-2010-0970	10-08-21	36	103	85	*22*	-18.2	0.4	14.1	0.5
	ARSQ-2010-0971	10-08-21	38	97.5	94	*26*	-18.4	0.2	14.2	0.4
	ARSQ-2010-0972	10-08-21	43	98	103	*32*	-17.7	0.4	14.7	0.6
	ARSQ-2010-0973	10-08-21	33	101	87	*32*	-18.1	0.2	12.5	0.8
Average			**40**	**102**	**94**	**27**	**-17.8**	**0.30**	**14.32**	**0.72**

Group	ID	Capture Date	Mass (kg)	Length (cm)	Girth (cm)	No. of 2 mm vibrissae Segments	$\delta^{13}C$	SD	$\delta^{15}N$	SD
Juvenile Male	ARSQ-2006-0529	06-09-15	39	109	92.5	*27*	-17.7	0.2	14.9	0.7
	ARSQ-2007-0641	07-09-17	33	89	88	*27*	-17.1	0.2	16.3	0.4
	ARSQ-2008-0781	08-09-01	36.5	102	97	*27*	-17.4	0.2	15.4	0.3
	ARSQ-2008-0784	08-09-02	35	89	94	*26*	-17.6	0.2	14.7	1.1
	ARSQ-2010-0907	10-10-19	60	103	115	*31*	-18.6	0.3	13.8	0.7
	ARSQ-2010-0964	10-08-22	46	106	101.5	*34*	-18.2	0.1	13.1	0.9
	ARSQ-2010-0968	10-08-21	41	116	95	*25*	-17.8	0.2	14.8	0.6
	ARSQ-2010-0976	10-10-17	46	108	96	*37*	-18.4	0.2	14.0	0.5
Average			42	103	97	29	-17.8	0.2	14.6	0.6
PUPS	ARSQ-2006-0523	06-09-11	26.2	89	84.5	*18*	-17.8	0.7	14.7	1.2
	ARSQ-2006-0524	10-10-19	16.2	75	70	*30*	-18.8	0.3	12.9	0.7
	ARSQ-2006-0527	06-09-14	30	99	83	*29*	-18.2	0.2	12.8	0.7
	ARSQ-2007-0638	07-09-14	24	78	76	*18*	-17.8	0.1	12.1	0.5
	ARSQ-2007-0640	08-08-31	26.5	91	84	*27*	-17.8	0.2	13.6	0.6
	ARSQ-2007-0640	09-07-31	26.5	91	84	*20*	-16.7	0.7	15.2	0.5
Average			25	87	80	24	-17.8	0.3	13.5	0.7

Table 3.2. Variation in nitrogen isotope ratios from mean vibrissae segemnets from 42 ringed seals captured around the Belcher Islands, Nunavut in 2006- 2010 explained by covariates in generalized linear mixed effect model selection. These models related the nitrogen isotope ratios to age, sex and year of each individual where individual ID was a random effect. Models are ranked by Akaike weights, K is the number of estimated parameters, and Log L is the maximized log-likelihood of the model, AICc is selection criteria.

Model	K	LogL	AICc	ΔAIC	AICw
All Seals					
age + year + sex |seal	7	-62.039	141.372	0.000	0.656
age + year + sex + length |seal	8	-62.017	144.398	3.027	0.144
age | seal	5	-66.924	145.515	4.143	0.083
year | seal	4	-68.565	146.211	4.839	0.058
|seal	3	-70.701	148.033	6.661	0.024
age + sex + length |seal	7	-65.766	148.826	7.454	0.016
sex | seal	4	-70.006	149.093	7.721	0.014
age + sex | seal	8	-65.233	150.829	9.458	0.006
Adult Females					
year +|seal	4	-9.498	40.329	0.000	0.483
|seal	3	-14.218	40.436	0.108	0.458
girth +|seal	4	-11.796	44.925	4.597	0.049
length +|seal	4	-13.312	47.958	7.629	0.011
year + length +|seal	5	-9.323	58.645	18.317	0.000
length + girth, random +|seal	5	-11.675	63.350	23.021	0.000
year + length + girth + |seal	6	-8.952	113.904	73.576	0.000
Adult Males					
|seal	3	-12.898	37.795	0.000	0.949
girth +|seal	4	-11.806	44.945	7.150	0.027
year +|seal	4	-12.403	46.140	8.345	0.015
length +|seal	4	-12.855	47.044	9.249	0.009
length + girth, random +|seal	5	-11.007	62.014	24.218	0.000
year + length +|seal	5	-12.403	64.805	27.010	0.000
year + length + girth + |seal	6	-10.840	117.679	79.884	0.000
Juvenile females					
length +|seal	4	-11.042	36.750	0.000	0.704
girth +|seal	4	-12.719	40.105	3.354	0.132
|seal	3	-15.450	40.328	3.578	0.118
length + girth, random +|seal	5	-10.962	43.924	7.174	0.020
year + length +|seal	5	-11.018	44.036	7.286	0.018
year +|seal	4	-15.418	45.504	8.753	0.009
Model	**K**	**LogL**	**AICc**	**ΔAIC**	**AICw**

year + length + girth + |seal	6	-10.946	54.892	18.142	0.000
Juvenile males					
|seal	3	-10.769	33.537	0.000	0.850
year +|seal	4	-8.033	37.399	3.862	0.123
length +|seal	4	-10.014	41.361	7.823	0.017
girth +|seal	4	-10.522	42.377	8.840	0.010
year + length +|seal	5	-7.947	55.895	22.358	0.000
length + girth, random +|seal	5	-8.843	57.686	24.149	0.000
year + length + girth + |seal	6	-7.331	110.662	77.125	0.000
Pups					
year + length + girth + |seal	1	-5.420	-61.170	0.000	0.978
|seal	4	-9.030	36.070	97.230	0.001
length + girth, random +|seal	6	-6.770	61.530	122.700	0.001
length +|seal	7	-7.740	63.480	124.650	0.000
girth +|seal	8	-7.740	63.480	124.650	0.000
year +|seal	3	-9.000	66.000	127.170	0.000

Table 3.3. Variation in carbon isotopic ratios from mean vibrissae from 42 ringed seals captured around the Belcher Islands, Nunavut in 2006- 2010 explained by covariates in generalized linear mixed effect model selection. These models related the isotopic ratios to age, sex and year of each individual where individual ID was a random effect. Models are ranked by Akaike weights, K is the number of estimated parameters, and Log L is the maximized log-likelihood of the model, AICc is selection criteria.

Model	K	LogL	AICc	ΔAIC	AICw
All Seals					
|seal	3	-44.740	96.112	0.000	0.318
age + year + sex |seal	4	-43.550	96.181	0.069	0.307
year | seal	4	-43.679	96.439	0.327	0.270
age | seal	5	-44.044	99.754	3.642	0.051
age + year + sex |seal	7	-41.813	100.920	4.809	0.029
age + sex | seal	7	-42.816	102.925	6.813	0.011
age + year + sex + length |seal	7	-42.816	102.925	6.813	0.011
sex |seal	8	-42.144	104.651	8.539	0.004
Adult Females					
girth |seal	4	-0.941	23.216	0.000	0.794
|seal	3	-7.428	26.856	3.641	0.129
length |seal	4	-3.586	28.504	5.289	0.056
year |seal	4	-4.577	30.488	7.272	0.021
length + girth |seal	5	-0.566	41.132	17.916	0.000
year + length | seal	5	-1.014	42.029	18.813	0.000
year + length + girth |seal	6	-0.412	96.824	73.609	0.000
Adult Males					
|seal	3	-11.311	34.621	0.000	0.971
girth +|seal	4	-11.231	43.794	9.173	0.010
length +|seal	4	-11.253	43.840	9.219	0.010
year +|seal	4	-11.310	43.952	9.331	0.009
length + girth, random +|seal	5	-11.228	62.456	27.835	0.000
year + length +|seal	5	-11.252	62.505	27.884	0.000
year + length + girth + |seal	6	-11.222	118.443	83.822	0.000
Juvenile females					
|seal	3	-8.552	26.532	0.000	0.814
year +|seal	4	-8.516	31.699	5.168	0.061
length +|seal	4	-8.516	31.700	5.168	0.061
girth +|seal	4	-8.541	31.749	5.217	0.060
year + length +|seal	5	-8.484	38.968	12.436	0.002

length + girth, random +|seal	5	-8.512	39.024	12.492	0.002
Model	**K**	**LogL**	**AICc**	**ΔAIC**	**AICw**
year + length + girth + |seal	6	-8.476	49.953	23.421	0.000
Juvenile male					
|seal	3	-5.473	22.946	0.000	0.790
year +|seal	4	-2.286	25.906	2.960	0.180
length +|seal	4	-4.468	30.269	7.323	0.020
girth +|seal	4	-5.251	31.835	8.890	0.009
length + girth, random +|seal	5	-1.140	42.280	19.334	0.000
year + length +|seal	5	-2.088	44.175	21.230	0.000
year + length + girth + |seal	6	0.999	94.002	71.056	0.000
Pups					
year + length + girth + |seal	6	-1.080	-69.830	0.000	1.000
|seal	3	-5.710	29.420	99.250	0.000
length + girth, random +|seal	4	-5.230	58.470	128.300	0.000
length +|seal	4	-5.680	59.370	129.200	0.000
girth +|seal	4	-5.680	59.370	129.200	0.000
year +|seal	4	-5.700	59.410	129.240	0.000

Table 3.4. Total niche breadth of ringed seals captured between 2006 – 2010 from the Belcher Islands, Nunavut. Niche breadth is representated by the calculated variance component analysis of the most optimal model from Tables 3.2 and 3.3 for all ringed seals and each demographic group separately. Total niche breadth is the sum of both the intercept and residual variances for $\delta^{15}N$ and $\delta^{13}C$. Total intercept variance represented the variance between individuals and the total residual variance is within individual.

Group	n	*δ*15N		*δ*13C		Total Intercept (BIC)	Total Residual (WIC)	Total Niche breadth (BIC + WIC)
		Intercept Variance	Residual Variance	Intercept Variance	Residual Variance			
All seals	42	1.47	0.21	0.99	0.14	2.46	0.35	2.81
Adult Females	8	0.74	0.10	0.09	0.02	0.83	0.12	0.95
Adult Males	8	1.12	0.16	0.38	0.05	1.50	0.21	1.71
Juvenile Females	12	0.47	0.07	0.27	0.04	0.74	0.11	0.85
Juvenile Males	8	0.87	0.12	0.23	0.03	1.00	0.15	1.15
Pups	6	0.36	0.14	0.13	0.22	0.49	0.36	0.85

Table 3.5. Mean estimated diet proportions ± SD for each ringed seal demographic group calculated from vibrissae segments from 42 individual ringed seals captured around the Belcher Islands, Nunavut in 2006- 2010.

Group	n	Themisto (%)	Sand lance (%)	Capelin (%)	Squid & Shanny (%)	Gammarids (%)	Cod & Sculpin (%)
All Seals	42	29±9	17±11	13±4	13±5	16±10	12±8
Adult Female	8	17±9	32±11	13±8	12±8	15±7	12±9
Adult Male	8	19±2	17±10	16±10	16±7	15±10	18±7
Juvenile Female	12	32±9	17±11	16±9	11±5	17±10	11±5
Juvenile Male	8	30±8	17±9	12±8	10±8	16±3	10±6
Pups	6	39±11	16±12	10±7	8±6	17±11	8±11

Figures

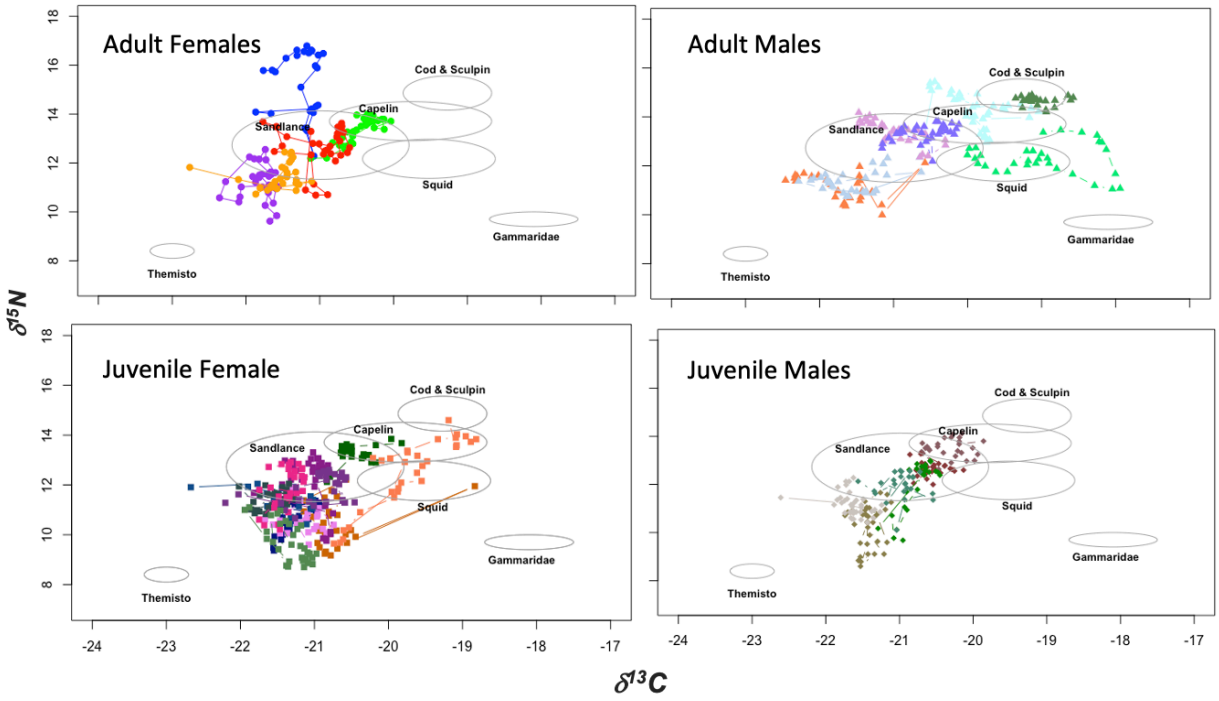

Figure 3.1. Isotopic biplot $\delta^{13}C$ and $\delta^{15}N$ of chronological ringed seal vibrissae segments separated by age and sex categories. Each colour/symbol is unique to an individual ringed seal captured between 2006 – 2010 from the Belcher Islands, Nunavut. Prey isotopic ellipses are represented by the mean +SD

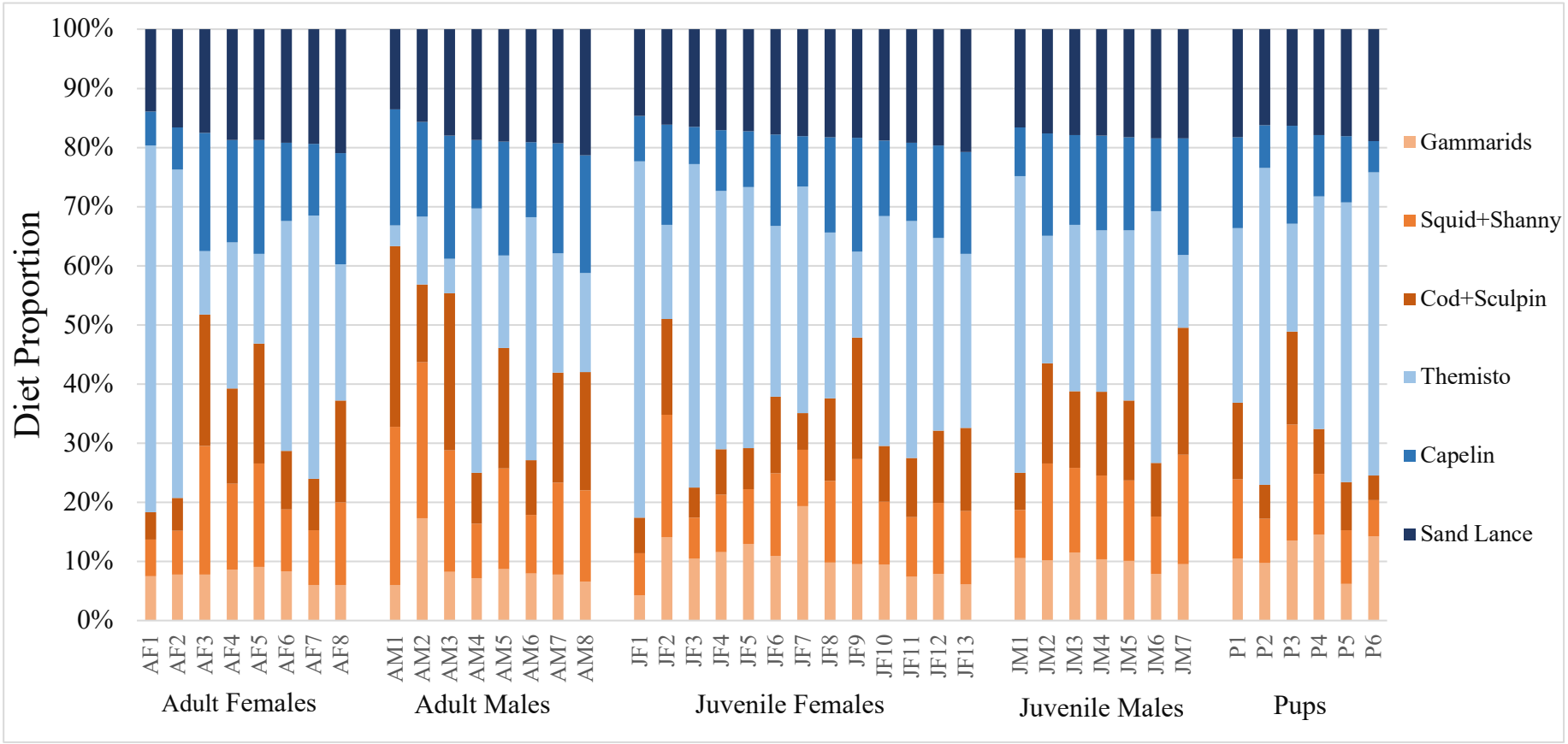

Figure 3.2. Mean diet proportions using $\delta^{13}C$ and $\delta^{15}N$ of combined ringed seal vibrissae segments separated by age and sex categories. Ringed seals were captured between 2006 – 2010 from the Belcher Islands, Nunavut.

Connecting Statement

In the previous chapter, I identified that ringed seals exhibit high inter-individual variability among conspecifics. Indeed, seals of all age classes showed higher between individual variation in diet biomarkers than within individual. However, an additional interaction that was not considered previously was possible interspecific interactions of sympatric species. That is, how do ringed seal diets compare to those of other phocid species in Hudson Bay? The next chapter investigates the interspecific isotopic, dietary and carbon source overlap between three phocids species.

Chapter 4: Estimating dietary overlap between three phocid species using stable isotopes and sea ice carbon biomarkers

Abstract

Temperate species distributional poleward shifts presents potential competition for species endemic to the Arctic. Harbour seal (*Phoca vitulina*) populations are increasing in Hudson Bay, an area at the southern extent of ringed (*Pusa hispida*) and bearded seals (*Erignathus barbatus)* range. The competitive interaction between these three species is not well understood in Hudson Bay and with poleward retreats of endemic Arctic fish, niche expansion of seals would be expected. I used stable isotope ratios (δ^{13}C, δ^{15}N) derived from liver tissue to investigate the amount of isotopic niche overlap among all three seal species, while highly branch isoprenoids were used to determine the primary sources of dietary carbon. I found that 83.8% of the ringed seals isotopic niche was overlapped by bearded seals, and 54% by harbour seals. I also found the 45.5% of harbour seals' isotopic niche was overlapped by bearded seals, both of which predominantly relied on sea ice algae produced sympagic carbon sources. In contrast, ringed seals exhibited a higher proportion of pelagic carbon source, 54.7%, contributing to the niche. Furthermore, the estimated dietary proportions harbour and bearded seals were similar with 50% of their diet comprised with cod+sculpin compared to only 6% in ringed seal diets, consistent with the trends observed in sympagic carbon proportions of these three species. These findings suggest that ringed seals have flexible foraging strategies to capitalize on energy sources beyond sympagic carbon, thereby displaying a nuanced relationship with sea-ice derived carbon energy. This adaptation in ringed seals has significant implications for energy transfer within ecosystems, particularly concerning apex predators, like polar bears (*Ursus maritimus*).

Keywords: niche overlap, isotopic breadth, stable isotopes, highly branched isoprenoid, ringed seals

Introduction

A species' niche breadth balances the effects of both intraspecific and interspecific competition. Interspecific interactions within a community can constrain a species' niche (Van Valen 1965). When this happens, the competitive exclusion principle states that similar species sharing the same resource or set of resources in limited supply would not be able to coexist (Hardin 1960). Interspecific competition is when one species affects the ability of another to forage, grow, survive, and reproduce (Hardin 1960; May and MacArthur 1972; Pianka 1981; Schoener 1983). Conversely, similar species can coexist provided that at least one of the niche dimensions differs among species (niche partitioning) and that the habitat has enough resources to sustain multiple individuals within each species' ecological niche (Hutchinson 1959; Huey and Pianka 1981). As interspecific competition between predators increases, niche overlap is predicted to decrease, resulting in niche partitioning (May and MacArthur 1972). While at the same time competition theory predicts that a species' niche will expand when prey availability becomes limited, and individual predators consume a higher variety of less preferred prey (Svanback and Bolnick 2007).

Many temperate species have also shifted their distributions towards the poles in response to warming temperatures (Parmesan et al. 1999; Araújo et al. 2004; Parmesan 2006). The poleward shifts of species represent one possible perturbation to the marine food web structure and dynamics, through top-down effects (Carpenter et al. 1987) and bottom-up effects (i.e. increase primary production) on the food web. Ringed seals (*Pusa hispida*) are subject to changes in their Arctic marine habitat with ongoing environmental change, which may include the increase of coexistence and/or competition of interspecific phocid species that are found in temperate and sub arctic regions (e.g., harbour [*Phoca vitulina*]), and in Arctic regions bearded [*Erignathus*

barbatus], and harp seals [*Pagophilus groenlandicus*]). Ringed seals in Hudson Bay are already sympatric with both bearded and harbour seals (Young et al. 2010), but harbour seals have been increasing in abdundance in the sub-Arctic waters such as Hudson Bay (Florko et al. 2018).

Changes to sea ice phenology has led to increased primary production throughout areas of the Arctic (Tremblay et al. 2015; Ardyna et al. 2020; Ardyna and Arrigo 2020). The extent of Arctic sea ice and timing of seasonal sea ice melt can directly influence the abundance and diversity of sympagic algae and carbon production (Post et al. 2013; Brown et al. 2020). The energy transformed from atmospheric CO_2 into organic carbon by primary producers has a peak in spring due to sea-ice associated algal production followed by a smaller peak later in the spring and early summer due to pelagic phytoplankton production (Leu et al. 2011; Ji et al. 2013). The production of organic carbon by these two groups of algal species are different enough that they can be traced in predator diets (Brown et al. 2014; 2018). Specific marks of algal carbon production are found in the form of highly branched isoprenoids (HBIs), a class of lipids, that can be differentiated based on the number and position of double bonds (Belt et al. 2007). While HBIs can be produced by a diversity of diatom genera, only a few species produce a monounsaturated 25 carbon HBI termed "Ice Proxy with 25 carbons" or IP_{25}, as they are species associated with Arctic sea ice, sympagic diatoms (Belt et al. 2007; Brown et al. 2014; Koch et al. 2020). Reduction of sea ice may result in declines in sympagic algae that produce up to 57% of overall Arctic marine primary productivity, including IP_{25}, with links through the food web to marine mammals (Brown et al. 2018). Ongoing changes to primary productivity in the Arctic are related to sea ice conditions and the mismatch of the spring melt and sympagic algal blooms (Søreide et al. 2006; Leu et al. 2015). Regional differences can occur, whereby areas with high ice coverage favour sympagic

algal species (Brown et al. 2014), while areas with seasonal ice and more open water are associated with phytoplankton blooms (Arrigo and van Dijken 2015). With ongoing environmental change, it is crucial to understand marine predator use of ice algal primary production and contribution to tissues of consumers within the Arctic marine food web.

Both ringed and bearded seals forage extenstively on Arctic marine prey, forage fish and invertebrates, as they are ice obligate species (Laidre et al. 2008;2015). Conversely, harbour seals have been documented to forage on both marine and freshwater prey (Bowen et al. 1996;1999, Smith et al. 1996) and in the sub-Arctic marine environment, stable isotopes indicate they may be gaining more energy from marine sources (St. George et al. 2023). Ringed seals primarily feed in the water column on fish and invertebrates, while bearded seals primarily feed on benthic invertebrates and fish (Lowry et al. 1980; Hjelset et al. 1999; Young et al. 2010). Conversely, harbour seals are generalist predators, and generally perform shallow dives and, thus, occupy areas along coastal regions (Bowen et al. 1999). Ringed and harbour seals are known to be predators that consume predominiately pelagic prey in temperate to subarctic regions (Bowen et al. 1996; Hammill et al. 2000). Ringed seals have exhibited niche overlap with sympatric phocid species in other parts of their range (Wathne et al. 2000; Ogloff et al. 2019; Kunisch et al. 2021; Desforges et al. 2022). The degree of niche overlap has also been associated with dietary overlap between ringed seals and conspecifics; however, prey size still varies, revealing ways of resource partitioning between the two species (Ogloff et al. 2019). Ringed and bearded seal stomach contents also showed high dietary overlap, but in different frequencies that vary amoung age classes (Crawford et al. 2015).

An aspect that has been overlooked is linking seal isotopic ratios to that of the primary producers to determine potential competition and dietary niche overlap. Primary production in the Arctic is changing, as the climate continues to warm and different climatic conditions yield different algal communities assemblages, and thus lipids that fuel the Arctic marine food web (Duerksen et al. 2014; Lange et al. 2019). Combining multiple dietary tracers together can provide a more detailed understanding of these phocid species' dietary composition and eludicate niche dynamics and partititioning (Leu et al. 2020). Understanding ringed seal dietary niches have commonly used bulk stable isotopes, but more recently using HBI biomarkers, has revealed 80% of ringed seal dietary carbon is sympagically dervived in regions of the high Canadian Arctic (Carlyle et al. 2022, Desforges et al. 2022).

The main objective of this study was to use a multi-dietary tracer approach to investigate the foraging ecology of three sympatric phocid species in western Hudson Bay. Specific objectives were to examine the amount of niche overlap, describing potential competition, by (1) determining isotopic niche breadth and overlap, (2) estimate species-specific dietary proportions, and (3) quantify the contribution of sympagic and pelagically derived carbon in the diets of all species. I hypothesized that niche overlap and dietary composition would vary between the three phocid species specifically between ice-obligate species and temperate species in this western Hudson Bay area. I predicted that diet proportions estimated with Bayesian mixing models would reveal different proportions of prey in the diet composition of the three phocid species and that both harbour and ringed seals will have a great proportion of pelagic forage fish in the diet , and overall broader niches, compared to the benthic invertebrate specialist, bearded seal. To better understand the influence of sympagically dervived carbon on the dietary composition, niche breadth and

ultimately dietary overlap of these three phocids, I compared the contributions of sympagic versus pelagically dervived carbon. I hypothesized that contribution of sea-ice dervived carbon would vary between ice-obligate species and temperate species. I predicted that bearded and ringed seals would have a higher proportion of sympagic carbon as ice obligate species. Investigating potential overlap and competition between ringed seals and sympatric species will increase our understanding of the foraging ecology of ringed seals and their interactions with interspecific competititors and can be used to determine the diet flexibility of predators during ongoing climate change. The intereactions between these mesopredators can be important in the overall understanding of how the Hudson Bay marine food web is functioning.

Methods

Sample Collection

Seal liver samples were collected in Arviat, Nunavut (61° N, 94 ° W) from ringed seals (n = 50), bearded seals (n = 39), and harbour seals (n = 6) by Inuit subsistence hunters during part of their annual fall community-based monitoring program (Table 4.1). Samples were collected from the years 2006 – 2017, though most of the samples of all species came from 2014 – 2017. Sex was recorded during collection by hunters, and were aged by Matson's Laboratory LLC (Missoula, MT, USA) by counting annual growth layer groups in cementum of the lower right canine (Stewart et al. 1996, Young and Ferguson 2014). I used age estimates to classify seals as pups (< 1 year of age), juvenile (1 – 4 years), or adult (≥ 5 years; Stewart et al. 1996; Quakenbush et al. 2011).

I focused the analyses on liver tissue because all biomarkers of interest can be examined using liver (Brown & Belt 2012; Brown et al. 2014). Liver has a relatively quick turnover rate of

approximately 1 – 2 months (Vander Zanden et al. 2015), and therefore I limited the analyses to samples that were collected in the fall months (October and November) immediately following the period where ringed seals are known to be foraging intensely (Young and Ferguson 2013). Possible seal prey species, such as fish and invertebrate species, were collected from coastal Hudson Bay communities between 2004 – 2007 and used for previous stable isotope studies (Elliott and Gaston 2008; Chambellant et al. 2013) and in Chapter 2 of this thesis.

Laboratory analyses

To prepare the liver samples for stable isotope analysis, all samples were freeze dried at − 50 °C for 48 hours and homogenized using a mortar and pestle. Lipids were extracted using a 2:1 chloroform: methanol solvent following a modified method from Bligh and Dyer (1959) and ~ 400 µg of tissue was weighed into tin capsules. The use of chemical lipid extraction may influence the ratios of nitrogen stable isotopes in the tissue samples, but many studies, including those of marine mammals, have found the effects to be minimal (Ingram et al. 2007; Yurkowski et al. 2015). Samples were then combusted to measure $\delta^{13}C$ and $\delta^{15}N$ using a continuous flow isotope ratio mass spectrometer (Delta V Plus; Thermo Scientific) interfaced with an elemental analyzer (ECS 4010; Costech Instruments) and connected via a Conflo IV interface (Thermo Scientific) at the Freshwater Institute (Fisheries and Oceans Canada, Winnipeg, MB, Canada).

The relative difference between isotope ratios (δ) was expressed as parts per thousand (‰) deviation from the standards measured against those in Vienna Pee Dee Belemnite for carbon, and atmospheric nitrogen standards for nitrogen, using the following formula:

$$\delta X = [(Rsample/Rstandard) - 1] \times 1000$$

Where X refers to $\delta^{13}C$ or $\delta^{15}N$, and R refers to the ratio of heavy to light isotope (^{13}C:^{12}C or ^{15}N:^{14}N). Both precision and accuracy were assessed using replicates of standard reference material (USGS 40 and USGS41a) spaced throughout runs and was determined to be ≤ 0.25‰ for $\delta^{13}C$ and ≤ 0.30‰ for $\delta^{15}N$. Every tenth seal liver sample was run in duplicate resulting in standard deviations ranging from 0.01 to 0.66‰ for $\delta^{13}C$ and 0. to 0.70‰ for $\delta^{15}N$.

Liver samples prepared for stable isotope analysis were also used for measurement of HBIs, as this is where most vertebrates store these specific lipid compounds (Brown et al. 2014b). Freeze dried (−50 °C, 0.2 mbar, 24 h) and homogenized liver tissue subsamples of ~ 0.4 – 1.0 g were prepared for analysis following established methods (Belt et al. 2013; Brown et al. 2014b) and sent to the Scottish Association for Marine Sciences at the Scottish Marine Institute (Oban, Argyll, UK). Briefly, lipid samples were saponified in methanolic KOH solution containing 5 mL H20:MEOH, 20% KOH for 60 minutes at 80 °C. Hexane (4 mL) was added to the saponified samples and were centrifuged at 2000 rpm for two minutes, three times. The supernatant containing non-saponifiable lipids were transferred to a new glass tube, dried with N_2 and resuspended in 0.5 mL of hexane. The dried lipid extracts were then fractionated with 5 mL of hexane using column chromatography (SiO2; 0.5g). Using the method outlined in Belt et al. (2012), the non-polar lipids containing the HBIs were analyzed with gas chromatography -mass spectrometry and quantified as described by Brown et al. (2014, 2018). The percentages of primary produced carbon were quantified from analytical intensities of three HBI masses to specific charge (m/z) (IP25: m/z 350.3, II: m/z 348.3, III: m/z 346.3) according to an established equation known as H-Print (Brown et al. 2014a and b), seen below:

$$H - Print\ (\%) = \frac{III}{IP25 + II + III}\ x\ 100$$

To differentiate the proportion of sea ice-derived carbon from planktonic carbon as a proportion of marine origin carbon within samples, I used a previous H-Print calibration equation to determine percent sympagic carbon use (Brown et al. 2018):

$$Sympagic\ carbon\ (\%) = 101.8 - 1.02 \times H - Print$$

Data analysis

To examine niche breadth and overlap, liver $\delta^{13}C$ and $\delta^{15}N$ were analysed using the SIBER package in R (Legendre and Vaudor 1991; Jackson et al. 2011). I used isotopic niche breadth as an indicator of the variety of resources consumed by a predator, where a narrower isotopic niche breadth reflects a small set of resources, whereas a broader niche breadth reflects a larger set of resources (Jackson et al. 2011; Yurkowski et al. 2016). For each species, a standard ellipse area corrected for small sample sizes (SEA_c) was calculated and plotted, which represents the standard deviation around the bivariate mean and encompasses ~ 40% of the individuals. I also measured the Bayesian standard ellipse area for each species along with 95% Bayesian ellipses. Bayesian ellipses were estimated for each seal species using 100,000 iterations with a burn in of 10,000. The posterior distribution was thinned by 10, and two chains were run. I calculated overlap following Ogloff et al. (2019) using the following formula:

$$\%\ Overlap = \frac{AO}{A1 + A2 - AO} \times\ 100$$

Where AO represents the overlap area, that can be calculated by the percent of A1 isotopic niche that overlapped A2 isotopic niche, and A1 and A2 are the SEA of two different species being compared. To determine how much one species overlaps the niche of another species was calculated by dividing the overlap area (AO) between both species by the area of the species (A1 or A2). For example to determine the percentage of ringed seal niche overlapped by bearded seal, the total overlap area between both ringed and bearded seal would be divided by the area of ringed seal niche.

To estimate the contribution of various prey species in each seal species' diet, I used stable isotope mixing models in the Bayesian Mixing Models in R (MixSIAR) package (Stock et al. 2018). Diet estimation models use Bayesian methods to determine possible prey proportions as probability distributions. I ran the models using uninformative priors because these models had improved convergence. Models were formulated with a chain length of 1 000 000, thinned by 500, and a burn-in of 10 000 with three chains. To assess model convergence, I used the Gelman-Rubin diagnostic (Gelman and Rubin 1992). Models were considered to converge if all variables fell below 1.05 Gelman-Rubin diagnostic value (Brooks and Gelman 1998).

I used prey samples from previously collected and published data on species that have been documented in ringed seal stomach contents (Chambellant et al. 2013). The prey type groups I used were *Themisto libellula* (mean ± SD of 7: δ^{15}N= 8.4 ± 0.3‰, δ^{13}C = -23.0 ± 0.2‰), capelin (*Mallotus villosus*) (mean ± SD of 46: δ^{15}N= 13.7 ± 0.8‰, δ^{13}C = -19.8 ± 1.1‰), sand lance (*Ammodytes sp.*) (mean ± SD of 47: δ^{15}N= 12.7 ± 1.4‰, δ^{13}C = -21.0 ± 1.2‰), *Gammarus sp.* (mean ± SD of 4: δ^{15}N= 9.7 ± 0.3‰, δ^{13}C = -18.1 ± 0.6‰), and (both Greenland (*Gadus ogac*) and Arctic cod and sculpin(*Cottoidea sp.*)) (mean ± SD of 61: δ^{15}N= 14.9 ± 0.7‰, δ^{13}C = -19.2 ±

0.6‰). Fish muscle and whole bodied invertebrates were homogenized and lipid extracted following the modified Blight & Byer (1959) method using a chloroform:methona solvent with a 2:1 ratio, a complete detail of the modified lipid extraction is outlined in Logan et al. (2008), and were processed at the University of Winnipeg Isotope Laboratory (Chambellant et al. 2013). In brief, samples were combusted to measure $\delta^{13}C$ and $\delta^{15}N$ using a continuous flow isotope ratio mass spectrometer (Delta V Plus; Thermo Scientific) interfaced with an elemental analyzer (ECS 4010; Costech Instruments) and connected via a Conflo IV interface (Thermo Scientific). To account for trophic discrimination, species-specific trophic discrimination factors estimated from harp seals (*Pagophilus groenlandicus*) by Hobson et al. (1996) (liver $\delta^{15}N = 3.1$, $\delta^{13}C = 0.6$) with an arbitrary standard deviation of 0.2 were used for all species.

To investigate the mean differences of bulk stable isotopes ($\delta^{13}C$, $\delta^{15}N$), and percent sympagic carbon among species, I used two-factor ANOVAs that included species and age class as factors, and performed post-hoc Tukey HSD tests when significance was found. Sympagic carbon was transformed using the arcsine transformation, to improve normality and homoscedasticity (Quinn and Keough 2002). The effect of year on mean sympagic carbon was assessed using simple linear regression for ringed seals and bearded seals, but not harbour seals due to sample size limitations. The significance of statistical tests was assessed at $\alpha = 0.05$ and analyses were conducted in JMP Pro 16 (SAS Institute Inc 2021) and R version 3.4.4 (R Core Team 2021).

Results

The 95% ellipse area was narrowest for harbour seals (2.0‰^{2}) with the highest δ^{15}N isotopic ratio of 18.1, broadest for bearded seals (6.9‰^{2}) and was intermediate for ringed seals (3.76‰^{2}; Figure 4.1; Table 4.1). When corrected for small sample sizes, SEA_c was also broadest for bearded seals (2.0‰^{2}) but narrowest for ringed seals (1.0‰^{2}) and was 1.9‰^{2} for harbour seals (Figure 4.1;Table 4.2) Bearded and ringed seal isotopic niches had the highest overlap (39.0%), whereas harbour and ringed seals had the lowest (23.1%) (Figure 4.1). The overlap between bearded and harbour seal was 4.6% greater compared to the shared area between ringed and harbour (Figure 4.1; Table 4.2). Niche overlap by harbour or bearded seal on the ringed seal niche was higher, than ringed seal niche overlap on bearded and harbour niche (Figure 4.1; Table 4.2). Ringed seal niche was overlapped 83.8% and 54% by bearded seal and harbour seal, respectively (Figure 4.1 and Table 4.2).

Liver δ^{13}C differed significantly between the three species ($F_{2,82} = 33.03$, $p<0.001$) where ringed seals had the most depleted values, compared to both bearded and harbour seals. Bearded seals had the least depleted liver δ^{13}C (Table 4.1). Liver δ^{13}C did not differ by age class ($F_{2,82} = 1.74$, $p=0.172$), as values were within 1‰, though the greatest variation was in bearded seals. There was a significant interaction between species and age ($F_{8,82} = 12.51$, $p<0.005$). Liver δ^{15}N varied significantly between the three species ($F_{2, 82} = 37$, $p<0.001$), where ringed seals had the lowest valus, 16.04 ‰ compared to 18.1 ‰ in harbour seals (Table 4.1). Liver δ^{15}N also varied significantly by age ($F_{2,82} = 3.51$, $p=0.001$), where adults had the highest δ^{15}N for ringed and harbour seals, and was highest in bearded seal pups, though not all species-specific age class comparisons were significant (Table A4.3).

When combining age groups and year together for dietary estimations, the cod+sculpin prey type represented 51% and 53% of the diet in bearded and harbour seals, respectively, compared to the 6% in ringed seal diet (Figure 4.2). By contrast, ringed seal diets were primarily comprised of sand lance (78%), followed by capelin (7%) and *Themisto* (7%; Figure 4.2). Capelin was found to be 22% of the estimate diet in harbour seals and 24% in bearded seals (Figure 4.2). Sand lance contributed less to harbour seals (16%) and bearded seals (18%) compared to ringed seals. Gammarids were in smallest proportion for all three species (<5%; Figure 4.2).

When all age groups and years were combined, the percentage of sympagic carbon use was highest in harbour and bearded seals compared to ringed seals (70.13, 66.40 and 45.33% respectively; Table 4.1; Figure 4.3) The–mean annual sympagic carbon (%) in ringed seals significantly increased from 2011 to 2017 by 36.67% from 25.9 to 62.56% ($r^2 = 0.909$, $F_{1,58} = 19.998$, $p = 0.012$; Figure 4.4). There was a decline in sympagic carbon (%) in bearded seals from 2005to 2017, though the relationship was not significant ($r^2 = 0.06$, $F_{1,72} = 4.279$, $p = 0.0685$; Figure 4.4). Absolute concentration of IP_{25} was measured for only harbour seal and a subset of ringed seal livers. The absolute concentration of IP_{25} in ringed seals was 17.96 ng/g compared to 10.88 ng/g in harbour seals. Bearded seals samples were not run with a standard so absolute concertation of IP_{25} could not be measured.

Discussion

This study revealed that there is isotopic niche overlap between three endemic Arctic phocid species; However, I demonstrate that although the isotopic niches of these three phocids overlap, they do partition energetic dietary resources and sources thereby reducing direct competition (Hardin 1960). Notably sympagic derived carbon does not contribute to bearded and

ringed seal diets equally, even though both are ice-obligate species (Laidre et al. 2008). Estimated diet proportions further elucidate some of the ways seals within Hudson Bay may be partitioning resources. Using a complementary biomarker approach, I can further infer niche differences between sympatric species, even when foraging location, and geographical distributions are not available.

There was limited isotopic overlap (21%) between ringed seals and harbours and $\delta^{13}C$ did not vary significantly between the two species, but $\delta^{15}N$ did, implying that harbour seals are likely consuming higher proportions of prey types that are more enriched with nitrogen given their higher isotope value (Hobson & Welch 1992) that could be larger predatory fish such as trout or pike species that are in the Churchill estuary and have high trophic position (St.George et al. 2024) . The dietary proprotions estimated here show that ringed seals are predominantely consuming sand lance, whereas cod, sculpin, and capelin are important contributions to the diet of harbour seals. Harbour seals in Svalbard, Norway have been documented to consume high proportions of cod and sculpins in their diet with smaller invertebrates not significantly contributing to the diet, in an area where harbour and ringed seals overlap in range (Labansen et al. 2007). While both predators are feeding on sand lance and capelin it is likely that they may be consuming different sized forage fish as this has been previously shown as strategy ringed seals partition resources when sympatric with interspecific competitors (Wathne et al. 2000; Ogloff et al. 2019). For instance, when ringed seals are sympagic with harp seals in the Barents Sea there is nearly 100% dietary overlap between the two species using stomach content analysis; However, ringed seals did feed on smaller forage fish compared to harp seals, which demonstrated how prey resources can be partitioned among similar phocid predators allowing them to coexist in the same habitat (Wathne et al. 2000).

Differences in dietary proportions between harbour and ringeds seals could also be attributed to the potential foraging locations of the two species. Harbour seals have been known to occupy freshwater and estuary areas in Hudson Bay (Bajzak et al. 2013; Florko et al. 2018), but there has not been the same documentationed for ringed seals. Harbour seals may be consuming a greater proportion of freshwater prey compared to ringed seals. This study did not use any freshwater prey species in the diet mixing model and thus, exact freshwater versus marine prey proportions cannot be eludicated. Based on the two elements used in this study, it is difficult to tease apart specific carbon source (marine vs. freshwater) in the diet of each predator (Szpack and Buckley 2020), but the evidence of the combination of the dietary markers in this study support previously reported dietary differences.

The overlap between harbour and bearded seals is likely due to the coastal or benthic feeding areas of the two species, respectively (Hobson & Welch 1992; Crawford et al. 2008). Bearded seals feed extensively in the benthic environment and harbour seals feed in coastal habitats (Smith & Hammill 1981, Planque et al. 2020), which would yield similar $\delta^{13}C$ between these two species. Bearded seals overlapped more with ringed seals and there were no significant differences between the juvenile and adult age classes. Bearded seals and ringed seals do overlap in their dietary niche elsewhere in their range. For instance in Alaskan waters, stomach contents showed that the two species consume the same prey types but in a short time period (<8 hours) in significantly different frequencies (Crawford et al. 2016). Ringed seals also showed an increase in the frequency of fish consumed in older individuals compared to pups, with the most frequent fish species found in both species stomachs was Arctic cod (Chambellant et al. 2013; Crawford et al. 2016). It is likely that juvenile predators have a more generalized diet because of their inexperience

capturing prey; conversely adults can specialize because of their previous foraging experience (Werner and Gilliam 1984) and the physiological capabilities of juvenile ringed seals is limited to those of adults (Teilmann et al. 1999). Comparison between the three species should be interpreted with caution given the low sample size of harbour seals that were available.

The contributions of sympagic carbon were higher in bearded seal and harbour seals compared to ringed seals, suggesting that ringed seals are consuming pelagically produced carbon compared to relying on sea ice algal production (Brown et al. 2014). Given that previous HBI studies had found sympagic carbon in the diets of ringed seals (Brown et al. 2014, Carlyle et al.2002, Desforges et al. 2022), it was suprising that a lower contribution was found in this study. The lower absolute concentration of IP_{25} found in the harbour seals and a portion of the ringed seals in this study further supports the likelihood that other non-marine derived carbon sources are contributing to the diets of these species (Pedro et al. 2020). The sub-Arctic fish in Arviat are known to have broader niche breadth compared to higher Arctic areas (Pedro et al. 2020). Therefore, it is not surprising that the niche breadth of the seals examined in Arviat also have broader niche breadth in comparison to seals in higher areas of the Arctic (Carlyle et al. 2022). Ringed seals may be shifting their diet to more estuarian signal (freshwater energy sources) as some freshwater fish species sulphur, nitrogen and carbon isotopic ratios recorded just south of Arviat in Churchill by St. George et al. (2023), but still find a high contribution of marine sources for both harbour and ringed seals. Limitations to our study include the temporal collection of the samples, wherein the seals were harvested in the fall months after the algal bloom (Matthes et al. 2021). Little is known about the latency of the sympagic biomarkers in the liver of consumers, and the lower concentrations found in this study compared to ringed seals at higher latitudes (Brown

et al. 2014; Carlyle 2022; Koch et al. 2023) could be attributed to a weakened signal in ringed seals. Stable isotope ratios in Hudson Bay ringed seals do vary seasonally (Young and Ferguson 2014), which is one possibility as to why there are lower absolute IP_{25} concentrations recorded in ringed seals in this study. All seals were harvested following the intensive foraging period as liver has a ~1 – 2-month turnover rate (Budge et al. 2008; Brown et al. 2014). Decreased sympagic algal production is unlikely, given that polar bears from the same locations during the same years were found to have a dietary average of 86% derived from sympagic carbon (Brown et al. 2018). With high sympagic carbon found in polar bear diets during the same years, it is clear the HBI signal was indeed present and can be detected. Brown et al (2018) did report that areas of polar bear habitat that had the longest open water period (Baffin Bay) coincided with the lowest sympagic carbon estimates.

The low value of sympagic carbon in ringed seals here in Hudson Bay is also an area where the sea ice free season is lengthening (Stroeve and Notz 2018), and it could be that ringed seals have less time to forage on prey species that have high concentrations of symagically produced carbon, that are likely ice-associated. Furthermore, sea ice thickness is also known to influence the production of sympagic algae and pelagic phytoplankton changing the primary carbon available in the system (Leu et al. 2015). It could be possible that less sympagic carbon is being produced in Hudson Bay compared to Phytoplankton. Alternative explanations to the lower sympagic carbon contribution in ringed seals can be explained by the increased consumption of temperate and/or freshwater prey species that are not as tied to the sympagic zone. It is unlikely that I am not picking up the signal in ringed seals given the measurements found in apex predators and interspecific competitors. Yurkowski et al. (2020) found a weakening predator-prey relationship in western

Hudson Bay due interannual changes in carbon production which could be explained by a more pelagic sourced carbon diet (54.77%) in ringed seals found in this study. In Hudson Bay, there are increased productivity in areas (Matthes et al. 2021), which may explain the significant increase in ringed seal sympagic carbon contribution in the diet over time. The changes to ringed seal diet contributions could likely be tied to environmental conditions, as diet has been previously empirically linked to climate variables, sea surface temperatures, sea ice phenology, and changes to diet contributions in the Beaufort Sea region of ringed seals' range (Boucher et al. 2020).

With an environment that is undergoing rapid change, interspecific competition may cause species to partition their niche (Hardin 1960). I have documented evidence that niche partitioning may happening between three phocid species in Hudson Bay, whereby using a variety of dietary markers, I was able to highlight differences in isotopic niche overlap and compare sympagic and pelagic carbon sources. Future research should examine the latency and abundance of HBIs in the environment seasonally, and annually to better understand patterns that were revealed here. Gaining an understanding of how three phocid species are able to coexist in an area with ongoing changes to the food web will allow for a better understanding of the community's structure and function.

This study was the first to compare the sympagic and pelagic carbon contributions to three Arctic phocid species and evaluate their niche overalp at the southern extent of their range. The liver biomarker estimates varied between ringed seals and the two other seal species. The results from this study can be used as a reference for future research comparisons in this study area to investigate the use of freshwater sources to further discriminate carbon source differences between these predator species and use multiple biomarkers, such as fatty acids to further estimate dietary

propotions in mixing models with increased prey types. In conclusion, results from this study support the use a multi-biomarker approach (stable isotopes and HBI) to better understand resource overlap of these phocid predators. Stable isotope ellipses offer two-dimensional insight into resources being consumed and can provide further support when paired with diet estimations. Understanding seal diet overlap and changes to carbon resources will be essential in determining community level impacts in a warming climate.

Literature Cited

Araújo, M. B., Cabeza, M., Thuiller, W., Hannah, L., & Williams, P. H. (2004). Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global change biology*, *10*(9), 1618-1626.

Ardyna, M., & Arrigo, K. R. (2020). Phytoplankton dynamics in a changing Arctic Ocean. *Nature Climate Change*, *10*(10), 892-903.

Ardyna, M., Mundy, C. J., Mayot, N., Matthes, L. C., Oziel, L., Horvat, C., ... & Arrigo, K. R. (2020). Under-ice phytoplankton blooms: Shedding light on the "invisible" part of Arctic primary production. *Frontiers in Marine Science*, *7*, 608032.

Arrigo, K. R., & van Dijken, G. L. (2015). Continued increases in Arctic Ocean primary production. *Progress in Oceanography*, *136*, 60-70.

Bajzak, C. E., Bernhardt, W., Mosnier, A., Hammill, M. O., & Stirling, I. (2013). Habitat use by harbour seals (*Phoca vitulina*) in a seasonally ice-covered region, the western Hudson Bay. *Polar Biology*, *36*, 477-491.

Belt, S. T., Brown, T. A., Ringrose, A. E., Cabedo-Sanz, P., Mundy, C. J., Gosselin, M., & Poulin, M. (2013). Quantitative measurement of the sea ice diatom biomarker IP25 and sterols in Arctic sea ice and underlying sediments: Further considerations for palaeo sea ice reconstruction. *Organic Geochemistry*, *62*, 33-45.

Belt, S. T., Massé, G., Rowland, S. J., Poulin, M., Michel, C., & LeBlanc, B. (2007). A novel chemical fossil of palaeo sea ice: IP25. *Organic Geochemistry*, *38*(1), 16-27.

Bligh, E. G., & Dyer, W. J. (1959). A rapid method of total lipid extraction and purification. Canadian journal of biochemistry and physiology, 37(8), 911-917.

Boucher, N. P., Derocher, A. E., & Richardson, E. S. (2020). Spatial and temporal variability in ringed seal (*Pusa hispida*) stable isotopes in the Beaufort Sea. *Ecology and Evolution*, *10*(10), 4178-4192.

Bowen, W.D., Boness, D.J., & Iverson, S.J. 1999. Diving behaviour of lactating harbour seals and their pups during maternal foraging trips. *Canadian Journal of Zoology*, 77, 978–988.

Bowen, W. D., & Harrison, G. D. (1996). Comparison of harbour seal diets in two inshore habitats of Atlantic Canada. *Canadian Journal of Zoology*, *74*(1), 125-135.

Brown, T. A., Alexander, C., Yurkowski, D. J., Ferguson, S. H., & Belt, S. T. (2014). Identifying variable sea ice carbon contributions to the Arctic ecosystem: A case study using highly branched isoprenoid lipid biomarkers in Cumberland Sound ringed seals. *Limnology and Oceanography*, *59*(5), 1581-1589.

Brown, T. A., Belt, S. T., & Cabedo-Sanz, P. (2014b). Identification of a novel di-unsaturated C 25 highly branched isoprenoid in the marine tube-dwelling diatom Berkeleya rutilans. *Environmental Chemistry Letters*, *12*, 455-460.

Brown, T. A., & Belt, S. T. (2012). Identification of the sea ice diatom biomarker IP 25 in Arctic benthic macrofauna: direct evidence for a sea ice diatom diet in Arctic heterotrophs. *Polar Biology*, *35*, 131-137.

Brown, T. A., Galicia, M. P., Thiemann, G. W., Belt, S. T., Yurkowski, D. J., & Dyck, M. G. (2018). High contributions of sea ice derived carbon in polar bear (*Ursus maritimus*) tissue. *PloS one*, *13*(1), e0191631.

Brown, T. A., Rad-Menéndez, C., Ray, J. L., Skaar, K. S., Thomas, N., Ruiz-Gonzalez, C., & Leu, E. (2020). Influence of nutrient availability on Arctic sea ice diatom HBI lipid synthesis. *Organic Geochemistry*, *141*, 103977.

Budge, S. M., Wooller, M. J., Springer, A. M., Iverson, S. J., McRoy, C. P., & Divoky, G. J. (2008). Tracing carbon flow in an arctic marine food web using fatty acid-stable isotope analysis. Oecologia, 157(1), 117-129.

Carpenter, S. R., Kitchell, J. F., Hodgson, J. R., Cochran, P. A., Elser, J. J., Elser, M. M., ... & von Ende, C. (1987). Regulation of lake primary productivity by food web structure. *Ecology*, *68*(6), 1863-1876.

Carlyle, C. G., Roth, J. D., Yurkowski, D. J., Kohlbach, D., Young, B. G., Brown, T. A., ... & Ferguson, S. H. (2022). Spatial variation in carbon source use and trophic position of ringed seals across a latitudinal gradient of sea ice. *Ecological Indicators*, *145*, 109746.

Chambellant, M., Stirling, I., & Ferguson, S. H. (2013). Temporal variation in western Hudson Bay ringed seal *Phoca hispida* diet in relation to environment. *Marine Ecology Progress Series*, 481, 269-287.

Crawford, K., Mcdonald, R. A., & Bearhop, S. (2008). Applications of stable isotope techniques to the ecology of mammals. Mammal Review, 38(1), 87-107.

Crawford, J. A., Quakenbush, L. T., & Citta, J. J. (2015). A comparison of ringed and bearded seal diet, condition and productivity between historical (1975–1984) and recent (2003–2012) periods in the Alaskan Bering and Chukchi seas. *Progress in Oceanography*, 136, 133-150.

Desforges, J. P., Kohlbach, D., Carlyle, C. G., Michel, C., Loseto, L. L., Rosenberg, B., ... & Ferguson, S. H. (2022). Multi-dietary tracer approach reveals little overlap in foraging ecology between seasonally sympatric ringed and harp seals in the high Arctic. *Frontiers in Marine Science*, *9*, 969327.

Duerksen, S. W., Thiemann, G. W., Budge, S. M., Poulin, M., Niemi, A., & Michel, C. (2014). Large, omega-3 rich, pelagic diatoms under Arctic sea ice: sources and implications for food webs. *PloS one*, *9*(12), e114070.

Elliott, K. H., & Gaston, A. J. (2008). Mass-length relationships and energy content of fishes and invertebrates delivered to nestling thick-billed murres *Uria lomvia* in the Canadian Arctic, 1981-2007. *Marine Ornithology*, *36*, 25-34.

Florko, K. R., Bernhardt, W., Breiter, C. J. C., Ferguson, S. H., Hainstock, M., Young, B. G., & Petersen, S. D. (2018). Decreasing sea ice conditions in western Hudson Bay and an increase in abundance of harbour seals (Phoca vitulina) in the Churchill River. *Polar Biology*, *41*, 1187-1195.

Hamilton, C. D., Lydersen, C., Ims, R. A., & Kovacs, K. M. (2015). Predictions replaced by facts: a keystone species' behavioural responses to declining arctic sea-ice. Biology Letters, 11(11), 20150803.

Hammill, M. O., & Stenson, G. B. (2000). Estimated prey consumption by harp seals (*Phoca groenlandica*), hooded seals (*Cystophora cristata*), grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) in Atlantic Canada. *Journal of Northwest Atlantic Fishery Science*, *26*, 1-24.

Hardin, G. (1960). The competitive exclusion principle. *Science*, 131(3409), 1292-1297.

Hjelset, A. M., Andersen, M., Gjertz, I., Lydersen, C., & Gulliksen, B. (1999). Feeding habits of bearded seals (*Erignathus barbatus*) from the Svalbard area, Norway. *Polar Biology*, 21(3), 186-193.

Hobson, K. A., Schell, D. M., Renouf, D., & Noseworthy, E. (1996). Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. Canadian Journal of Fisheries and Aquatic Sciences, 53(3), 528-533.

Hobson, K. A., & Welch, H. E. (1992). Determination of trophic relationships within a high Arctic marine food web using δ 13 C and δ 15 N analysis. Marine Ecology Progress Series, 9-18.

Huey, R. B., & Pianka, E. R. (1981). Ecological consequences of foraging mode. *Ecology*, 62(4), 991-999.

Hutchinson, G. E. (1959). Homage to Santa Rosalia or why are there so many kinds of animals?. The American Naturalist, 93(870), 145-159.

Ingram, T., Matthews, B., Harrod, C., Stephens, T., Grey, J., Markel, R., & Mazumder, A. (2007). Lipid extraction has little effect on the δ15N of aquatic consumers. *Limnology and Oceanography: Methods*, *5*(10), 338-342.

Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, *80*(3), 595-602.

Ji, R., Jin, M., & Varpe, Ø. (2013). Sea ice phenology and timing of primary production pulses in the Arctic Ocean. *Global Change Biology*, *19*(3), 734-741.

Koch, C. W., Cooper, L. W., Lalande, C., Brown, T. A., Frey, K. E., & Grebmeier, J. M. (2020). Seasonal and latitudinal variations in sea ice algae deposition in the Northern Bering and Chukchi Seas determined by algal biomarkers. *PLoS One*, *15*(4), e0231178.

Kunisch, E. H., Graeve, M., Gradinger, R., Haug, T., Kovacs, K. M., Lydersen, C., ... & Bluhm, B. A. (2021). Ice-algal carbon supports harp and ringed seal diets in the European Arctic: evidence from fatty acid and stable isotope markers. *Marine Ecology Progress Series*, *675*, 181-197.

Labansen, A. L., Lydersen, C., Haug, T., & Kovacs, K. M. (2007). Spring diet of ringed seals (*Phoca hispida*) from northwestern Spitsbergen, Norway. *ICES Journal of Marine Science*, *64*(6), 1246-1256.

Laidre, K. L., Stirling, I., Lowry, L. F., Wiig, Ø., Heide-Jørgensen, M. P., & Ferguson, S. H. (2008). Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. Ecological Applications, 18(sp2).

Laidre, K. L., Stern, H., Kovacs, K. M., Lowry, L., Moore, S. E., Regehr, E. V., ... & Born, E. W. (2015). Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. Conservation Biology, 29(3), 724-737.

Lange, B. A., Haas, C., Charette, J., Katlein, C., Campbell, K., Duerksen, S., ... & Michel, C. (2019). Contrasting ice algae and snow-dependent irradiance relationships between first-year and multiyear sea ice. *Geophysical Research Letters*, *46*(19), 10834-10843.

Legendre, P., & Vaudor, A. (1991). The R package. *Montreal: Université de Montréal*.

Leu, E., Søreide, J. E., Hessen, D. O., Falk-Petersen, S., & Berge, J. (2011). Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: timing, quantity, and quality. *Progress in Oceanography*, *90*(1-4), 18-32.

Leu, E., Mundy, C. J., Assmy, P., Campbell, K., Gabrielsen, T. M., Gosselin, M., ... & Gradinger, R. (2015). Arctic spring awakening–Steering principles behind the phenology of vernal ice algal blooms. *Progress in Oceanography*, *139*, 151-170.

Lowry, L. F., Frost, K. J., & Burns, J. J. (1980). Feeding of bearded seals in the Bering and Chukchi Seas and trophic interaction with Pacific walruses. *Arctic*, 330-342.

MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. The American Naturalist, 100(916), 603-609.

Matthes, L. C., Ehn, J. K., Dalman, L. A., Babb, D. G., Peeken, I., Harasyn, M., ... & Mundy, C. J. (2021). Environmental drivers of spring primary production in Hudson Bay. *Elementa Science of the Anthropene*, *9*(1), 00160.

May, R. M., & Arthur, R. H. M. (1972). Niche overlap as a function of environmental variability. *Proceedings of the National Academy of Sciences*, *69*(5), 1109-1113.

Ogloff, W. R., Ferguson, S. H., Fisk, A. T., Marcoux, M., Hussey, N. E., Jaworenko, A., & Yurkowski, D. J. (2021). Long-distance movements and associated diving behaviour of ringed seals (*Pusa hispida*) in the eastern Canadian Arctic. *Arctic Science*, *7*(2), 494-511.

Ogloff, W. R., Yurkowski, D. J., Davoren, G. K., & Ferguson, S. H. (2019). Diet and isotopic niche overlap elucidate competition potential between seasonally sympatric phocids in the Canadian Arctic. *Marine Biology*, *166*(8), 103.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.*, *37*, 637-669.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., ... & Warren, M. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, *399*(6736), 579-583.

Pedro, S., Fisk, A. T., Ferguson, S. H., Hussey, N. E., Kessel, S. T., & McKinney, M. A. (2020). Broad feeding niches of capelin and sand lance may overlap those of polar cod and other native fish in the eastern Canadian Arctic. *Polar Biology*, *43*, 1707-1724.

Pianka, E. R. (1996). Long-term changes in lizard assemblages in the Great Victoria Desert. Longterm studies of vertebrate communities. Academic, San Diego, 191-216.

Pianka, E. R. (1981). Competition and niche theory. Ariel, 128, 205-172.

Planque, Y., Huon, M., Caurant, F., Pinaud, D., & Vincent, C. (2020). Comparing the horizontal and vertical approaches used to identify foraging areas of two diving marine predators. *Marine Biology*, *167*, 1-14.

Post, E., Bhatt, U. S., Bitz, C. M., Brodie, J. F., Fulton, T. L., Hebblewhite, M., ... & Walker, D. A. (2013). Ecological consequences of sea-ice decline. *Science*, *341*(6145), 519-524.

Quakenbush, L., Citta, J., & Crawford, J. (2011). Biology of the ringed seal (*Phoca hispida)* in Alaska, 1960–2010. *Final Report to: National Marine Fisheries Service*.

Schoener, T. W. (1983). Field experiments on interspecific competition. The American Naturalist, 122(2), 240-285.

Smith, T. G., & Hammill, M. O. (1981). Ecology of the ringed seal, *Phoca hispida*, in its fast ice breeding habitat. *Canadian Journal of Zoology*, 59(6), 966-981.

Smith, R. J., Hobson, K. A., Koopman, H. N., & Lavigne, D. M. (1996). Distinguishing between populations of fresh-and salt-water harbour seals (*Phoca vitulina*) using stable-isotope ratios and fatty acid profiles. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*(2), 272-279.

Søreide, J. E., Hop, H., Carroll, M. L., Falk-Petersen, S., & Hegseth, E. N. (2006). Seasonal food web structures and sympagic–pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. *Progress in Oceanography*, *71*(1), 59-87.

St George, J. R., Petersen, S. D., Roth, J. D., Ferguson, S. H., & Yurkowski, D. J. (2023). Habitat coupling dynamics of mobile consumers along a freshwater and marine resource gradient in a sub-Arctic estuarine system. *Estuarine, Coastal and Shelf Science*, *292*, 108449.

Stroeve, J., & Notz, D. (2018). Changing state of Arctic sea ice across all seasons. *Environmental Research Letters*, *13*(10), 103001.

Szpak, P., & Buckley, M. (2020). Sulfur isotopes (δ34S) in Arctic marine mammals: indicators of benthic vs. pelagic foraging. *Marine Ecology Progress Series*, *653*, 205-216.

Stewart, R. E., Stewart, B. E., Stirling, I., & Street, E. (1996). Counts of growth layer groups in cementum and dentine in ringed seals (*Phoca hispida*). *Marine Mammal Science*, *12*(3), 383-401.

Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L., & Semmens, B. X. (2018). Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ*, *6*, e5096.

Svanbäck, R., & Bolnick, D. I. (2007). Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1611), 839-844.

Teilmann, J., Born, E. W., & Acquarone, M. (2000). Behaviour of ringed seals tagged with satellite transmitters in the North Water polynya during fast-ice formation. *Canadian Journal of Zoology*, *77*(12), 1934-1946.

Tremblay, J. É., Anderson, L. G., Matrai, P., Coupel, P., Bélanger, S., Michel, C., & Reigstad, M. (2015). Global and regional drivers of nutrient supply, primary production and CO2 drawdown in the changing Arctic Ocean. *Progress in Oceanography*, *139*, 171-196.

Vander Zanden, M. J., Clayton, M. K., Moody, E. K., Solomon, C. T., & Weidel, B. C. (2015). Stable isotope turnover and half-life in animal tissues: a literature synthesis. *PloS one*, *10*(1), e0116182.

Van Valen, L. (1965). Morphological variation and width of ecological niche. The American Naturalist, 99(908), 377-390.

Young, B. G., Loseto, L. L., & Ferguson, S. H. (2010). Diet differences among age classes of Arctic seals: evidence from stable isotope and mercury biomarkers. *Polar Biology*, 33(2), 153-162.

Young, B. G., & Ferguson, S. H. (2013). Seasons of the ringed seal: pelagic open-water hyperphagy, benthic feeding over winter and spring fasting during molt. *Wildlife Research*, 40(1), 52-60.

Young, B.G., & Ferguson, S.H. (2014). Using stable isotopes to understand changes in ringed seal foraging ecology as a response to a warming environment, *Marine Mammal Science*, 30(2), 706-725.

Yurkowski, D. J., Ferguson, S. H., Semeniuk, C. A., Brown, T. M., Muir, D. C., & Fisk, A. T. (2016). Spatial and temporal variation of an ice-adapted predator's feeding ecology in a changing Arctic marine ecosystem. Oecologia, 180(3), 631-644.

Yurkowski, D. J., Hussey, N. E., Semeniuk, C., Ferguson, S. H., & Fisk, A. T. (2015). Effects of lipid extraction and the utility of lipid normalization models on δ13C and δ15N values in Arctic marine mammal tissues. *Polar Biology*, 38(2), 131-143.

Yurkowski, D. J., Richardson, E. S., Lunn, N. J., Muir, D. C., Johnson, A. C., Derocher, A. E., ... & Ferguson, S. H. (2020). Contrasting temporal patterns of mercury, niche dynamics, and body fat indices of polar bears and ringed seals in a melting icescape. *Environmental Science & Technology*, *54*(5), 2780-2789.

Wathne, J.A, Haug, T., & Lydersen, C. (2000). Prey preference and niche overlap of ringed seals *Phoca hispida* and harp seals *P.groenlandica* in the Barents Sea. *Marine Ecology Progress Series*, 194, 233-239.

Werner, E.E., & Gilliam, J.F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*, 15:3.

Tables

Table 4.1. Mean (± SE) $\delta^{13}C$, $\delta^{15}N$, and C: N of liver and calculated sympagic carbon (%) from bearded, harbour and ringed seals sampled from 2005-2017 in Arviat, Nunavut, during October-November. Age classes are classified by pups = 0 years of age, juvenile = 1 – 5 years of age, and adult = ≥5 years of age. Multiple pairwise comparisons (Tukey's post-hoc test) between $\delta^{13}C$, $\delta^{15}N$, and Sympagic carbon are described with different letters which indicate significant differences ($\alpha = 0.05$).

	n	$\delta^{13}C$		$\delta^{15}N$		C: N	Sympagic Carbon (%)	
Bearded Seal		**-19.41(0.17)**		**16.69 (0.12)**		**3.26 (0.03)**	**66.40 (2.12)**	
pups	15	-18.78 (0.25)	A	17.38 (0.15)	A	3.21 (0.04)	68.60 (3.37)	A
juvenile	8	-19.93 (0.31)	BC	16.59 (0.21)	B	3.56 (0.07)	61.22 (5.34)	A
adult	14	-19.86 (0.26)	B	16.12 (0.09)	B	3.27 (0.07)	66.34 (3.50)	A
Harbour Seal		**-19.62 (0.32)**		**18.1(0.28)**		**3.43 (0.05)**	**70.13 (4.48)**	
pups	3	-19.36 (0.62)	AB	17.93 (0.78)	A	3.37 (0.03)	71.23 (6.33)	A
juvenile	2	-19.69 (0.62)	ABC	17.97 (0.05)	A	3.4 (0.05)	76.08 (5.34)	A
adult	1	-19.29	ABC	18.87	A	3.64	54.96	A
Ringed Seal		**-20.78 (0.07)**		**16.04 (0.09)**		**3.32 (0.02)**	**45.33 (2.35)**	
pups	18	-20.88 (0.13)	C	15.51 (0.17)	C	3.27 (0.04)	53.51 (3.08)	B
juvenile	14	-20.88 (0.12)	C	16.27 (0.08)	B	3.38 (0.05)	40.27 (4.90)	B
adult	18	-20.59 (0.12)	BC	16.40 (0.06)	B	3.33 (0.03)	41.09 (3.77)	B

Table 4.2. Isotopic niche overlap calculated from the standard ellipse area and 95% predicted isotopic ($\delta^{13}C$, $\delta^{15}N$) among ringed, bearded and harbour seals liver tissue collected from seals hunted during the open-water period in Arviat, Nunavut from 2006 – 2017.

	Standard ellipse	95% ellipse
Bearded and Ringed		
% Shared Area	3.1	39.0
% Ringed seal ellipse overlapped by bearded	4.5	83.8
% Bearded seal ellipse overlapped by ringed	9.0	42.2
Harbour and Ringed		
% Shared Area	-	23.1
% Ringed seal ellipse overlapped by harbour	-	54.0
% Harbour seal ellipse overlapped by ringed	-	28.7
Harbour and Bearded		
% Shared Area	-	27.7
% Bearded seal ellipse overlapped by harbour	-	45.9
% Harbour seal ellipse overlapped by bearded	-	43.4

Figures

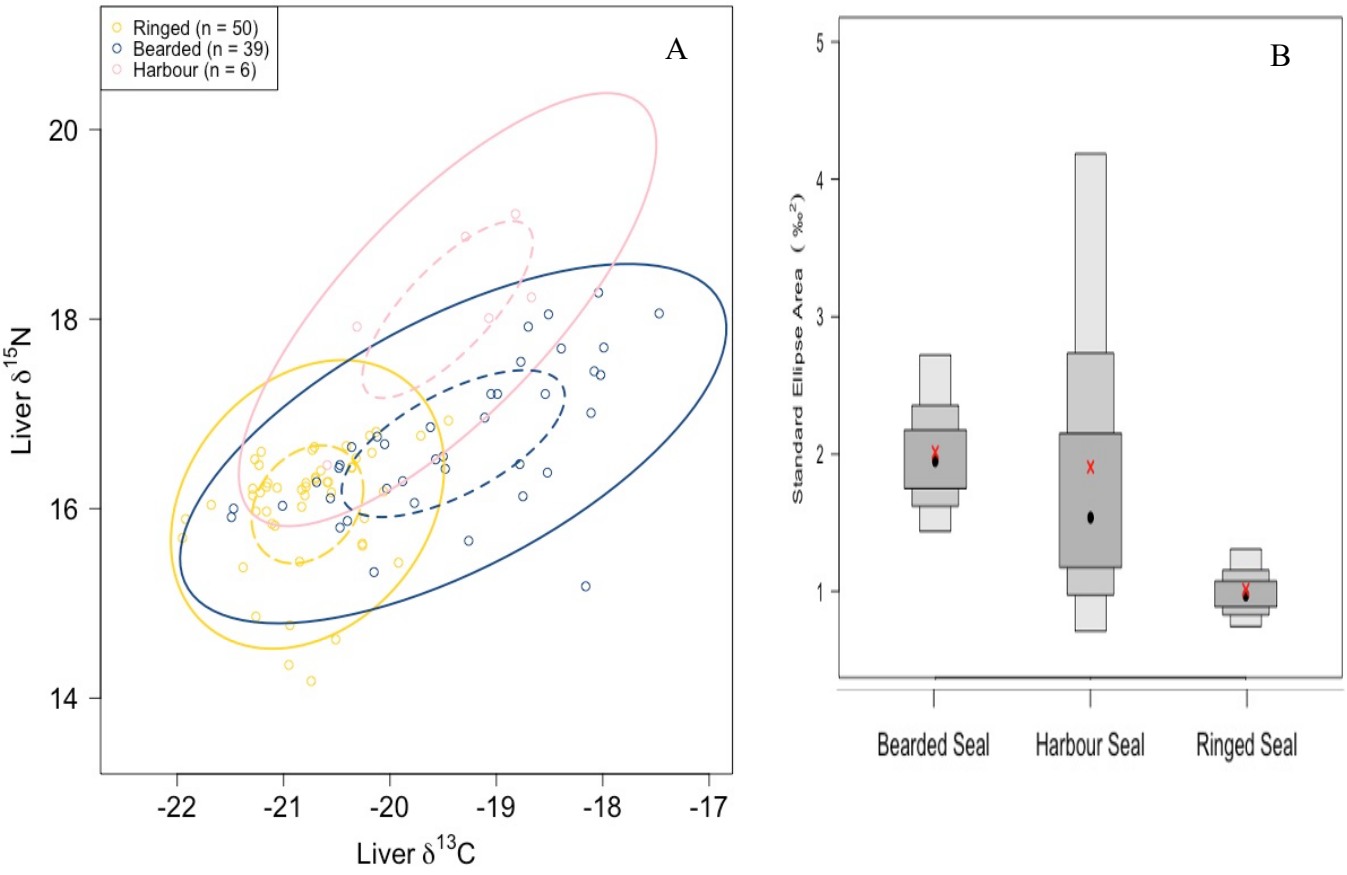

Figure 4.1. Isotopic biplot (A) of liver $\delta^{13}$and δ^{15}N for ringed (yellow), bearded (blue) and harbour seals (pink), both standard ellipse areas (SEA, dashed line) and 95% prediction ellipses (solid line) are shown. Bayesian standard ellipse areas (‰^{2}) estimates (isotopic niche breadth) (B) from harvested seals in Arviat in 2005—2017. On the boxplots, the black circle represents the Bayesian modal SEA estimates and the boxes indicate the Bayesian credible intervals at 50 % (dark gray), 75 % (medium gray), and 95 % (light gray). The red x represents the single standard ellipse area corrected for small sample size (SEA_C).

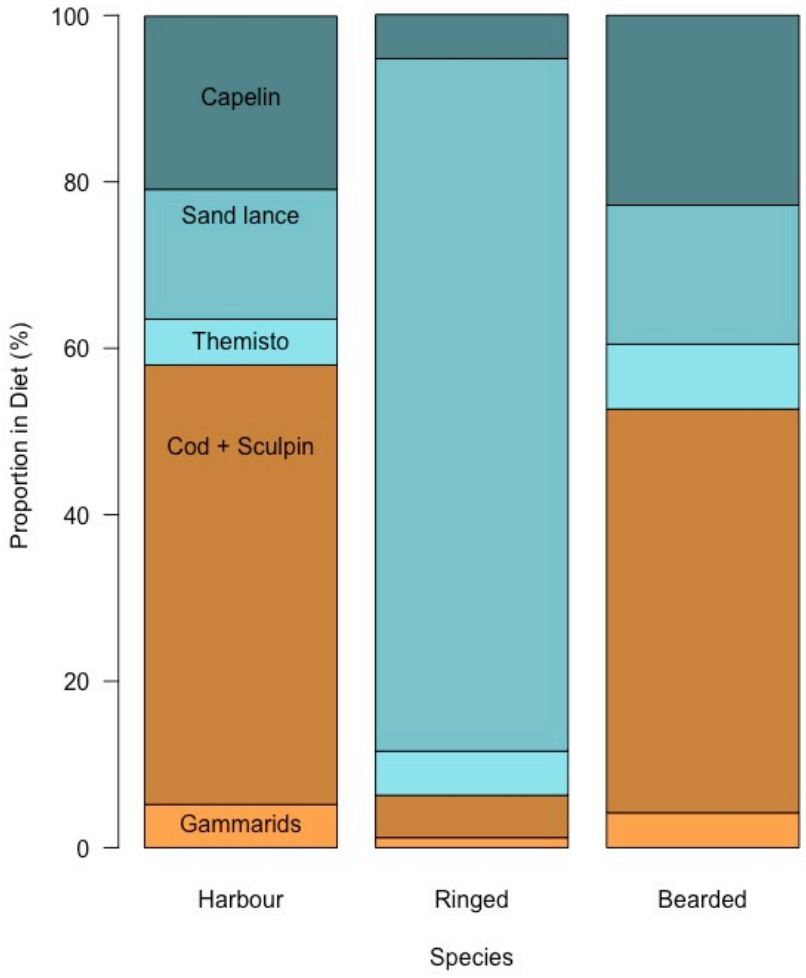

Figure 4.2. Mean liver MixSIAR prey portions of ringed (n=50), bearded (n=39) and harbour seal (n=6) diet from Arviat, Nunavut sampled 2006 – 2017 during the fall harvest.

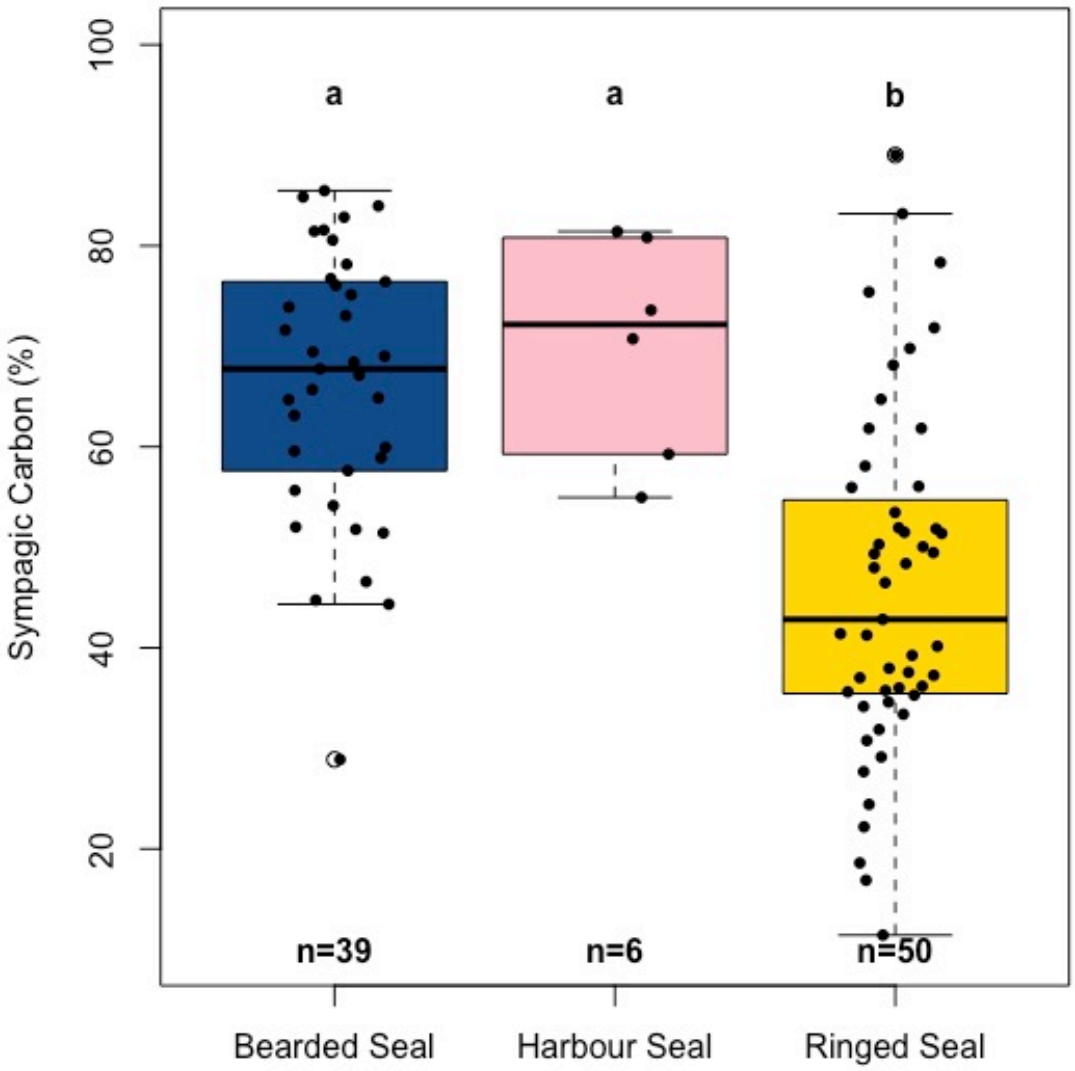

Figure 4.3. Comparison of sympagic carbon (%) as percentage of marine carbon among seal species. Horizontal bars represent median values, and upper and lower portions of the boxes are the 1st and 3rd quartile range. Each black point represents a single individual sympagic carbon (%) value sampled from liver tissues collected from 2005 – 2017 in Arviat, Nunavut.

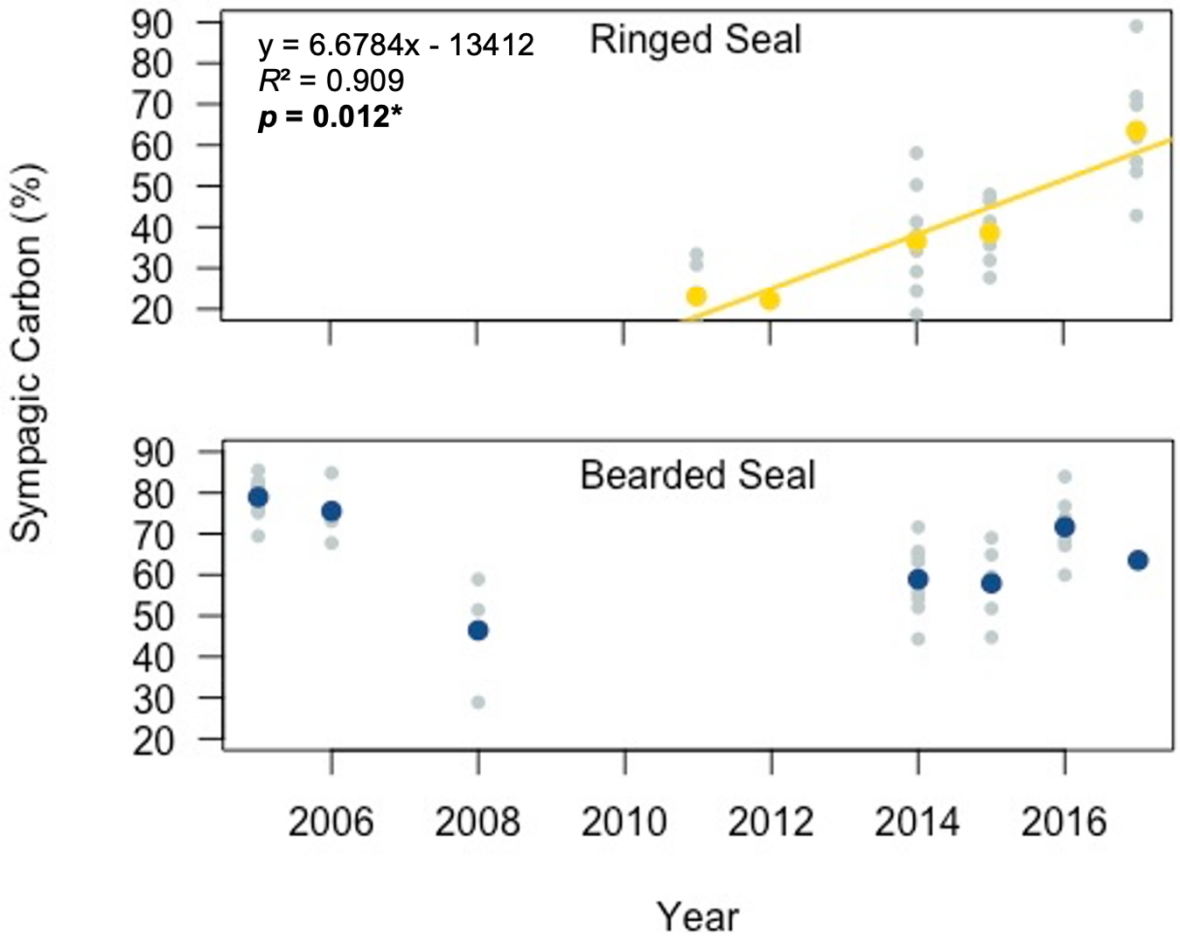

Figure 4.4. Temporal trends of Sympagic carbon (%) of Arviat ringed seals (yellow [top]) and bearded seals (blue [bottom]) from 2005 – 2017. Linear regression (yellow line) was performed on mean annual values. Grey points represent individuals and coloured represent the annual mean.

Appendices

Table A4.1. Tukey's post hoc test comparing nitrogen stable isotope ratios ($\delta^{13}C$) (‰) between Arviat seal species (bearded, harbour and ringed) and age classes (pups, juvenile and adult). Significant differences between age/sex classes are indicated in bold.

Species	Age Class	n	Bearded Seal			Harbour Seal			Ringed Seal		
			Pups	Juvenile	Adult	Pups	Juvenile	Adult	Pups	Juvenile	Adult
Bearded Seal	Pups	15	-	**0.015**	**0.004**	0.939	0.767	0.999	**<0.0001**	**<0.0001**	**<0.0001**
	Juvenile	8		-	1.000	0.998	1.000	0.996	0.069	0.098	0.456
	Adult	14			-	0.977	1.000	0.998	**0.005**	**0.012**	0.124
Harbour Seal	Pups	3				-	1.000	1.000	**0.033**	**0.041**	0.161
	Juvenile	2					-	1.000	0.426	0.449	0.769
	Adult	1						-	0.469	0.482	0.723
Ringed Seal	Pups	18							-	1.000	0.960
	Juvenile	14								-	0.975
	Adult	18									-

Table A4.2. Tukey's post hoc test comparing nitrogen stable isotope ratios ($\delta^{15}N$) (‰) between Arviat seal species (bearded, harbour and ringed) and age classes (pups, juvenile and adult). Significant differences between age/sex classes are indicated in bold.

Species	Age Class	n	Bearded Seal			Harbour Seal			Ringed Seal		
			Pups	Juvenile	Adult	Pups	Juvenile	Adult	Pups	Juvenile	Adult
Bearded Seal	Pups	15	-	**0.028**	**<0.0001**	0.736	0.861	0.150	**<0.0001**	**<0.0001**	**<0.0001**
	Juvenile	8		-	0.533	**0.009**	**0.038**	**0.003**	**0.0002**	0.906	0.993
	Adult	14			-	**<0.0001**	**0.0004**	**<0.0001**	**0.046**	0.998	0.826
Harbour Seal	Pups	3				-	1.000	0.835	**<0.0001**	**0.0001**	**0.0004**
	Juvenile	2					-	0.895	**<0.0001**	**0.002**	**0.004**
	Adult	1						-	**<0.0001**	**0.0003**	**0.0006**
Ringed Seal	Pups	18							-	**0.004**	**<0.0001**
	Juvenile	14								-	0.999
	Adult	18									-

Table A4.3. Tukey's post hoc test comparing sympagic carbon (%) between Arviat seal species (bearded, harbour and ringed). Significant differences between species are indicated in bold.

Species	n	Bearded Seal	Harbour Seal	Ringed Seal
Bearded Seal	39	-	0.9956	**<0.001**
Harbour Seal	6		-	**0.005**
Ringed Seal	50			-

Table A4.4. Mean and Bayesian 95% credible intervals of MixSIAR estimated prey proportions (%) in the diet of combined age/sex groups of harbour, ringed and bearded seal liver tissues collected from 2005 – 2017 in Arviat.

Species	n	Mean prey contribution (%) to seal diet (95% CI)				
		Gammarids	Cod+Sculpin	Themisto	Sand lance	Capelin
Harbour Seal	6	5.2 (0, 15.1)	52.8 (16.3, 80.2)	5.5 (1, 14.6)	15.6 (1.2, 39.2)	20.8 (1.5, 53.5)
Ringed Seal	50	1.2 (0, 3.4)	5.1 (0, 13.4)	5.3 (0, 11.6)	83.2 (69, 93.7)	5.3 (1, 14.3)
Bearded Seal	39	4.2 (1, 9.8)	48.5 (22.5, 69.1)	7.8 (1, 15.3)	16.7 (2.4, 36.1)	22.8 (2.3, 54.9)

Chapter 5: General Conclusion

Examining factors that influence a species realized ecological niche assists in completing our understanding of food web dynamics, particularly in a time of rapid ecosystem change. Investigating the variations of a species realized niche better able us to define a species fundamental niche. In this thesis, I examined the isotopic niche breadth and diet proportions of ringed seals (*Pusa hispida*) at the population and individuals levels to better understand the adaptive responses to a changing environment. Considering the ecological niche concept, I was able to test foraging theory over time and locations to provide support for the niche variation hypothesis (Van Valen 1965; Chapter 3), and evidence of intra- and interpopulation niche partitioning (Schoener 1974; Chapter 3 and 4). I also used a combination of dietary markers that can be used to investigate niche expansion and foraging plasticity (Chapters 2 and 4).

In this thesis, I examined the foraging ecology of ringed seals in Hudson Bay, an area at the southern extent of their range, where presumably continued climate warming is likely going to have the largest influences (Hoover et al. 2013a; 2013b), I investigated changed in ringed seal diet by analyzing stable isotopes and highly branched isoprenoid (HBI) biomarkers in three tissues that have been used to investigate dietary changes in other marine predators (Iverson et al. 2004; Beck et al. 2007; Yurkowski et al. 2016; Brown et al. 2014). Overall, the findings in this thesis provide an understanding of prey contributions to the diet of Arctic endemic phocid species. Furthermore, I highlighted the increase in sympagic carbon contribution to ringed seal diet overtime. However, the HBI data presented in Chapter 4 may not indicate a weakened association between ringed seals and sympagically derived carbon. Yurkowski et al. (2020) found that ringed seal niche breadth

remained relatively constant throughout during a period similar to that in this thesis, using only muscle tissues, and in Chapter 2, I documented a decreasing niche breadth from 2003 – 2017. Ringed seals may be attempting foraging on sympagically linked prey, but not consuming in high enough proportions. I found spatial difference in isotopic niche breadth of ringed seals between western and eastern Hudson Bay (Chapter 2) which provides support for the for variation in spatial foraging of the species. Specifically, I found contrasting patterns in that ringed seals in western Hudson Bay have narrowing isotopic niche breadth and seals in eastern Hudson Bay have expanding isotopic niche breadth. The seals examined in this study follow ontogenetic niche shifts, where adults isotope ratios represent that they are feeding on higher trophic level compared to pups and juveniles.

This thesis found little evidence for dietary resource competition between ringed seals within the same age classes (Chapter 3) and harbour seals (*Phoca vitulina*) when comparing liver stable isotopes from Arviat (Chapter 4). While competition theory states that species that occupy similar ecosystem roles that feed on similar prey will exhibit niche partitioning (Schoener 1974), it could be that these two species are already partiting available resources given the low overlap. Bearded seals (*Erignathus barbatus*) were found to have more similar diets to harbour seals (Chapter 4) and both species had higher dependence on sympagically dervived carbon. Additionally, as this thesis focused only on two elements in stable isotope niche determination, the inclusion of other elements such as sulpher or oxygen could eludicate proportions of marine and freshwater carbon contributions to stable isotope ratios (Finlay and Kendall 2007). In Chapter 2, I found that seals in Sanikiluaq have an expanding niche at the population level, which based on the strong evidence from Chapter 3 that indicates the high intra-individual diet consistency and high

degree of individual specialization is an explanation to the widening population level niche breadth observed.

Stable isotope ecology can be useful to describe trophic interactions within a foodweb. Aspects of isotope ecology that this study has not be able to take into consideration are abiotic, such as sea ice phenology. In the Arctic, sea ice decline has contributed to species dietary and distributional shifts, particularly for species strongly associated with sea ice habitat (Laidre et al. 2008). Studies have linked variation in sea-ice phenology with aspects of foraging ecology, including niche breadth, diet estimates, body condition and movement (Johnson et al. 2019; Reimer et al. 2019). An investigation that models sea ice dynamics and seal dietary biomarkers together in a empirical model could further endhnace our understanding of the energy transfer from sympagic carbon producers to ringed seals.

Biotic factors that were not included in this study include a lack of consideration for parasite ecology. Parasites can influence an individual's stable isotope signature (Lafferty et al. 2008), Indeed, this has been documented in wolves (*Canis lupus*), where alternative prey use increased parasite infections (Friesen and Roth 2016). Presumably as other taxa are experiencing poleward shifts, parasites are also likely expanding into regions previously not occupied. For instance, Kutz et al. (2013) reports parasites range changes into the Arctic, and like other species are also shifting their distributions towards the poles. Parasites have been documented to alter Arctic fish measured isotopic niches due to the changes of lipid routing (Molbert et al. 2022). Arctic food web modelling has typically not included parasites in the community structure and thus, I may be missing information regarding changes to baselines or signatures of species that I am tracking. Given that the seals investigated in this thesis are at the southern extent of their range

and are known to have decreased body condition (Ferguson et al. 2020), and Ogloff et al. (2022) found support that seals in this area may be undergoing a stress response as an adaption to food scarcity, and mobilizing their energy stores, altering the chemical signals for diet estimation. Parasites further exacerbate this by removing chemical signatures for their own tissues that do not get incorporated into the seal's tissues. Indeed, Barratclough et al. (2023) summarize Arctic marine mammal health, with a diversity of parasite taxa being found within the digestive tracts of some marine mammals.

Additional biotic factors that were not included in this study include prey abundance and distribution. There is documented heterogeneity among esturasy areas of Hudson Bay (Morin et al. 1980), that likely influence the prey type availability in the different regions of Hudson Bay. Wassmann et al. (2011) highlight the expansion of subarctic fish, including sand lance (*Ammodytes spp.*) and capelin (*Mallotus villosus*), two fish that were dominate in seal diets estimated in this thesis; However, there is a lack of understanding of the abundance of these species and I am unable to describe the foraging behaviours and ecology of ringed seals. Current predictive models do indicate that there will be changes to the biomass, abundance and distribution to key forage fish in Hudson Bay (Florko et al. 2021), which predict increases of sand lance abdundance. Ultimately, changes to biomass of forage fish will impact the niche of phocid predators, potentitally leading to increased isotopic and dietary overlap between ringed seals and harbour seals.

Fundamental studies that describe dietary patterns enable us to better understand the food web and strength of connections within (Paine 1980). This thesis provides the first estimated ringed seal dietary proportions and comparisons using Bayesian mixing models in this southern part of their range. The ringed seals studied here at southern extent of their range is where climate

warming is likely going to have the largest influences. Characterizing changes ringed seal diet by analyzing stable isotopes and highly branched isoprenoid biomarkers in three tissues that have been used to investigate dietary changes in other marine predators (Iverson et al. 2004; Beck et al. 2007; Yurkowski et al. 2016; Brown et al. 2014) will help us establish baselines for projected change in other areas less studied, or yet to experience environment degradation. Overall, the findings in this thesis provide an understanding of prey contributions to the diet of Arctic endemic phocid species. Collectively, this thesis contributes to our fundamental understanding of the ringed seals realized niche and how intrapopulation niche variation.

Literature Cited

Barratclough, A., Ferguson, S. H., Lydersen, C., Thomas, P. O., & Kovacs, K. M. (2023). A review of circumpolar Arctic marine mammal health—a call to action in a time of rapid environmental change. *Pathogens*, *12*(7), 937.

Beck, C. A., Iverson, S. J., Bowen, W. D., & Blanchard, W. (2007). Sex differences in grey seal diet reflect seasonal variation in foraging behaviour and reproductive expenditure: evidence from quantitative fatty acid signature analysis. *Journal of Animal Ecology*, *76*(3), 490-502.

Brown, T. A., Alexander, C., Yurkowski, D. J., Ferguson, S. H., & Belt, S. T. (2014). Identifying variable sea ice carbon contributions to the Arctic ecosystem: A case study using highly branched isoprenoid lipid biomarkers in Cumberland Sound ringed seals. *Limnology and Oceanography*, *59*(5), 1581-1589.

Ferguson, S. H., Yurkowski, D. J., Young, B. G., Fisk, A. T., Muir, D. C., Zhu, X., & Thiemann, G. W. (2020). Comparing temporal patterns in body condition of ringed seals living within their core geographic range with those living at the edge. *Ecography*, *43*(10), 1521-1535.

Finlay, J. C., & Kendall, C. (2007). Stable isotope tracing of temporal and spatial variability in organic matter sources to freshwater ecosystems. *Stable isotopes in ecology and environmental science*, 283-333.

Florko, K.R.N., Tai, T.C., Cheung, W.W.L., Ferguson, S.H., Sumaila, U.R., Yurkowski, D.J. & Auger-Méthé, M. (2021). Predicting how climate change threatens the prey base of Arctic marine predators. *Ecology Letters, 24*, 2563–2575.

Friesen, O. C., & Roth, J. D. (2016). Alternative prey use affects helminth parasite infections in grey wolves. *Journal of Animal Ecology*, *85*(5), 1265-1274.

Hoover, C., Pitcher, T. & Christensen, V. (2013a) Effects of hunting, fishing and climate change on the Hudson Bay marine ecosystem: I. Re-creating past changes 1970–2009. *Ecological Modelling, 264*, 130–142.

Hoover, C., Pitcher, T. & Christensen, V. (2013b) Effects of hunting, fishing and climate change on the Hudson Bay marine ecosystem: II. Ecosystem model future projections. *Ecological Modelling, 264*, 143–156

Iverson, S. J., Field, C., Don Bowen, W., & Blanchard, W. (2004). Quantitative fatty acid signature analysis: a new method of estimating predator diets. *Ecological Monographs*, *74*(2), 211-235.

Johnson, A. C., Hobson, K. A., Lunn, N. J., McGeachy, D., Richardson, E. S., & Derocher, A. E. (2019). Temporal and intra-population patterns in polar bear foraging ecology in western Hudson Bay. *Marine Ecology Progress Series*, *619*, 187-199.

Kutz, S. J., Hoberg, E. P., Molnár, P. K., Dobson, A., & Verocai, G. G. (2014). A walk on the tundra: host–parasite interactions in an extreme environment. *International Journal for Parasitology: Parasites and Wildlife*, *3*(2), 198-208.

Lafferty, K. D., Allesina, S., Arim, M., Briggs, C. J., De Leo, G., Dobson, A. P., Dunne, J. A., Johnson, P. T., Kuris, A. M., Marcogliese, D. J., Martinez, N. D., Memmott, J., Marquet, P. A., McLaughlin, J. P., Mordecai, E. A., Pascual, M., Poulin, R., & Thieltges, D. W. (2008). Parasites in food webs: the ultimate missing links. *Ecology letters*, *11*(6), 533–546.

Laidre, K. L., Stirling, I., Lowry, L. F., Wiig, Ø., Heide-Jørgensen, M. P., & Ferguson, S. H. (2008). Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. *Ecological Applications*, *18*(sp2), S97-S125.

Molbert, N., & Goutte, A. (2022). Narrower isotopic niche size in fish infected by the intestinal parasite *Pomphorhynchus sp*. compared to uninfected ones. *Journal of Fish Biology*, *101*(6), 1466-1473.

Morin, R., Dodson, J., & Power, G. (1980). Estuarine fish communities of the eastern James-Hudson Bay coast. *Environmental Biology of Fishes*, *5*, 135-141.

Ogloff, W. R., Anderson, R. A., Yurkowski, D. J., Debets, C. D., Anderson, W. G., & Ferguson, S. H. (2022). Spatiotemporal variation of ringed seal blubber cortisol levels in the Canadian Arctic. *Journal of Mammalogy*, *103*(5), 1208-1220.

Paine, R. T. (1980). Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology*, *49*(3), 667-685.

Reimer, J. R., Brown, H., Beltaos-Kerr, E., & de Vries, G. (2019). Evidence of intraspecific prey switching: stage-structured predation of polar bears on ringed seals. *Oecologia*, *189*(1), 133-148.

Schoener, T. W. (1974). Resource Partitioning in Ecological Communities: Research on how similar species divide resources helps reveal the natural regulation of species diversity. *Science*, *185*(4145), 27-39.

Van Valen, L. (1965). Morphological variation and width of ecological niche. *The American Naturalist*, *99*(908), 377-390.

Wassmann, P., Duarte, C.M., Agustí, S. & Sejr, M.K. (2011) Footprints of climate change in the Arctic marine ecosystem. *Global Change Biology, 17*, 1235–1249.

Yurkowski, D. J., Ferguson, S. H., Semeniuk, C. A., Brown, T. M., Muir, D. C., & Fisk, A. T. (2016). Spatial and temporal variation of an ice-adapted predator's feeding ecology in a changing Arctic marine ecosystem. *Oecologia*, *180*, 631-644.

Yurkowski, D. J., Richardson, E. S., Lunn, N. J., Muir, D. C., Johnson, A. C., Derocher, A. E., ... & Ferguson, S. H. (2020). Contrasting temporal patterns of mercury, niche dynamics, and body fat indices of polar bears and ringed seals in a melting icescape. *Environmental Science & Technology*, *54*(5), 2780-2789.