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Using isotopic niche dynamics to predict resiliency to climate change in an Arctic seabird.

By

Kyle J. L. Parkinson

A Thesis
Submitted to the Faculty of Graduate Studies
through the Department of Integrative Biology
in Partial Fulfillment of the Requirements for
the Degree of Master of Science
at the University of Windsor

Windsor, Ontario, Canada

2020

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Using isotopic niche dynamics to predict resiliency to climate change in an Arctic seabird

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DECLARATION OF CO-AUTHORSHIP

I. Co-Authorship

I hereby declare that this thesis incorporates material that is result of joint research, as follows:

The thesis incorporates the results from a collaboration with researchers at Environment and Climate Change Canada (Dr. H. Grant Gilchrist and Dr. Holly L. Hennin; chapters 2,3), Western University (Dr. Keith A. Hobson, chapters 2,3), La Rochelle Université (Dr. Jerome Fort, chapters 2,3), University of Windsor (Dr. Nigel Hussey; chapters 2,3), University of Iceland (Dr. Jón Einar Jónsson, chapter 3), the Faroese Marine Research Institute (Dr. Jóhannis Danielsen, chapter 3), the Russian Academy of Sciences (Dr. Grigori Tertitski, chapter 3), Acadia University (Dr. Mark Mallory, chapter 3), and the Norwegian Polar Institute (Dr. Børge Moe and Dr. Sveinn Are Hanssen, chapter 3), all under the supervision of Dr. Oliver P. Love. In all cases, the key ideas, primary contributions, experimental designs, data analysis, interpretations, and writing were performed by the author with input from each of the co-authors on writing and idea development in their respective chapters. In chapter 2, all co-authors assisted with idea development, Dr. Hennin and Dr. Love assisted with writing and statistical analyses, while Dr. Hussey and Dr. Hobson provided guidance in stable isotope interpretation. Dr. Hussey provided laboratory space for sample preparation, and Dr. Hobson provided laboratory space to analyze all samples. In chapter 3, Dr. Hennin and Dr. Love assisted with statistical analyses and writing, Dr. Fort provided laboratory space for sample preparation and stable isotope interpretation. Drs. Jónsson, Danielsen, Mallory, Moe, and Hanssen assisted with sample collection, with Dr. Hobson providing further stable isotope interpretations.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis, and have obtained written permission from each of the co-author(s) to include the above material(s) in my thesis.

I certify that, with the above qualification, this thesis, and the research to which it refers, is the product of my own work.

II. General

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ABSTRACT

Resource limitation drives fitness-related decisions and constrains the ability of organisms to invest in energetically demanding life history stages. Environmental factors (e.g., temperature) play an important role in affecting resource availability and quality which can downstream effect the ability of individuals to invest in energetically demanding life history stages, including reproduction. Human-induced climate change is generating increasingly variable environmental conditions, impacting the abundance and distribution of prey items and therefore the ability of individuals to successfully reproduce, and these effects are especially pronounced in the Arctic. However, it is currently unknown whether Arctic organisms possess the ability to adjust foraging decisions and prey selection to overcome newly emerging environmental constraints. Quantifying stable isotopes in the tissues of consumers provides a minimally invasive method of inferring foraging niche; however, has yet to be validated as a method of predicting population-level resiliency to climate change. Seabirds are a useful system to test these linkages in because they are wide-ranging, predominantly oceanic-based group, reliant on marine-based resources and they are often widely distributed across polar regions. Using common eiders (*Somateria mollissima*), an Arctic diving seabird, as a model organism, this thesis examines the linkages between environmental variation, isotopic variation in foraging niche, and breeding parameters, as a means of predicting the resiliency of Arctic seabirds to the effects of climate change. Using a long term data set from a focal breeding colony, I found significant inter-annual and inter-breeding stage variation in isotopes and isotopic niche. Although environmental cues only weakly predicted variation in isotopic niche, variation in isotopic niche was a key predictor of breeding probability. Given that variation in isotopic niche has fitness-related impacts, I then took a species-wide approach to assess inter-colony variation in isotopic niche by sampling 8 breeding colonies across the distribution of eiders. While common eiders are a generalist species overall, individual colonies had significantly different foraging strategies and levels of generalization. Taken together, these results suggest that common eiders are likely to be resilient in the face of climate change, but some colonies may be more at risk from the ongoing effects of climate change. This thesis provides the first steps towards developing a minimally invasive method for foraging flexibility as a means of assessing the resiliency of Arctic seabirds to climate change.

DEDICATION

To my parents, this is as much yours as it is mine. Thank you.

ACKNOWLEDGEMENTS

I want to start by acknowledging my primary supervisor, Dr. Oliver Love. With every new idea I thought of, you never wavered, and always supported me with long meetings and often looking for additional graduate students to take on everything I could not. You have pushed me harder than anyone ever has, and I cannot thank you enough for this. The experiences that I have had during my time in your lab are unforgettable and would not have been possible without your support and encouragement. Thank you, Oli.

I also want to thank my co-supervisor, Dr. Grant Gilchrist for helping take my thesis project to an international scale. Grant, your positivity in and out of the field is infectious, and your input to my thesis has been instrumental. Thank you for providing access to one of the most amazing field sites I have ever worked in.

Dr. Holly Hennin, you are my supervisor, my mentor, and my friend. You really have taught me how to be a fully-fledged scientist. Through editing my drafts, interpreting my thoughts and refining them into actual questions, and always supporting me, you have been by my side every step of the way. The 2017 field season was life changing for me, and I am so grateful to have gone through that experience with you.

Thank you to Dr. Keith Hobson for helping me understand stable isotopes and providing analytical services. Your wealth of knowledge has been instrumental throughout the progression of my thesis.

I would also like to thank Dr. Jerome Fort for his support in analyzing all of the international eider samples. The service you provided was key to my thesis, and your continued support is very appreciated. My time in La Rochelle will always be a highlight of my degree.

I would like to thank my committee (Dr. Nigel Hussey & Dr. Scott Mundle) for their feedback throughout my degree. I want to give a special mention to Stephanie Isaac for teaching me how to prepare all my isotope samples. I hope to continue applying the skills you have given me for the rest of my career.

I would like to thank all my sources of funding, particularly Ontario Graduate Scholars for my graduate scholarship, and the University of Windsor for the tuition waiver and additional funding.

To every EBI field crew member, thank you for your hard work in assisting with data collection. My thesis includes nearly a decade of data collected from East Bay, as such there are countless people that need to be acknowledged. In particular, I would like to give nod to the 2017 crew (Holly Hennin, Michael Janssen, Frankie Jean-Gagnon, Catherine Geoffroy, Alexandra Langwieder, Brandon Norman, Rolanda Steenweg, and Patrick Jagielski) and the 2018 crew (Reyd Smith, Frederic Dulude-de Broin, and Russell Turner). You all share the passion I have for field work, and you have made my Arctic adventure one to remember. I am forever grateful to the experiences I have shared with you.

East Bay would not be the field site that it is without the continued support from the Environment and Climate Change Canada field technicians, specifically Michael Janssen, Nik Clyde, Amie Black, and Christie Macdonald. Additionally, Rob Kelley and Isabel Buttler, thank you for carefully managing all the data we collect each summer. Your organizational skills are impeccable and have always been ready with my data queries. Thank you!

To all the international collaborators (Dr. Jón Einar Jónnson, Dr. Mark Mallory, Dr. Sveinn Are Hannsen, Dr. Børge Moe, Dr. Jóhannis Danielsen, Dr. Grigori Teritski, Dr. Christopher Latty) and everyone else that assisted with our world-wide data collection effort, thank you. The idea of running an inter-colony analysis was a lofty goal for a master's thesis, but with all your hard work, we pulled it off!

Love lab and fellow Biology graduate students, you are an amazing group of talented researchers, and it has been a pleasure working alongside you. With that, I need to thank my lab mates: Theresa Warriner, Colin Finerty, Sydney Courier, Erica Geldart, Alyssa Eby, Madison Sturba, and Reyd Smith.

To my lab manager, Christopher Harris. You are always a rock for me, providing sound advice and calming words. You taught me to think carefully and critically about some of the (even I will say it) farfetched ideas I come up with.

To the staff in Biology and GLIER, in particular Nancy Barkley and Mary-Lou Scratch, thank you for all the work you do for the graduate students. You are kind, organized, and keep everyone's degrees running smoothly.

This degree has been challenging at times, and the support of my friends has made this possible. In particular I would like to thank Amy Ketch, you are my oldest friend and I cherish you so much. Bethany Nordstrom and Eric Sylvester, thank you for always pushing me to be the best version of myself. Finally, I need to give, possibly the biggest acknowledgment, to Reyd Smith. Our friendship will last a lifetime, even while I continue to crush you in leg wrestles.

A quick shout-out to the coffee shops in Windsor, and FO and AG for getting me through sample prep.

To my family: Dad, you have taught me how to work hard, to face adversity head on, and never give up. Kristina, you understand me better than most, and our talks on the phone have fueled me through challenging moments. Ann and Jim, thank you for providing me a sense of family while I have been away from mine. You have both done so much for me over these past two years, and I appreciate you so much. Mom, I don't have the words to explain how much I appreciate you. You are inspiring with your generosity, your unwavering love, and unconditional support. I love you all, and this thesis is as much yours as it is mine.

Finally, that leaves Shayne. You have seen me through it all, and here we are. We made it. You have changed my life, and I am forever grateful to you. I want to go on and on but know that everything you have done has not gone unnoticed. I cannot wait to start the next chapter with you.

TABLE OF CONTENTS

DECLARATION OF CO-AUTHORSHIP	iii
ABSTRACT	v
ACKNOWLEDGEMENTS	vii
LIST OF TABLES	xiii
LIST OF FIGURES	xvi
Chapter 1 : General Introduction	1
<i>Roles of foraging flexibility in overcoming resource limitation</i>	1
<i>Using stable isotopes and isotopic niches to assess resiliency to change</i>	2
<i>Effects of climate change on resources and reproduction</i>	5
<i>Seabirds as useful models to assess resiliency to environmental change</i>	6
<i>Study species</i>	7
<i>Thesis goals and chapter objectives</i>	9
<i>References</i>	10
Chapter 2 : Estimating resiliency to environmental change in an Arctic seabird using inter-annual and breeding stage related variation in isotopic niche dynamics	17
<i>Introduction</i>	17
<i>Methods</i>	21
<i>Study system and breeding parameters</i>	21
<i>Environmental indices</i>	23
<i>Stable isotope analysis, niche metrics, and interpretation</i>	24
<i>Statistical analyses</i>	26
<i>Results</i>	27
<i>Inter-annual and breeding stage variation in isotopic signatures</i>	27
<i>Changes in isotopic values across breeding stages</i>	27
<i>Using climate to predict isotopic metrics</i>	27
<i>Using isotopic metrics to predict breeding parameters</i>	28
<i>Discussion</i>	28

<i>Interactions between inter-annual and breeding-stage related variation in $\delta^{15}\text{N}$ and $\delta^{35}\text{C}$ values</i>	29
<i>Links between isotopic niche variation and breeding investment decisions</i>	30
<i>Lack of a detectable relationship between environmental conditions and isotopic characteristics</i>	32
<i>Conclusions and future directions</i>	32
<i>Acknowledgements</i>	33
<i>References</i>	34
Chapter 3 : Investigating resiliency to climate change in an Arctic seabird using inter-colony isotopic niche variation	53
<i>Introduction</i>	53
<i>Methods</i>	57
<i>Study sites and blood sample collection</i>	57
<i>Environmental indices</i>	57
<i>Stable isotope analysis</i>	58
<i>Calculation and interpretation of niche dynamics</i>	60
<i>Statistical analyses</i>	61
<i>Results</i>	61
<i>Inter-colony variation in isotopic values</i>	61
<i>Spatial predictors of isotopic variation</i>	61
<i>Inter-colony variation in environmental variables</i>	62
<i>Relationship between isotopic niche and environmental variables</i>	62
<i>Discussion</i>	62
<i>Inter-colony variation in isotopic niches</i>	63
<i>Environmental variation weakly relates to inter-colony variation in isotopic niches</i>	64
<i>Using isotopic niche specialization to predict resiliency across colonies</i>	65
<i>Conclusions and future directions</i>	67
<i>Acknowledgments</i>	68
<i>References</i>	69
Chapter 4 : A novel application of stable isotopes: using isotopic variation to link environmental conditions, breeding parameters, and resiliency to change	88
<i>Interpreting a novel application of stable isotopes</i>	89

<i>Spatiotemporal isotopic variation</i>	90
<i>Life history investment modulated through foraging decisions</i>	91
<i>Flexible foraging in response to broad- and fine-scale environmental variation</i>	92
<i>A novel technique estimating resiliency through stable isotope analysis</i>	92
<i>Environmental constraints driving foraging decisions</i>	93
<i>Modulating foraging decisions across multiple temporal scales</i>	95
<i>Future directions and conclusions</i>	95
<i>References</i>	98
VITA AUCTORIS	102

LIST OF TABLES

Table 2.1 - Summary of key common eider parameters collected from Mitivik Island, Nunavut used in the current analyses. Parameters include relative arrival date (RAD), breeding propensity (BP), laying interval (LI), relative lay date (RLD).	41
Table 2.2 - Summary of isotopic metrics from female common eiders breeding at the Mitivik Island colony, Nunavut, Canada.	42
Table 2.3 - Summary of average Winter North Atlantic Oscillation (Winter NAO), Spring North Atlantic Oscillation (Spring NAO), and mean relative ambient temperature (Ta) for the 7 days leading up median arrival date, from Coral Harbour Airport Weather Station, Nunavut, Canada (closest weather station to the Mitivik Island colony).	43
Table 2.4 - List of principal component correlation values based on plasma isotopic metrics of female common eiders breeding at the Mitivik Island colony, Nunavut, Canada and environmental metrics (see Methods for details). Bold values indicate statistically significant relationships.	44
Table 2.5 - Summary of analyses examining predictors of variance in plasma $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in female common eiders breeding at the Mitivik Island colony, Nunavut, Canada. Bold values indicate statistically significant relationships.	45
Table 2.6 - Summary of regression analyses using environmental metrics (ENVPC1 (Spring Weather); and ENVPC2 (NAO)) to predict variation in plasma isotopic metrics (ISOPC1 (Foraging Location); ISOPC2 (Niche Breadth); and ISOPC3 (Trophic Position)) in female common eiders breeding at the Mitivik Island colony, Nunavut, Canada. Bold values indicate statistically significant relationships.	46
Table 2.7 - Summary of regression analyses between breeding parameters (relative arrival date (RAD); percent breeding propensity (BP); laying interval (LI); relative lay date (RLD)) and isotopic metrics (ISOPC1 (Foraging Location); ISOPC2 (Niche Breadth); and ISOPC3 (Trophic Position)).	47
Table 3.1 – Summary of common eider colonies sampled for stable isotopic analysis. Eiders have an expansive range, as such samples from multiple independent colonies provides a metric of population-level resiliency. We used red blood cells (RBC) for eiders	

sampled while incubating their nest, and plasma for eiders that were sampled during the pre-breeding period to assess pre-breeding isotopic signatures. 76

Table 3.2 – Summary of average and percent coefficient variation in inter-colony sea surface temperature (SST) for the relative pre-laying month for each common eider colony. The breeding phenology of eiders varies across their range, with certain colonies laying earlier than other. As such, average values (AVG) and percentage of coefficient of variation (%CV) include SSTs for the relative month leading up to average colony lay dates. 77

Table 3.3 – Average prey isotopic signatures were collected from the literature to correct common eider isotopic values in order to be able to compare inter-colony isotopic niche. Prey isotopic values (also referred to as baseline) vary across the globe, thereby making untreated isotopic values collected from multiple source locations non-comparable. 78

Table 3.4 – Summary of mean \pm standard error of mean, percent coefficient of variation (%CV) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ raw values, and average trophic position (TP) of common eiders nesting across 8 colonies. Prey values (Table 3) are applied to these values in order to make inter-colony comparisons. These values are for both breeding and non-breeding eiders, depending on sampling method. 79

Table 3.5 – Summary of inter-colony common eider stable isotopic metrics calculated using SIBER. Isotopic metrics, standard ellipse area corrected for small sample size (SEAc), mean next neighbor distance (MNND), range of $\delta^{13}\text{C}$ values, and range of $\delta^{15}\text{N}$ range, characterize foraging dynamics. All metrics are calculated using corrected $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, thereby are comparable across colonies. 80

Table 3.6 – List of principal component correlation values based on common eider plasma and red blood cell isotopic metrics. Bold values reflect metrics which significantly loaded and included in the principal component. 81

Table 3.7 – Regression analysis between isotopic metrics and principal component residuals as dependent variables, and latitude and longitude and independent variables. Bold p-values reflect a significant (or marginally significant at the $p=0.1$ level) relationship between dependent and independent variables. 82

Table 3.8 – Regression analysis between residual PC scores and sea surface temperature (both average (AVG) and percent of coefficient of variation (%CV)). Bold values indicate a significant result. 83

LIST OF FIGURES

- Figure 2.1** - Inter-annual variation in plasma isotopic niche of eiders nesting at Mitivik Island, NU. Each colour is an independent year. Ellipses represent 40% of the individuals' isotopic signatures within each year. 40% ellipses are used to represent the placement of birds within each year in isotopic space and compare placement among years. 48
- Figure 2.2** - Isotopic variation from plasma across breeding stages of eiders nesting at Mitivik Island, NU. PR (green line; pre-recruiting), shows 40% of the individuals which started laying at least 8 days post-capture; RFG (blue line; rapid follicle growth), is characterized by birds that are delayed between 8-1 days before they breed; and Lay (red line; laying or incubating) is the 40% ellipse of birds which were laying or incubating the same day of capture. 49
- Figure 2.3** - Boxplot of inter-annual variation in plasma $\delta^{13}\text{C}$ values of female eiders nesting at Mitivik Island, Nunavut, Canada. High $\delta^{13}\text{C}$ values represent an inshore benthic diet, while a low $\delta^{13}\text{C}$ value represent an offshore pelagic diet. 50
- Figure 2.4** - Boxplot of inter-annual variation in plasma $\delta^{15}\text{N}$ values of female eiders nesting at Mitivik Island, Nunavut, Canada. High $\delta^{15}\text{N}$ values represent a higher trophic diet, compared to low $\delta^{15}\text{N}$ values. 51
- Figure 2.5** - Variation in plasma $\delta^{13}\text{C}$ (A), and $\delta^{15}\text{N}$ (B) values across breeding stages of female eiders nesting on Mitivik Island, Nunavut, Canada. Values are represented as mean \pm SEM provided for each day during pre-breeding (black circle), rapid follicle growth (black square), and laying (black triangle)..... 52
- Figure 3.1** – Map of 8 breeding common eider colonies. Each location was sampled during the pre-breeding or breeding period. 84
- Figure 3.2** – Inter-colony variation in isotopic niche of eiders nesting at 8 different breeding colonies. Each colour is an independent colony. Ellipses represent 40% of the individuals' isotopic signatures within each year. 40% ellipses are used to represent the placement of birds within each colony in isotopic space and compare placement among years. Isotopic values are corrected for baseline variation in prey isotopic signatures (i.e., $\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{prey}}$). 85

Figure 3.3 – Inter-colony variation in trophic position, with tukey-HSD groups listed above each colony. SPIT = *Kongsfjorden, Norway*; GRIN = *Grindoya, Norway*; RUSS = *Oneaga Bay, Russia*; ICE = *Breiðafjörður, Iceland*; MI = *Mitivik Island, Canada*; JOHN = *Johns Island, Canada*; TERN = *Tern Island, Canada*; FAR = *Kirkjubøhólmur, Faroe Islands*. Different letters above boxplots represent distinct groups based on the out of variance in trophic position. Groups with two letters were described as in between two groups. See methods for description of trophic position calculation. 86

Figure 3.4 – Inter-colony variation in $\delta^{13}\text{C}_{\text{corr}}$ values, which have been corrected by baseline prey values to make comparable across colonies. See table 3 for further information on prey values, and methods for information on correcting values. SPIT = *Kongsfjorden, Norway*; GRIN = *Grindoya, Norway*; RUSS = *Oneaga Bay, Russia*; ICE = *Breiðafjörður, Iceland*; MI = *Mitivik Island, Canada*; JOHN = *Johns Island, Canada*; TERN = *Tern Island, Canada*; FAR = *Kirkjubøhólmur, Faroe Islands*. 87

Chapter 1 :
General Introduction

Roles of foraging flexibility in overcoming resource limitation

Resources are essential for life history investment in all species, and the availability of resources is often highly influenced by environmental conditions (Stephens and Krebs, 1986; Newton, 1998). To adapt to the constraints associated with environmentally-induced resource limitation, species have evolved differing anatomical, behavioural or physiological phenotypes to obtain and process resources more readily or efficiently (Stearns, 1992; West-Eberhard, 1989). This phenotypic variation in turn shapes species assemblages and therefore trophic dynamics, as some species are able to take advantage of a wide array of resources (i.e., generalists), while others have a smaller breadth of dietary decisions (i.e., specialists; Kassen, 2002; Ryall & Fahrig, 2006). For example, Darwin's finches are a group of birds found on a few islands in the South Pacific where the combination of exposure to harsh conditions, resource limitation, and competition, have selected for a diversity of anatomical morphologies and therefore speciation (Grant & Estes, 2009; Grant & Grant 2002). One foraging behavioural phenotype that has been shown to have impacts on fitness (Ronconi & Burger, 2008) and can inform conservation measures (Granadeiro et al., 1998; Miller et al., 2009; Nakano et al., 1999) is foraging flexibility; when individuals or populations can flexibly adjust to novel environmental conditions and unpredictable resource abundance. For instance, common murre (*Uria aalge*) forage predominantly on capelin (*Mallotus villosus*) but have been shown to flexibly adjust their foraging behaviour by increasing their daily foraging distance to search out capelin or by locating larger prey when capelin are low in abundance (Burke and Montevecchi, 2009). In addition to foraging flexibility impacting fitness (Hamer et al., 2007) it also varies across species, populations, and individuals (Boggs, 1992). As such, phenotypes associated with foraging flexibility are under selection, and individuals must adaptively switch between phenotypes to match expected variation in environmental conditions (Piersma & Drent, 2003). This flexibility provides organisms important fitness-related adaptive functions to then invest in life history stages (Miner et al., 2005).

An important constraint to consider when investigating the degree of foraging flexibility found within a species and individual is the level of foraging niche overlap (inter- and intra-specific competition) among competing individuals and species (Kronfeld-Schor & Dayan, 2003;

Schoener, 1974). An organism's foraging niche is the range of prey items a consumer can acquire within the range of environments it can forage (Davis & Smith, 2001; Sabo & Holmes, 1983), which can often impact and shape the population dynamics of consumers and prey (Bolnick et al., 2012; Holt, 2009; Schoener, 1989). As such, there is an evolutionary benefit to being flexible in foraging decisions, which allows consumers to avoid niche overlap and competition to take advantage of particular prey items which are inaccessible to other consumers (Robinson & Wilson, 1998), or prey items that lack variability over time or space (Garthe et al., 2007). As such, species that forage on a limited number of prey items, which often fill a specific ecological niche, are known as foraging specialists, whereas individuals that forage more generally on multiple prey items are considered foraging generalists (Strickler, 1979). Indeed, investigating variation in foraging strategies among individuals and populations can provide critical information on the level of generalist vs specialist foraging behaviours (Garthe et al., 2007) which can then be used to estimate how resilient a population or species may be to fluctuations in resource abundance (Paredes et al., 2012; Perez et al., 2016; Smith & Reeves, 2012), and therefore their adaptive capacity to respond to rapid environmental change (Sydeman et al., 2012) .

Using stable isotopes and isotopic niches to assess resiliency to change

Trophic dynamics are the interactions between consumers and their prey (Lindeman, 1942; Ware & Thomson, 2005) (where typically higher order consumers forage on lower-order prey) and can reflect the response of individuals and populations, and therefore species and even entire ecosystems, to environmentally-driven variation in resources (van der Putten et al., 2004). Importantly, these trophic estimations can provide key quantitative information on a species or population's adaptive capacity to respond to environmental change (Moon & Stiling, 2002; Moore et al., 2004). The ability to quantify this resilience to rapid environmental change has been particularly important in recent decades, as climate change is directly and indirectly impacting how trophic dynamics impact key ecological processes (Post et al., 2009). Many foundational dietary studies relied on highly invasive sampling techniques (i.e., destructive sampling of individuals), which is problematic for obtaining large enough sample sizes to make reliable assessments of adaptive responses to change, as well as for studying species-at-risk.

The quantification of stable isotopes in organismal tissues has emerged over the past three decades as a means of overcoming these limitations to investigate trophic dynamics and

foraging decisions (Boecklen et al., 2011; Hobson & Clark, 1992a,b; Newsome et al., 2007; Petersen & Fry, 1987). Typically, elements (e.g., Nitrogen and Carbon) will have a light and heavy form, which is dependent on their atomic mass (i.e., number of neutrons) and these are referred to as isotopes. Both light and heavy isotopes are incorporated into the body of organisms through ingestion and inhalation, with heavier isotopes fractionating from lighter forms and remaining in the body of consumers (Rundel et al., 1989). Isotopic fractionation is measured as a ratio of heavy to light forms and expressed in delta (δ) notation as parts per thousand (Petersen & Fry, 1987). This rate of fractionation, or incorporation, depends on the metabolic rate of specific tissues, where metabolically inert tissues (e.g., bone, hair, and nails) stop incorporating isotopes once fully grown, while metabolic activity keeps tissues turning over stable isotopes (Hobson & Clark, 1992b). As such, isotopes can be used as chemical markers which contain information regarding trophic dynamics, and when an organism has ingested certain resources based on an understanding of the isotopic discrimination factors of tissues (also called “isotopic fractionation”, “isotopic enrichment”, “diet-to-tissue discrimination”, or “trophic discrimination factors”, hereby referred to as DF) (Gannes et al., 1997; Wolf et al., 2009). Many studies have investigated the inter-tissue turnover rates of multiple tissues and have found that these values vary greatly across species, life history stages, and even isotopes (Hobson and Clark, 1992a). For example, nitrogen is found in two forms in the environment, with $^{15}\text{N}:^{14}\text{N}$ fractionating from diet to consumer in a stepwise rate of typically 2-5‰ across species (Fry, 1998; Wada et al., 1987). Therefore, nitrogen provides information on the trophic level in which a consumer is foraging (Mingawa & Wada, 1984), with nitrogen values increasing in higher trophic levels (Hobson & Welch, 1992; Vander Zanden et al., 1997). However, research has shown that the DF of $\delta^{15}\text{N}$ can be influenced by multiple extrinsic and intrinsic factors (Hobson et al., 2002). For example, some species of seabirds use a fasting strategy during incubation, where lipid stores are often completely depleted, and the fasting individual begins to utilize their protein stores which can skew their $\delta^{15}\text{N}$ signatures (Hobson et al., 1993). Currently, there is little information on the rate of enrichment of $\delta^{15}\text{N}$ during increased energetic demand (i.e., incubation), making comparisons of $\delta^{15}\text{N}$ values across life history stages challenging and better-suited to comparisons within a life history stage. In contrast, carbon is typically found as ^{13}C and ^{12}C , and vary significantly by the primary producers forming the foundation of a food web (Boecklen et al., 2011). As a result, carbon ($^{13}\text{C}:^{12}\text{C}$) fractionates a negligible amount, 0-2‰, therefore making them a strong proxy for the location in which a consumer is foraging (i.e., inshore versus offshore, pelagic versus

benthic) (Hobson & Clark, 1992a). In this way, combining nitrogen and carbon stable isotope analyses provides a window into predator-prey dynamics within food-webs, and can provide dietary incorporation across time, instead of a single point (Hobson et al., 1994; Hussey et al., 2014). It is important to note that DF values can play an important role in the interpretation of isotopic signatures, and inter-specific variation in DFs can be extremely variable (Robbins et al., 2005). One of the largest gaps in our current understanding of isotopic ecology is generating species-specific DFs, largely due to the need for rigorous lab-based captive studies (Federer et al., 2010). As such, many studies tend to use an average value of 3.4, or will use a DF from a closely related species. This can be problematic, and results should be interpreted with care since research has shown that even Bayesian models are sensitive to these values (Bond & Diamond, 2011).

The development of isotopic niche theory has prompted a resurgence of interest in the field of isotope ecology (Newsome et al., 2007), as isotopes are able to reflect dietary niche characteristics and comparisons within and across individuals (Vander Zanden et al., 1997). Importantly, isotopic niche has been shown to reflect foraging niche (Bearhop et al., 2004; Newsome et al., 2007), and act as a predictor of individual- and population-level responses to climate change and disrupted trophic webs (Hobson, 1994; Martinez del Rio et al., 2009). In addition, multiple analytical tools have been produced to calculate isotopic niche metrics (Jackson et al. 2011; Layman et al. 2007). These tools can produce metrics which represent the size and placement of a niche or group of individuals within isotopic-space, or the distribution of individuals within a niche (i.e., degree of spacing). Although the use of stable isotopes has proven a powerful means by which to assess trophic positioning, there remains a level of quantitative uncertainty in the values produced and as such stable isotopes in general should be interpreted with care (Martinez del Rio et al., 2009). Specifically, although many of these isotopic niche metrics can be used to make comparisons at multiple scales, they do not account for environmental impacts on primary producers' isotopic values (i.e., temperature effects on phytoplankton, Ventura et al., 2008; Bond & Jones 2009). This variation in primary producers is referred to as baseline isotopic variation and should not be left unaccounted for when comparing isotopic signatures across multiple scales (Boecklen et al., 2011).

Effects of climate change on resources and reproduction

Over the past 60 years, climate has been significantly altered due to human-induced increases in greenhouse gas emissions, resulting in an overall warming effect (IPCC, 2018). Associated increases in temperatures are causing a cascade of biotic and abiotic effects, especially with respect to oceanic patterns and conditions, and an overall reduction in organismal biomass (Edwards & Richardson, 2004). Novel abiotic trends caused by climate change are especially prevalent in the northern hemisphere, particularly in the Arctic (Hinzman et al., 2005; Post et al., 2009), although the scale of change varies substantially across the Arctic (Cohen et al., 2014). This variation is largely driven by a reduction in the albedo effect (Winton, 2006) in which snow and ice cover usually acts as a large reflective surface, sending large amounts of ultraviolet radiation back into the atmosphere. However, as temperatures continue to increase and snow and ice cover decreases, the rate of change in the Arctic is further increased as the albedo effect diminishes (Johannessern et al., 2004).

Due to the rapid pace of environmental change in the Arctic, it is important to determine how individuals and their associated populations are affected, which will provide a means of assessing the ability of species to adapt to this rapid change (Moore et al., 2008). To assess the broad impacts of climate change both within and across species, environmental indices are often used, and have been shown to be strongly correlated with localized environmental conditions (Stenseth et al., 2003). For example, the North Atlantic Oscillation (NAO) describes the oscillation of atmospheric mass between the Arctic and subtropical Atlantic Ocean (Hurrell & Deser, 2010) and has been validated in several studies as a key predictor of environmental impact on organisms (Descamps et al., 2010; Ottersen et al., 2001). The NAO index shifts between positive and negative phases, which describes the dynamics of pressure gradients in this region, and the corresponding environmental and oceanographic conditions that result from these changes. During a positive NAO phase, the pressure gradient over the North Atlantic is large, causing increased wind speeds and moisture transport along the Eastern Atlantic and Arctic, and fewer storms in the Western Atlantic Ocean. As such, a positive NAO is associated with colder temperatures increased storm activity especially during the winter (December to March) in the Eastern Atlantic and Arctic (Osborn, 2006). The shifts between positive and negative NAO phases have historically been predictable; however, in recent decades, NAO trends are inconsistent with simulated models and therefore less predictable,

which is reflective of the impacts of climate change on oceanographic cycles (Gillett et al., 2003). Although this makes interpreting associations between organismal responses and NAO values challenging, NAO still provides a strong metric of localized environmental conditions. As such, NAO provides a relevant proxy for the environmental conditions that Eastern Arctic species experience across life history stages (i.e., from wintering to migration to breeding) in the face of climate change (Hüppop et al., 2003; Ottersen et al., 2001; Weyhenmeyer et al., 1999). With increased levels of environmental variation, it is important to investigate how Arctic species are responding to these novel conditions, which has been a pressing question among ecologists over the past decade. Specifically, given that a wide range of taxa are facing substantial population declines, researchers are interested to determine whether organisms can adjust their life history stage decisions in pace with the ongoing changes in resource availability and unpredictable environmental conditions generated from climate change (Visser et al., 1998; Berteaux et al., 2004; Callaghan et al., 2004; Post & Forchhammer, 2008; Gustine et al., 2017).

Seabirds as useful models to assess resiliency to environmental change

Arctic species and ecosystems are at-risk due to environmental changes centered around climate change; however, little is currently known about the ability of these species to respond mechanistically to this new environmental norm, especially given the degree of heterogeneity in environmental change across the circumpolar Arctic (Ford et al., 2006). A useful way to begin examining the mechanisms at the heart of these broad-scale effects, and by extension the resiliency of Arctic biota to climate change, may be to quantify variation across individuals and populations in the limited resources used to fuel important life history stages, determine whether these resource patterns are influenced by climatic variation, and then assess whether environmentally-driven resource patterns predict key life history decisions. The ability to researchers to generate models to make directed, but broadly applicable inferences about how we expect ecologically similar Arctic-breeding species respond to environmental variability is now critical given the current rate of environmental change in the Arctic (Descamps et al., 2017; Legagneux et al. 2012, 2014). Large, top order vertebrates can be some of the best models to test these questions, as they are highly constrained by lower order trophic interactions, and their life-histories are often evolutionarily tied to the timing of changes in key environmental conditions (i.e., prey emergence) (Dell et al., 2013). As such, these organisms are constrained by multiple extrinsic factors, and stage-specific responses can be examined to determine their

ultimate impact on key life history decisions. Of these, seabirds can be ideal model organisms to assess resiliency to climate change for many reasons (Grémillet et al., 2009; Moe et al., 2009). Firstly, seabirds have a global distribution, with many being colonial nesting, with a strong nest site fidelity, making the collection of multiple samples across time, easy to accomplish (Furness, 2012). Second, seabirds are often at the top of their food-web, making them dependent on low trophic-interactions (Cury et al., 2011; Santora et al., 2011), and their life histories are associated with environmental variation (Wolf et al., 2009; Piatt & Sydeman, 2007; Sydeman et al., 2012). Further, as seabirds typically have both extensive foraging and migratory spatial ranges, which exposes them to a range of different environmental conditions, they can provide key broad information on the condition of the environment (Wolf et al., 2010). Finally, seabirds are often long-lived and as a result, have been shown to be robust to sampling and disturbances. Unfortunately, many seabird species are now at risk, with the potential root-cause being rapid environmental change across key foraging locations (Einoder, 2009). Given the rapid change occurring in the Arctic, it is highly pertinent to assess seabirds in an Arctic system, especially long-lived colonial seaducks, because they meet many of the criteria listed above for seabirds in general (Mallory et al., 2010).

Study species

Common eider (*Somateria mollissima*; hereafter eider) are a long-lived, diving seaduck and broadly distributed across the northern hemisphere (Goudie et al., 2000). Eiders spend most of their annual cycle on oceanic waters, generally only coming to land to breed (Goudie et al., 2000). Northern populations typically nest in large congregations on rocky coastlines and islands (Robertson, 1995), whereas more Southern populations often exhibit less colonial nesting behaviours and will often nest solitarily in tall grass or near trees along coastlines and on island (Gerell, 1985). Eiders typically forage on benthic macroinvertebrates, such as bivalves and crustaceans, diving up to 30 meters to forage (Heath & Gilchrist, 2010; Heath et al., 2006), but are also known to forage on amphipods and benthic fish (e.g., sculpin) (Goudie & Ankney, 1986; Guillemette et al., 1993). Nonetheless, there is limited information on the diet of eiders within and across populations, or whether foraging decisions and differences in prey selection vary across their range.

In preparation for breeding, access to resources are critical for female eiders. Following arrival on the breeding grounds females must gain sufficient body condition to initiate

reproduction (i.e., yolk follicle recruitment) (Hennin et al. 2015, 2018). The faster females can meet this condition threshold, the earlier they can initiate follicle recruitment and laying which has fitness-related benefits; previous research has shown that earlier laying dates result in both larger clutch sizes (Descamps et al., 2011a; Hennin et al., 2018) and higher duckling recruitment back into the population (Love et al., 2010; Descamps et al., 2011b). Finally, because females are the sole incubators of their clutch and incubate continually for approximately 24 days while fasting (Parker & Holm, 1990), they must also acquire enough stored lipid reserves prior to incubation to ensure that they can successfully complete incubation to hatch their ducklings. Therefore, the careful accumulation and management of resources is critical in pre-breeding female eiders.

Despite the significant resource accumulation required to successfully invest in reproduction, we know little about how prey selection and foraging decisions may vary leading up to laying, or how environmental variation may play a role in driving foraging decisions at the individual or population levels. The few dietary studies that have been conducted suggest that eiders (as a species) have an overall generalist diet, which is largely limited to nearshore, shallow regions, consisting mostly of sedentary macro invertebrates (Guillemette, 2001; Player, 1971; Sénéchal et al., 2011). However, given the substantial variation that exists in environmental and oceanographic conditions across the range of eiders, it is likely that their diet is more variable than currently assumed. In addition, the ability to forage following arrival from migration is likely highly constrained in many populations by the timing of ice breakup on the breeding grounds impacting resource availability, thereby affecting downstream variation in breeding investment decisions both within and across individuals (Love et al., 2010; Jean-Gagnon et al., 2018). With climate change having such varied effects across the northern hemisphere (IPCC, 2018), including potential bottom-up trophic disruptions (Beukama & Dekker, 2005), there may be direct impacts of climate change on the distribution and abundance of eider prey items, with indirect downstream effects on eider populations (Sydeman et al., 2012). It is therefore useful to assess both intra- and inter-colony variation in dietary characteristics of eiders as a means of predicting whether different populations might differentially cope with changing environments across their range. Further, estimating the degree of niche diversity within and across populations (i.e., specialist versus generalist foraging strategies) has the potential to inform researchers of the relative resiliency of different eider populations to the effects of environmental change. These relationships have yet to be broadly investigated in any

Arctic vertebrate at this level and results have the potential to uncover key responses that influence fitness in the context of a rapidly changing Arctic.

Thesis goals and chapter objectives

The overall goal of my thesis is to use isotopic niche dynamics within and across common eider breeding colonies to predict their potential resiliency to further environmental change. To address this overall goal, my first data chapter (Chapter 2) uses a long-term dataset from a focal breeding colony to relate inter-annual and inter-breeding stage variation in isotopic niche parameters to environmental conditions and downstream breeding parameters. My second data chapter (Chapter 3) extends these concepts and takes a broader-scale geographic approach to quantify inter-colony isotopic variation, and then examine whether this variation can be linked to environmental conditions. Finally, in my discussion chapter (Chapter 4) I synthesize my findings to address key gaps in: 1) how flexible foraging strategies may allow species to invest in reproduction; 2) the relationships between foraging decisions and environmental conditions across multiple scales; and 3) the overall ability of stable isotopes to predict resiliency. Overall, the thesis is designed to assess whether environmentally-driven variation in resources influences the breeding decisions that affect population resiliency in Arctic consumers.

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Chapter 2 :

Estimating resiliency to environmental change in an Arctic seabird using inter-annual and breeding stage related variation in isotopic niche dynamics

Introduction

Resource limitation is one of the greatest constraints influencing the ability of individuals to maximize fitness (Newton, 1998; Stephens & Krebs, 1986). A combination of variability in abiotic environmental variables that effect affect the quantity and quality of resources, as well as the ability of organisms to access those resources, therefore plays an important role in resource-based limitations on fitness and population demography (Boggs, 1992). As such, natural selection has shaped species-, population- and even individually-specific phenotypes (i.e., morphology, physiology, behaviour) to optimize foraging performance to exploit unoccupied dietary niches (Stephens & Krebs, 1986). Overall then, the degree to which organisms can navigate environmental variability to locate, exploit, and assimilate limited resources plays a major role in shaping variation of the life history strategies that ultimately maximize fitness (Stearns, 1989).

One of the most important and energetically demanding life history stages that also influences variation in fitness is reproduction (Drent and Daan, 1980). Individuals that can overcome extrinsic constraints, such as environmentally-driven, intra- or inter-annual variation in resource limitation, are predicted to meet the energetic demands associated with breeding and successfully reproduce (Daunt et al., 2006). However, in recent decades, there has been growing evidence suggesting that breeding decisions (i.e., breeding phenology) are being disrupted (Both et al., 2006; Visser & Both, 2005) and that there are long-term negative effects on breeding success (Root et al., 2003). A unifying, mechanistic hypothesis for this effect is that increased levels of environmental variation are resulting in a global reduction in prey biomass (Watson et al., 1998), while simultaneously altering prey distribution and diversity (Bakun et al., 2015). Together, these effects on prey bases are expected to affect the foraging success of individuals and their resulting ability to reproduce and rear offspring successfully, generating downstream impacts on population demography (Murawski 1993; Post and Forchhammer 2008; Selden et al., 2018; Simmonds & Isaac 2007; Tulloch et al., 2019; Watson et al., 1998).

Climate change is a global phenomenon, generating increases in annual temperatures, altering oceanographic cycles, and prompting a new global extinction (IPCC, 2018). Importantly, the timing of key resource abundance has shifted with warming air temperatures and a shortened non-breeding season for many species (Aubry et al., 2013; Hjort, 1914). Migratory species may be particularly sensitive to these changes since they have been selected to time their movements to their breeding grounds to match historically predictable timing in peak prey abundances. However, the timing of migration is now often mismatched to the timing of peak prey abundance causing downstream negative effects on breeding outcomes (Durant et al., 2007; Post & Forchhammer, 2008; Visser et al., 1998). In addition to changes in prey phenology, the global environmental conditions that often drive this match in timing are also often less consistent, further affecting the abilities of consumers to obtain the resources needed to optimally time life history events to maximize fitness (Tøttrup et al., 2008). The Arctic is currently showing amplified rates of climate change and subsequent alterations in prey abundance and diversity (Gaston et al., 2009; Screen & Simmonds, 2010). Indeed, Arctic regions are warming at a rate 2-4% faster than anywhere else on earth (Wassmann et al., 2011), with significant declines in the extent of sea ice (Ciancio et al., 2016; Comiso et al., 2008; Hoegh-Guldberg & Bruno, 2010; Johannessen et al., 2004), generating many bottom-up trophic disruptions (Boeitus et al., 2013; Jones et al., 2014; Meier et al., 2014; Wassmann et al., 2011). However, whether Arctic species have the ability to proximately keep pace with the current rate of environmental change, and therefore whether they ultimately possess the adaptive capacity to be flexible in the associated foraging strategies that optimize breeding decisions, has become an important topic of investigation (Descamps et al., 2017; Kovacs et al., 2010; Moore & Huntington, 2011). Changes in the abundance and phenology of primary producers, such as phytoplankton, have already been linked to declines in key prey species in Arctic food webs (e.g., Arctic cod) (Gradinger & Bluhm, 2004). As such, quality prey items that individuals or populations have historically relied on, are in decline or their distributions have shifted, now making them an unreliable food source (Both et al., 2006). These rapid and unpredictable shifts in prey demography has made it more challenging for consumers to acquire the necessary resources that enable them to optimize reproductive investment and maximize breeding success (Seyboth et al., 2016; Ward et al., 2009).

A potentially useful tool to assess and measure prey choice by predators and by proxy, potentially shifting prey availability in response to environmental change, are stable isotopes

(Herman et al., 2017; Hobson, 1992a,b, 1999; Newsome et al., 2007) as they have been validated for the use in representing the foraging niche of an individual or population (Bearhop et al. 2004). A foraging niche represents both resource and habitat usage of a consumer, and this metric can therefore provide insight into key fitness-related decisions that individual, populations and even entire species make (Alatalo, 1982; Bolnick et al., 2003; Hutchinson, 1957; Vandermeer, 1972). Stable isotopes of carbon ($\delta^{13}\text{C}$ - used to infer habitat usage) and nitrogen ($\delta^{15}\text{N}$ - used to infer resource usage) can together provide a non-lethal method of quantifying the foraging niche of multiple individuals or populations, and provides a framework to investigate links between resource usage and extrinsic constraints, such as environmental variability. For example, larger foraging niches are expected to represent a greater diversity of foraging decisions that should then translate into an increased likelihood of breeding success during times of environmental change (Seamon & Adler 1996). Overall then, quantifying isotopic niche dynamics has been proposed as a useful means of increasing our ability to predict the downstream consequences of environmentally-driven changes in resource bases on reproductive parameters and fitness, and as a consequence, the resiliency of populations to further change (Polito et al., 2015).

Here, we investigate whether environmental variability can be used to predict inter-annual and breeding stage related variation in isotopic niche dynamics in a high trophic, marine Arctic vertebrate species, and whether this variation predicts variability in key breeding decisions. We test these questions using a 9-consecutive-year (2010-2018) dataset collected from over 700 females in a diving seabird, the common eider (*Somateria mollissima*; hereafter eiders) a species which has a wide-spread distribution across the Arctic. A focus on Arctic-breeding eiders to examine these questions in is strategic for a number of reasons. First, the ability of this species to invest in reproduction is contingent on their capacity to meet a minimum body condition threshold, which is expected to be significantly influenced by adequate access to environmentally-limited resources (Jean-Gagnon et al. 2018; Love et al. 2010). Second, eiders use a mixed, capital-income breeding strategy and after arriving on the breeding grounds, females must forage to fatten to not only fuel follicle growth, but also to successfully complete their 24-day incubation fasting period (Gouette et al., 2010). Third, some of the mechanisms underlying variation in the timing of reproductive investment have been characterized (Hennin et al. 2015), providing a framework to interpret links between environmental variation, isotopic variation and breeding investment. For example, previous research has shown that females

which fatten more quickly during pre-breeding are able to lay earlier (Hennin et al. 2017; 2019), and that earlier-laying females are able to lay larger clutch sizes (Descamps et al. 2011; Hennin et al. 2018) and recruit more ducklings back into the breeding population (Love et al. 2010). Considering that prey items differ in nutritional value and composition, which can impact fattening rates (Paiva et al., 2013), the isotopic niche within which females forage should therefore play an important role driving variation in reproductive investment. Fourth, recent research has also demonstrated that variability in ice conditions (linked to broad environmental metrics; e.g., North Atlantic Oscillation (NAO) and ambient local temperatures) impacts access to foraging areas and the decision to breed, again mediated through impacts on individual body condition (Jean-Gagnon et al. 2018; Love et al. 2010). Overall, the need for females to fuel the energetics of breeding and the demonstrated impact of environmental variation in impacting access to foraging areas make this the ideal study system to link the influence of environmental variables to individual variation in isotopic niches and the influence isotopic niche has on key fitness-related life history decisions.

Our first goal was to quantify isotopic niche dynamics (calculated using carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes) across years and key breeding stages from blood samples collected from over 700 females breeding at a colony on Mitivik Island, Nunavut, Canada (Bottitta, 1999; Love et al., 2010; Mosbech et al., 2006). Next we examined whether variation in broad climatic metrics could be used to predict inter-annual variation in isotopic niche. Since the energetic demands leading up to laying are highly variable and there are known changes in physiology (Hennin et al., 2015, 2018), which may also directly impact isotopic values (Hobson et al., 1993; Sénéchal et al., 2011), we then examined whether niche dynamics varied at a finer inter-breeding-stage scale, by quantifying niche dynamics from pre-breeding, through yolk-follicle recruitment and leading up to laying (Hennin et al. 2015). Finally, to test whether variation in niche dynamics ultimately influences variation in actual breeding decisions, we related mean isotopic niche metrics to key fitness-related parameters known to influence fitness in this species (i.e., interval between arrival on the breeding grounds and laying, lay date, and breeding propensity; Descamps et al., 2011; Hennin et al., 2015, 2016, 2018; Love et al., 2010). Since ice conditions during the pre-breeding period at this colony are highly variable (Jean-Gagnon et al., 2018; Love et al., 2010), and local environmental conditions are known to influence the foraging behaviour of eiders (Hobson, 1999; Paiva et al., 2013), we first predicted significant amounts of inter-annual variation in isotopic niche. We also predicted that this variation would be impacted

by variation in broad climatic variables. Specifically, in years with warmer winters, warmer springs, and higher overall ambient temperatures (i.e., higher T_a , +/- NAO) female eiders should be able to exploit a wider variety of prey items due to a greater degree of open water to forage in, resulting in the colony that year having a broader isotopic niche. Given that energetic management is critical in driving reproductive investment decisions in this species (Descamps et al., 2010; Hennin et al., 2015, 2016, 2018, 2019; Love et al., 2010; Sénéchal et al., 2011), we expected that isotopic values and niche characteristics would be influenced by the energetic demand associated with breeding stages (Hennin et al., 2015), and therefore that both would vary across breeding stages and have downstream effects on key breeding decisions (i.e., breeding propensity, laying date) (Paiva et al., 2013). Specifically, in years where the eider colony exhibits a large isotopic niche and therefore a more generalized foraging strategy, we expected birds to be able to fatten more quickly and therefore have a shorter interval between arrival and laying, an earlier laying date and higher colony-level breeding propensity. The overall aim of our approach was to examine whether we can use information on isotopic niche dynamics to improve our ability to assess whether this species possesses the adaptive capacity (i.e., resiliency) to respond to current and expected environmental change due to climate change.

Methods

Study system and breeding parameters

Our research was conducted at Canada's largest and longest monitored Arctic-nesting colony of common eiders, located at Mitivik Island, Nunavut, Canada (64°02'N, 81°47'W). Mitivik Island (MI) is a small (800 m X 400 m), low lying island (<8m elevation), situated off the coast of Southampton Island, within the East Bay Migratory Bird Sanctuary. Females breeding at this colony migrate from their wintering grounds off the West coast of Greenland and the Northern coast of Newfoundland and Labrador, Canada annually in May (Mosbech et al., 2006; Steenweg et al., 2017), arriving at Mitivik Island in early to mid-June, and laying their eggs in mid-June to early-July (Jean-Gagnon et al. 2018; Hennin et al. 2015). We captured eiders from 2010-2018, in mid-June using flight nets as they flew over the colony, and we timed capture of birds to coincide with the timing of the bird's arrival at the breeding grounds (Descamps et al., 2010). Once captured, a blood sample was taken from the tarsal vein of females using a 1-mL heparinized syringe and 23G thin-wall, 0.5-inch needle. These samples were collected in tandem

with other studies examining baseline stress physiology (e.g., Hennin et al., 2016) and were therefore collected within 3 minutes of capture (Romero & Reed, 2005), although we do not expect any influence of capture stress on stable isotopes (Hobson et al., 1992). Samples were transferred to heparinized collecting tubes and kept cool for 2-6 hours. Samples were then centrifuged at 10,000 rpm for 10 minutes, plasma was separated from the red blood cells, and both components were frozen separately at -20°C until further processing. After blood sampling, females were banded with a government-issued metal band and alpha-numeric Darvic bands, then affixed with a unique combination of coloured and shaped nasal tag plastic discs. Nasal tags were threaded and tied through the nares (nostrils) using UV degradable monofilament to ensure they would allow individual identification within the season (see below) but fall off prior to fall migration. Although wing bar metrics have been used in other populations to assign age to nesting female birds, they are not a reliable measure of age in this breeding population (H. G. Gilchrist, unpublished) and we were therefore unable to assign age to our females.

Reproductive parameters were collected annually from experienced observers tracking nasal-tagged females in the colony using standardized protocols and spotting-scopes from 7 permanent blinds positioned around the periphery of the island (Table 1). Using these techniques, we were able to obtain accurate, individual data on breeding propensity, the delay between arrival at the colony and laying, and lay date which allowed us to calculate inter-annual colony-level means for these traits. Based on previous work categorizing the dynamics of breeding in this colony (see Hennin et al. 2015), birds captured 8 days or longer prior to laying were classified to be within the “pre-recruiting” (PR) stage (i.e., still fattening and not yet begun recruiting yolk follicles to produce eggs). Given the period of rapid follicle growth (RFG) stage (where birds have decided to invest in reproduction and are actively recruiting yolk follicles) in eiders has recently been estimated to be 7 days (Hennin et al., 2015), females captured between 7 and 1 day before laying were categorized to be within the “rapid follicle growth” (RFG) stage. Any females captured and known to be laying that day (or before that day) were categorized as “laying” (LAY). Finally, given that females at this colony have high breeding site fidelity (Jean-Gagnon et al. 2018), females that were captured and sampled, but not seen breeding at the colony within the given year, were considered non-breeders (NB). To facilitate inter-annual comparisons, we calculated relative arrival dates (RAD) and relative lay dates (RLD) for all

individuals (individual's arrival and lay date relative to the median arrival and lay dates for the colony in a given year) (Lepage et al., 2000). The interval in days between capture and laying was calculated as the "delay before laying" (Hennin et al., 2018) and was also used to assign birds to a given breeding stage at the time of capture and sample collection (see Hennin et al., 2015 for details). All work was conducted under University of Windsor Animal Utilization Protocol Permits (AUPP) 11-06 and 19-11 and Environment and Climate Change Canada Animal Care permit EC-PN-15-026.

Environmental indices

We assembled climatic variables previously shown to be predictive of storm activity and ice cover conditions that eiders face during the pre-breeding period while they are preparing to invest in reproduction (Table 3). The North Atlantic Oscillation (NAO) is a prominent pattern of atmospheric variation and an index of the severity of storms across the Eastern Canadian Arctic (Hurrell 1995). The NAO index is a commonly used proxy for broad environmental conditions, as its impact spans a wide area, and the relationship between temporal NAO values and energetic constraints has been validated in multiple seabird species (Hallett et al. 2004; Sandvik & Erikstad, 2008; Stenseth et al. 2003). Furthermore, the NAO overlaps with the annual distribution of females nesting at this colony (Mosbech et al. 2006; Descamps et al. 2010; Steenweg et al. 2017) and is therefore a relevant, broad scale environmental metric. A positive NAO value represents high storm activity and low temperatures in the Eastern Canadian Arctic, which represents a metric of environmental conditions which eiders face during important life history stages, and the demography of key prey species (Reusch & Chapman, 1995). We calculated the average winter NAO (December-March), which has been shown to directly impact the arrival body condition of eiders breeding at MI (Descamps et al., 2010) and impacts the average spring NAO (April-July; pre-breeding conditions for eiders at MI). NAO values were obtained from the National Weather Service (<https://www.cpc.ncep.noaa.gov/>). As a proxy for localized environmental conditions, we also used ambient temperature (Ta) measured at the Coral Harbour Airport Weather Station (approximately 70 Km from the MI breeding colony). Within a given year we calculated the mean Ta based on the date that coincides with the date of isotopic incorporation. Since stable isotopes in eider plasma has a turnover rate of roughly 2 days (see below), to capture the isotope incorporation date we used a conservative timeframe of 3 days pre-capture (Hahn et al., 2012; Hobson & Clark, 1993). We then calculated the average

Ta for a four-day window leading up to, and including, the isotope incorporation date and determined the mean Ta during that isotopic incorporation period.

Stable isotope analysis, niche metrics, and interpretation

Since the female eiders we catch are roughly 1.5-2 kg, and the half-life of plasma is around 3 days (Hahn et al., 2012; Hobson & Clark, 1992), we therefore used collected plasma samples as they provide the opportunity to analyze the most recent isotopic niche space used by individuals (Hobson & Clark, 1992, Table 2. Stable Isotope analyses were based on previously validated techniques (see Hobson & Clark 1992 for details). Briefly, we freeze-dried 100 uL of plasma from each individual until achieving a constant mass (minimum of 78 hours). All samples were then ground into a homogenized, fine powder using a metal spatula. Since plasma is often high in lipids we then performed a lipid extraction for all plasma samples using a 2:1 chloroform:methanol solution (based on Bligh and Dyer 1959). Post-lipid extraction, we used a fine-scale (4 digit) balance to weigh between 0.3-0.5 mg of each sample into individual 3.5x5 mm tin capsules for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis.

Analyses for plasma isotopes were conducted using continuous-flow isotope-ratio mass spectrometry (CFIRMS) at the Environment Canada Stable Isotope Hydrology and Ecology Research Laboratory in Saskatoon, Saskatchewan. Material was then combusted online using a Eurovector 3000 (Milan, Italy) elemental analyzer. We separated CO_2 and N_2 analyte gases resulting from the combustion of samples by gas chromatograph, and we introduced gases into a Nu Horizon triple-collector isotope-ratio mass-spectrometer (Nu Instruments, Wrexham, UK) *via* an open split and compared to a pure CO_2 or N_2 reference gas. Stable nitrogen ($^{15}\text{N}/^{14}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$) isotope ratios were expressed in delta notation (δ), as parts per thousand deviation from the primary standards: atmospheric nitrogen and Vienna Pee Dee Belemnite (VPDB) carbonate standards, respectively.

We used a bivariate approach to calculate the size of the isotopic niche for each year within the SIBER package (Jackson et al., 2011). The outputs we used from this model include mean next neighbor distance (MNND), maximum range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and 40% standard ellipse area corrected for small sample size (SEAc). These metrics have been used in multiple studies as a proxy for foraging decisions, habitat usage, and to represent of how a population is responding to environmental perturbations (Herman et al., 2017; Layman et al., 2007; Le Bot et

al., 2019). MNND measures the average distance between two points (in this study, individuals) in isotopic space with higher values representing a group that is accessing resources in multiple trophic levels (as opposed to single trophic levels; smaller MNND values). Calculating the range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ provides information on the breadth of dietary decisions eiders make within a given year. The size of the standard ellipse provides an estimate of the population niche width, with a larger value indicating higher amounts of individual spacing in isotopic space (Newsome et al., 2007).

Along with our estimation of niche breadth, we included the mean (AVG), standard error of the mean (SEM), and standard deviation (SD) for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for each year, as well as the coefficient of variation (%CV) to evaluate variation around these means (Table 2). Stable isotopes are useful to infer spatial movements of individuals, and trophic positioning (Boecklen et al., 2011). Nonetheless, understanding the degree of individual specialization is challenging with a dataset lacking prey data, however it is possible to use %CV as a qualitative proxy for the degree of colony-level specialization within a given year (Herman et al., 2017, Donnelly & Krammer, 1999). Finally, we used two principal component analyses (PCA) to collapse down our 1) eight isotopic metrics and 2) three environmental metrics into more manageable indices to simplify eventual analyses (Table 4). Principle components with eigen values of 1 or greater were used. The PCA for isotopic metrics detected 3 principal components, explaining 46.8, 18.6, and 16.0% of variance of isotopic metrics, with eigenvalues of 3.75, 1.49, and 1.28, respectively. For the first principal component, $\delta^{13}\text{C}$ range and SEAc were positively loaded (with correlation values of 0.46 and 0.47, respectively) and %CV $\delta^{13}\text{C}$ negatively loaded (-0.43, Table 4), overall representing a metric of *spatial foraging breadth*. For the second isotopic principal component, the $\delta^{15}\text{N}$ range and MNND were positively loaded (0.51 and 0.40, respectively), while AVG $\delta^{13}\text{C}$ was negatively loaded (-0.58), overall representing a metric of *niche breadth*. The third and final isotopic principal component included $\delta^{15}\text{N}$ range (which was negatively loaded onto the PC; -0.57), MNND and %CV $\delta^{15}\text{N}$, (both positively loaded onto the PC; 0.63 and 0.44, respectively), representing a metric of *trophic position*.

There were two environmental principal components detected, explaining 37.7 and 33.6% of variance, with eigenvalues of 1.14 and 1.01, respectively. Spring NAO positively loaded (0.60) and Ta negatively loaded (-0.72) onto PC1, representing a metric of *pre-breeding environmental conditions*. For the second environmental principal component, Spring NAO

negatively loaded (-0.53) and Winter NAO positively loaded (0.85) onto the PC score, together representing *pre-breeding NAO*.

Statistical analyses

We had three goals in our statistical analyses, namely examining whether: (1) Isotopic niche at the population level varies across years and breeding stages (Table 2, 2); (2) inter-annual variation in environmental indices (winter NAO, spring NAO; pre-breeding ambient temperature PC groups) predicts inter-annual variation in isotopic metrics (Table 3); and (3) inter-annual variation in isotopic metrics predicts variation in key breeding parameters (Table 4).

To examine inter-annual population-level variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, we ran a MANCOVA (with $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ as dependent variables) using the entire 9-consecutive-year database for common eider females including year, breeding stage, the interaction between year and breeding stage, body mass and relative arrival date as independent variables. Since each isotope represents a specific dietary variable (i.e., $\delta^{15}\text{N}$: trophic position; $\delta^{13}\text{C}$: spatial foraging), we then performed separate one-way ANCOVAs for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ that included year, breeding stage, the interaction between year and breeding stage, body mass and relative arrival date as independent variables. To examine finer-scale, breeding stage-specific changes in foraging strategies via variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, we conducted break-point analyses. Using a series of data points in time, this analysis identifies sudden and significant positive or negative changes in the dataset (Hennin et al., 2015). The procedure identifies and estimates breakpoints by iteratively fitting a model with a linear predictor. For each iteration, a standard linear model is fitted, and the breakpoint value is updated until algorithm convergence occurs. Using this procedure, we were therefore able to detect any significant changes (i.e., breakpoints) in the trophic position ($\delta^{15}\text{N}$) or spatial foraging ($\delta^{13}\text{C}$) of individuals (dependent variables) across the pre-laying period. We performed break point analyses for each dependent variable separately using the delay before laying as an independent variable. All segmented models were fitted using the Segmented R package (Muggeo 2003; R Core Team 2014).

To determine whether inter-annual variation in isotopic metrics can be predicted by inter-annual variation in environmental traits, we ran separate ANCOVAs with isotopic PC scores (see *Stable Isotope Analysis, Metrics and Interpretation*) as our dependent variables and environmental PC scores (see *Stable Isotope Analysis, Metrics and Interpretation*) as our

independent variables. Lastly, to test whether inter-annual mean isotopic metrics predicted variation in population mean arrival and breeding parameters (e.g., breeding propensity, the delay between arrival at the colony and laying, and relative lay date) we ran an ANCOVA. All of our analyses met the assumptions of a parametric test. All statistical tests were run using JMP (Version 14.1.0, SAS).

Results

Inter-annual and breeding stage variation in isotopic signatures

Using a MANOVA approach we found a significant year x breeding stage interaction explaining variation in the isotopic signatures ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of female common eiders (Table 5; Figure 1, 2, 3, 4). Using ANCOVAs to analyse the two isotopes separately revealed that only $\delta^{15}\text{N}$ showed significant year and breeding stage effects (with no year by stage interaction), while variation in $\delta^{13}\text{C}$ was only explained by highly significant negative relationship with relative arrival date where later arriving females had lower $\delta^{13}\text{C}$ values (more inshore foraging; Table 5).

Changes in isotopic values across breeding stages

A breakpoint was detected for $\delta^{15}\text{N}$, where values were relatively consistent throughout the pre-laying period and then increased significantly roughly two days prior to laying (breakpoint value: 1.8 ± 5.4 days, Fig. 5b). A breakpoint was also detected for $\delta^{13}\text{C}$ where values were relatively consistent across the pre-laying period, until 7.4 days prior to laying, roughly around the initiation of the RFG period when $\delta^{13}\text{C}$ values began increasing significantly (breakpoint value: 7.4 ± 2.5 days, Fig. 5a).

Using climate to predict isotopic metrics

We found a significant negative relationship between PCENV2, which represents North Atlantic Oscillation values, and PCISO3, which represents eiders trophic position (ANCOVA, $F_{1,1}=8.26$, $p=0.03$), suggesting that milder environmental conditions during spring are associated with more variable trophic dynamics. However, we did not detect any other relationships between environmental variables and isotopic metrics (Table 6).

Using isotopic metrics to predict breeding parameters

We detected a significant negative relationship between PCISO2 (isotopic niche breadth) and breeding propensity (one-way ANCOVA: $F_{1,7}=15.37$, $p=0.01$, Table 7), where foraging inshore and within a narrower niche was related to a higher probability of breeding. However, we did not detect any significant relationships between isotopic metrics and all other arrival or breeding parameters (Table 7).

Discussion

Using a 9-consecutive-year data set (2010-2018) collected from a focal breeding population of common eiders nesting at Mitivik Island, Nunavut, Canada, we used inter-annual and inter-stage variation in isotopic niche dynamics to assess the 'resiliency' of this species to current and expected environmental change. We found that eiders demonstrated both significant breeding stage-related and inter-annual variation in their $\delta^{15}\text{N}$ values, suggesting that access to certain trophic levels or foraging choices for certain trophic levels differ for specific breeding stages. This supports the idea that breeding stages require the input of specific resources; isotopic niche (specifically $\delta^{13}\text{C}$, i.e., the location of foraging) changed significantly from arrival on the breeding grounds leading up to laying, potentially supporting the idea that females in different stages are foraging in different areas and possibly targeting different prey items. For instance, we found that early arrival on the breeding ground was associated with foraging closer to shore within a narrower (i.e., more specialized) niche, which in turn predicted a higher probability of breeding. Despite these relationships, we only detected significant relationships between environmental conditions and trophic dynamics, but not spatial foraging indices (i.e., $\delta^{13}\text{C}$). Few studies are capable of obtaining large enough sample sizes from pre-breeding seabirds as they arrive to their breeding grounds (Sorensen et al., 2009), and currently no studies have been able to assess and relate isotopic variation across pre-breeding stages or to variation in broad-scale environmental indices. Our work suggests that flexible foraging may be a strategy that common eiders are able to use to overcome environmental constraints and accrue the required resources to invest in reproduction, particularly in the context of their rapidly changing environment. Considering the rapid and substantial changes occurring in Arctic marine ecosystems, our research is a first step towards bridging key mechanistic gaps in determining how large-scale environmental processes proximately impact the foraging decisions that ultimately influence fitness via effects on breeding decisions.

Interactions between inter-annual and breeding-stage related variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values

Given that energetic management is critical in driving reproductive investment decisions in this species (Hennin et al., 2015, 2016, 2018; Legagneux et al., 2016), we expected that isotopic niche would vary across breeding stages as the energetic demands for reproductive investment change. We found a significant interaction between year and breeding stage in our combined isotopic analysis, that largely appeared to be driven by $\delta^{15}\text{N}$ (i.e., significant year and breeding stage effects for $\delta^{15}\text{N}$) when analysing the isotopes. Variation in $\delta^{15}\text{N}$ can be used to infer trophic level and varies greatly among prey (Hobson et al., 2014), while $\delta^{13}\text{C}$ can be used to infer foraging location – inshore vs. offshore, pelagic vs. benthic (Kelly, 1999). We therefore expected breeding stage to be an important contributor to variation in $\delta^{15}\text{N}$, with more energetically demanding stages of breeding such as egg production (i.e., the RFG stage) likely requiring higher trophic level prey sources to fuel them. We found that $\delta^{15}\text{N}$ was higher at the pre-recruiting and RFG stages compared to the laying stages (Table 7; Fig. 2,5b) which agrees with previous research demonstrating that $\delta^{15}\text{N}$ becomes enriched during energetically demanding periods (Hobson & Clark, 1992; Hobson et al., 1993). During this time, eiders are rapidly trying to consume the required resources to invest in reproduction (pre-recruiting fattening) and then produce eggs (yolk development in RFG) (Descamps et al., 2010; Legagneux et al., 2016; Hennin et al. 2016, 2018). As such, we expected to find enriched $\delta^{15}\text{N}$ at the onset of RFG, as this is the most energetically demanding breeding stage (Hennin et al., 2015). It is likely that the combination of continued intense foraging during this time, and the increased energetic demand associated with egg production may play a role in generating higher $\delta^{15}\text{N}$. Given the importance of primary producers in Arctic food webs (Hobson, 1993), and the fact that eiders are closely associated with retreating ice for access to diving locations for foraging (Heath et al., 2006), we expected variation of $\delta^{13}\text{C}$ to play important roles in pre-breeding eiders. Interestingly, we did not detect significant inter-annual variation in $\delta^{13}\text{C}$ values, indicating that there may not be substantial differences in the relative abundance or importance of ice algae or phytoplankton (see below) as primary producers at East Bay.

Links between isotopic niche variation and breeding investment decisions

Common eiders must forage extensively after arriving on the breeding grounds to invest in reproduction (Sénéchal et al. 2011) and can therefore be constrained by the amount of sea ice impacting access to foraging areas (Goudie et al. 2000; Sénéchal et al., 2011). If important foraging areas are covered by ice when eiders arrive to the breeding grounds, they may be restricted to forage in sub-optimal (prey-poor) locations; possibly further from shore or deeper in the ocean (resulting in varied $\delta^{13}\text{C}$ values). Previous studies have demonstrated that in years with later ice breakup, females were less likely to breed, but this effect was exaggerated in females in low body condition (< 2000 g) compared to females in higher body condition (\geq 2000 g) (Jean-Gagnon et al., 2018). Supporting the idea that specific breeding stages require the input of specific resources, we detected a breakpoint in $\delta^{15}\text{N}$ values nearly two days prior to laying. Although this may suggest that females just prior to laying begin incorporating higher trophic prey into their diet, this may not be a biologically relevant result, given that the estimated error around the breakpoint is nearly 5 days. Therefore, females may be shifting their diet, but the evidence from these analyses is not particularly strong and requires further investigation.

Using breakpoint analyses we found that as females transition from pre-recruiting into the RFG period, there was an increase in the amount of $\delta^{13}\text{C}$ measured in their plasma. Since females are under a series of multiple energetic constraints leading up to reproduction, there may be different individual-based foraging strategies females have to accumulate the stores they need. Therefore, as females approach laying, they begin incorporating more inshore items into their diet. The timing of this shift in foraging location matches up with a previously documented change in corticosterone secretion at this colony; females just prior to entering RFG begin increasing baseline corticosterone secretion, presumably to promote an increase in foraging to support follicle growth (Hennin et al. 2015). It may be that the shift in corticosterone to promote foraging also plays a role in the shift in foraging behaviour given the role that corticosterone plays in mediating foraging behaviour (e.g., Angelier et al. 2007; Crossin et al. 2012) and mass gain (Holberton 1999; Holberton et al. 2007; Hennin et al. 2016). Alternatively, as females approach laying, and become increasingly heavy due to growing fat stores as well as reproductive organ and follicle growth (Williams, 2012), the energetic costs of deeper, pelagic dives for benthic prey may become greater. Females may instead opt to forage inshore on

smaller prey items (e.g., amphipods) more frequently to conserve their energy and fat stores for their upcoming incubation fast.

Interestingly, we found that higher breeding propensity was associated with an inshore, smaller niche diet (Table 7; Fig. 1, 5a). Based on our knowledge of ice dynamics at MI (Jean-Gagnon et al. 2018), the foraging ecology of eiders, and that Arctic environments are seasonally constrained (Lepage et al. 2000), it is likely that the ability of eiders to breed in a given year is highly influenced by their ability to locate resources across the different stages of the pre-laying period, especially in years with extensive ice-cover or late breakup. All of these factors combined make it difficult to disentangle the relationships between breeding propensity and inshore/specialized foraging. For example, breeding propensity is the cumulative result of at least three successful breeding decisions all driven by resource intake, which all build one upon the other. The initial decision to invest in reproduction within a given year (i.e., shift from the pre-breeding to the RFG stage) requires individuals to meet a minimum condition threshold following a rapid fattening period (Descamps et al., 2010; Hennin et al., 2015, 2016, 2018). Then individuals must successfully forage to fuel follicle production during the RFG stage to eventually ovulate follicles, complete the egg production process and lay successive eggs. We already know that unpredictable food shortages during the RFG stage reduce the chance an individual will reproduce, regardless of reproductive readiness and other breeding parameters (Legagneux et al., 2016), suggesting that investing in breeding is highly responsive to the impacts of climate change through changes in resource dynamics. Finally, during all of this, birds are continuing to top up lipid reserves to fuel the long 24 day fasting incubation period. As such, an inshore, smaller niche, diet could impact any (or all) of these stages to have positive downstream influences on breeding propensity. Therefore, either eiders may specifically target inshore resources, or given the severe constraints of ice cover eiders may be forced to fuel much of their reproductive investment using inshore resources around the edge of the melting bay in river mouths (Jean-Gagnon et al., 2018), especially in years with extensive ice or late ice breakup. Given all of this complexity, it is perhaps unsurprising that we did not detect predictive relationships between additional breeding parameters (i.e., laying interval, laying phenology) and isotopic metrics, especially with the broad, population-scale, analyses we have started with.

Lack of a detectable relationship between environmental conditions and isotopic characteristics

We predicted that in years with warmer winters, warmer springs, and higher overall ambient temperatures females (i.e., higher Ta, +/- NAO) female eiders should be able to exploit a wider variety of prey items due to a greater degree of open water to forage in, resulting in the colony that year having a broader isotopic niche. Surprisingly we found little evidence of environmental metrics being able to predict variation in isotopic niche, however we did detect a significant, negative relationship between trophic position (PCISO3) and pre-breeding NAO (PCENV2) (Table 6). More specifically, in years with higher winter storm activity and milder springs, females had a greater range and variance in $\delta^{15}\text{N}$ values, as well as the mean next neighbour distance (MNND). In years with harsh winter conditions, muscle beds and other prey sources for eiders may be depleted due to the increased storm activity (Reusch & Chapman, 1995). With depleted muscle beds, eiders may be forced to expand their spatial foraging range to locate additional prey, possible leading to increased variation in prey choice.

Similarly, we predicted that $\delta^{13}\text{C}$ would also be strongly related to environmental indices but, found no such relationships (Table 6). Given the impacts of environmental conditions (i.e., ambient temperature and storm activity) on sea ice dynamics, this result is surprising as eiders spatial foraging decisions are likely modulated and constrained by sea ice. However, it is possible that the primary production around MI lacks enough diversity to detect a relationship between $\delta^{13}\text{C}$ and environmental conditions in order to infer an interaction between foraging decisions and sea ice dynamics. Further, with key-fitness related decisions being modulated by both environmental conditions and physiological state in eiders, we may have not been able to capture all the relevant variables impacting isotopic signatures in our analyses.

Conclusions and future directions

We used a 9-year data set to examine the linkages between environmental conditions, foraging niche and reproductive parameters in pre-laying, wild-living common eiders. Although environmental conditions did not predict the isotopic niche of common eiders, the isotopic dynamics of pre-breeding females varied significantly across years and are likely mediated by the intensive energetic demands of the various breeding stages leading up to laying, and therefore also by the constraints that sea ice plays on restricting resource access in Arctic environments. It is also entirely possible that different breeding decisions in eiders are

differentially impacted by resources and changes in ice dynamics, suggesting that determining their adaptive capacity to change, as mediated by resources, will be a very complex undertaking. Although this research helps to establish links between climate, foraging decisions and reproduction, whether eiders possess the ability to mechanistically cope with the projected rate of environmental change and succeed is still unknown. Nonetheless, there may be a number of ways in which we might improve our predictive power. First, a focus on more specific environmental measures known to impact resource availability more directly, such as sea ice extent or sea-surface temperature, may help to explain some of the remaining variation. Second, our current analyses and scope has been an initial attempt to understand broad (i.e., inter-annual and inter-stage) variation in isotopic niches. Another fruitful step will be to examine these relationships at the individual level within years and in relations to what stage a given female is in at her time of capture. Finally, exploring the foraging decisions eiders across their circumpolar range will be an important next step to assessing how the species as a whole may be resilient to the predicted ecosystem changes as a result of climate change.

Acknowledgements

We thank the 2010-2018 Mitivik Island field crews for data collection and I. Butler and R. Kelly for data organization. We also thank the Natural Sciences and Engineering Research Council of Canada, Environment and Climate Change Canada, Canada Research Chairs Program, Northern Scientific Training Program, the Nunavut Wildlife Management Board, Polar Continental Shelf Project, and the Canadian Network of Centres of Excellence (ArcticNet), and Polar Knowledge Canada for logistical support and research or personal funding. Animal care approval for this project was granted through the University of Windsor Committee for Animal Care (AUPP #11-06; Reproductive Strategies of Arctic-Breeding Common Eiders) and ECCC Animal Care (EC-PN-15-026).

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Table 2.1 - Summary of key common eider parameters collected from Mitivik Island, Nunavut used in the current analyses. Parameters include relative arrival date (RAD), breeding propensity (BP), laying interval (LI), relative lay date (RLD).

Year	RAD	BP(%)	LI	RLD
2010	-0.56	45	3.67	0.78
2011	0.85	86	7.09	-1.25
2012	1.50	31	4.13	1.38
2013	0.09	51	5.09	-1.00
2014	-1.54	55	3.73	-0.19
2015	0.33	27	3.20	0.13
2016	0.68	35	3.59	-0.91
2017	-1.36	48	2.67	-1.03
2018	1.13	34	5.33	0.30

Table 2.2 - Summary of isotopic metrics from female common eiders breeding at the Mitivik Island colony, Nunavut, Canada.

Year	$\delta^{15}\text{N}$ (mean \pm sem)	$\delta^{15}\text{N}$ (%CV)	$\delta^{13}\text{C}$ (mean \pm sem)	$\delta^{13}\text{C}$ (%CV)	MNND	SEAc	$\delta^{15}\text{N}$ (Range)	$\delta^{13}\text{C}$ (Range)
2010	13.3 \pm 0.21	12.0	-17.5 \pm 0.13	5.60	0.3298986	4.126788	5.66	5.27
2011	12.3 \pm 0.09	9.1	-17.2 \pm 0.13	8.90	0.2403756	5.410365	6.07	5.26
2012	13.1 \pm 0.18	9.2	-17.3 \pm 0.15	5.70	0.2130465	3.732829	6.34	6.31
2013	13.3 \pm 0.14	9.1	-17.3 \pm 0.12	6.20	0.2900655	2.937805	4.94	3.95
2014	13.5 \pm 0.13	7.5	-17.5 \pm 0.09	3.80	0.2121922	2.046193	5.33	3.24
2015	12.4 \pm 0.18	10.4	-17.3 \pm 0.14	5.70	0.2213423	3.919739	6.41	5.97
2016	14.5 \pm 0.13	8.8	-17.6 \pm 0.09	5.20	0.2655668	3.30091	6.08	4.37
2017	13.3 \pm 0.17	11.1	-17.1 \pm 0.17	8.50	0.1741301	4.788338	5.75	6.42
2018	13.5 \pm 0.18	9.7	-18.2 \pm 0.15	6.10	0.2601373	3.841665	6.61	4.66

Mean \pm SEM, %CV $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ raw values were calculated to show broad population metrics. Isotopic metrics, Mean Next Nearest Neighbor (MNND), Standard Ellipse Area (SEAc), range of $\delta^{15}\text{N}$, and range of $\delta^{13}\text{C}$ infer annual foraging niche dynamics. All values are quantified from plasma samples and include a combination of breeding stages.

Table 2.3 - Summary of average Winter North Atlantic Oscillation (Winter NAO), Spring North Atlantic Oscillation (Spring NAO), and mean relative ambient temperature (Ta) for the 7 days leading up median arrival date, from Coral Harbour Airport Weather Station, Nunavut, Canada (closest weather station to the Mitivik Island colony).

Year	Winter NAO	Spring NAO	Ta
2010	-0.86	-4.45	6.60
2011	-0.09	-0.75	6.28
2012	-1.07	2.55	7.50
2013	0.61	-0.60	7.20
2014	-0.35	3.45	7.73
2015	-0.59	4.55	4.33
2016	-0.65	1.90	9.43
2017	0.28	1.05	8.40
2018	1.46	1.75	6.10

Table 2.4 - List of principal component correlation values based on plasma isotopic metrics of female common eiders breeding at the Mitivik Island colony, Nunavut, Canada and environmental metrics (see Methods for details). Bold values indicate statistically significant relationships.

Group	Variable	PC1 (Spatial Foraging)	PC2 (Niche Breadth)	PC3 (Trophic Position)
Isotopic	$\delta^{15}\text{N}$ Range	0.20201	0.51061	-0.57323
	$\delta^{13}\text{C}$ Range	0.45855	0.13017	-0.12389
	MNND	-0.17996	0.40414	0.63032
	SEAc	0.47159	0.1755	0.08766
	AVG $\delta^{13}\text{C}$	0.29675	-0.58426	0.19752
	%CV $\delta^{13}\text{C}$	-0.42799	0.08641	-0.13040
	AVG $\delta^{15}\text{N}$	-0.35635	0.21296	0.01793
	CV $\delta^{15}\text{N}$	0.30971	0.36609	0.44129
	<i>Eigenvalue</i>	3.7445	1.4859	1.2791
	<i>Cum. Percent</i>	46.806	18.574	15.989
Group	Variable	PC1 (Spring Conditions)	PC2 (NAO)	
Environmental	S NAO	0.6001	-0.53296	
	W NAO	0.35475	0.84569	
	Ta	-0.71696	-0.02764	
	<i>Eigenvalue</i>	1.1305	1.0078	
	<i>Cum. Percent</i>	37.685	33.592	

Table 2.5 - Summary of analyses examining predictors of variance in plasma $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in female common eiders breeding at the Mitivik Island colony, Nunavut, Canada. Bold values indicate statistically significant relationships.

Analysis	Variable	F value	df	p
MANCOVA ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$)	Full Model	4.35	74, 1198	0.0001
	Year	5.22	16, 1198	0.0001
	Breeding stage	2.97	2, 600	0.03
	Year*Breeding stage	1.41	48, 1198	0.04
	Relative arrival date	19.50	2, 599	0.0001
	Body Mass	0.50	2, 599	0.61
ACNOVA ($\delta^{15}\text{N}$)	Full Model	5.92	37, 600	0.0001
	Year	8.67	8, 8	0.0001
	Breeding stage	2.96	3, 3	0.03
	Year*Breeding stage	1.31	24, 24	0.15
	Relative arrival date	1.41	1, 1	0.23
	Body Mass	0.13	1, 1	0.71
ANCOVA ($\delta^{13}\text{C}$)	Full Model	2.82	37, 600	0.0001
	Year	1.15	8, 8	0.33
	Breeding stage	0.56	3, 3	0.64
	Year*Breeding stage	1.34	24, 24	0.13
	Relative arrival date	27.00	1, 1	0.0001
	Body Mass	0.51	1, 1	0.47

Table 2.6 - Summary of regression analyses using environmental metrics (ENVPC1 (Spring Weather); and ENVPC2 (NAO)) to predict variation in plasma isotopic metrics (ISOPC1 (Foraging Location); ISOPC2 (Niche Breadth); and ISOPC3 (Trophic Position)) in female common eiders breeding at the Mitivik Island colony, Nunavut, Canada. Bold values indicate statistically significant relationships.

Variable	ISOPC1			ISOPC2			ISOPC3		
	R ²	F _{2,6}	p	R ²	F _{2,6}	p	R ²	F _{2,6}	p
Model	0.02	0.07	0.93	0.10	0.35	0.72	0.62	4.88	0.06
ENVPC1	-	0.12	0.74	-	0.17	0.69	-	1.50	0.27
ENVPC2	-	0.03	0.86	-	0.53	0.49	-	8.26	0.03

Table 2.7 - Summary of regression analyses between breeding parameters (relative arrival date (RAD); percent breeding propensity (BP); laying interval (LI); relative lay date (RLD)) and isotopic metrics (ISOPC1 (Foraging Location); ISOPC2 (Niche Breadth); and ISOPC3 (Trophic Position)).

Variable	RAD			BP			LI			RLD		
	R ²	F _{1,1}	p	R ²	F _{1,1}	p	R ²	F _{1,1}	p	R ²	F _{1,1}	p
Model	0.34	0.84	0.53	0.73	4.48	0.07	0.01	0.02	1.00	0.23	0.51	0.70
ISOPC1	-	0.16	0.70	-	0.62	0.47	-	0.03	0.87	-	0.01	0.91
ISOPC2	-	1.57	0.27	-	12.67	0.02	-	0.00	0.97	-	1.25	0.31
ISOPC3	-	0.79	0.42	-	0.15	0.72	-	0.02	0.91	-	0.25	0.64

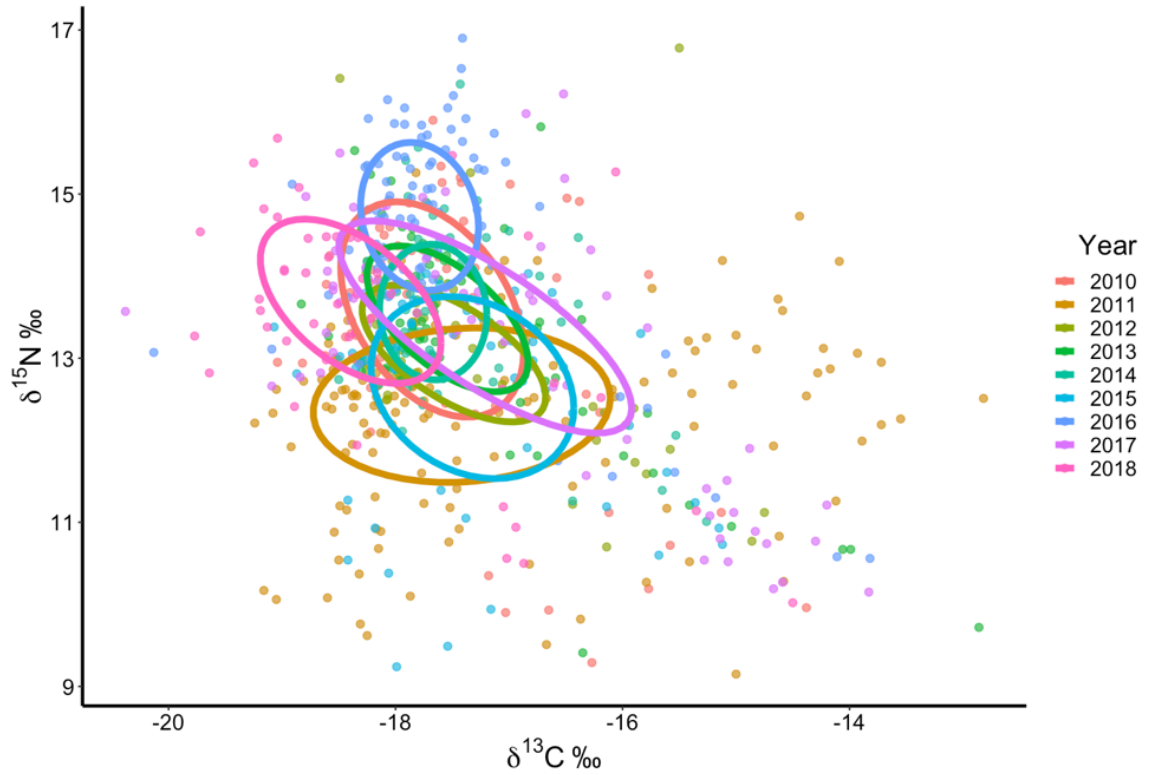


Figure 2.1 - Inter-annual variation in plasma isotopic niche of eiders nesting at Mitivik Island, NU. Each colour is an independent year. Ellipses represent 40% of the individuals' isotopic signatures within each year. 40% ellipses are used to represent the placement of birds within each year in isotopic space and compare placement among years.

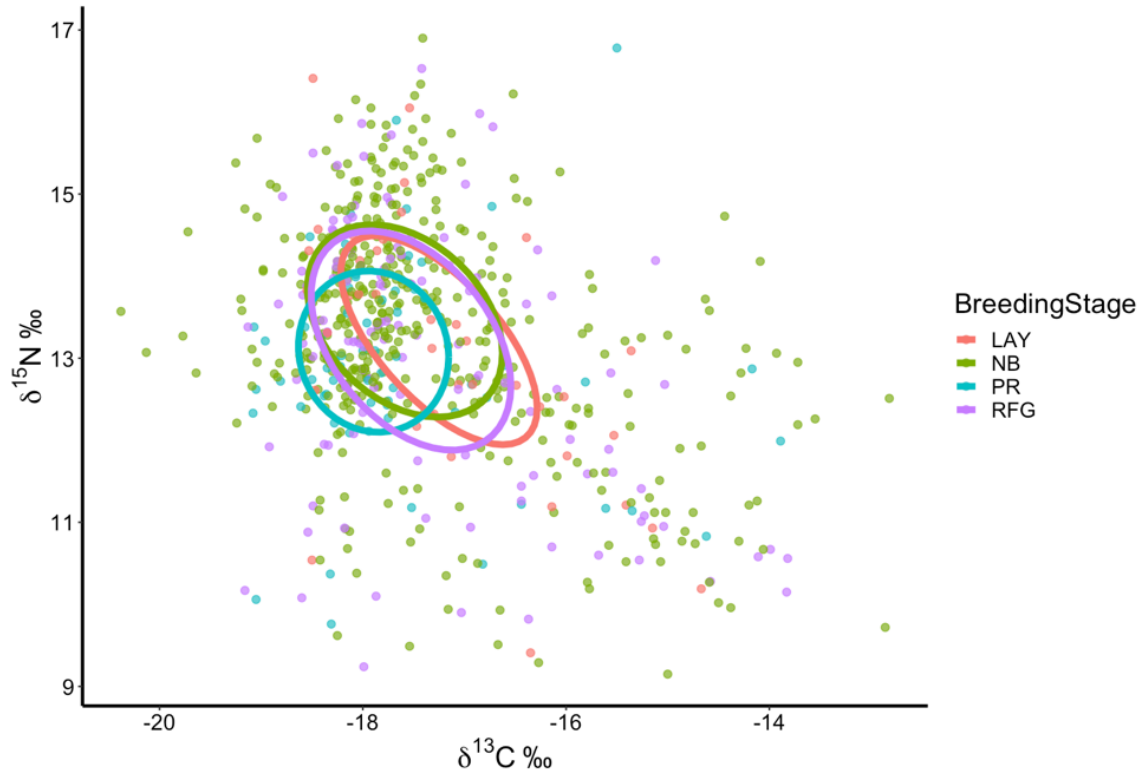


Figure 2.2 - Isotopic variation from plasma across breeding stages of eiders nesting at Mitivik Island, NU. PR (green line; pre-recruiting), shows 40% of the individuals which started laying at least 8 days post-capture; RFG (blue line; rapid follicle growth), is characterized by birds that are delayed between 8-1 days before they breed; and Lay (red line; laying or incubating) is the 40% ellipse of birds which were laying or incubating the same day of capture.

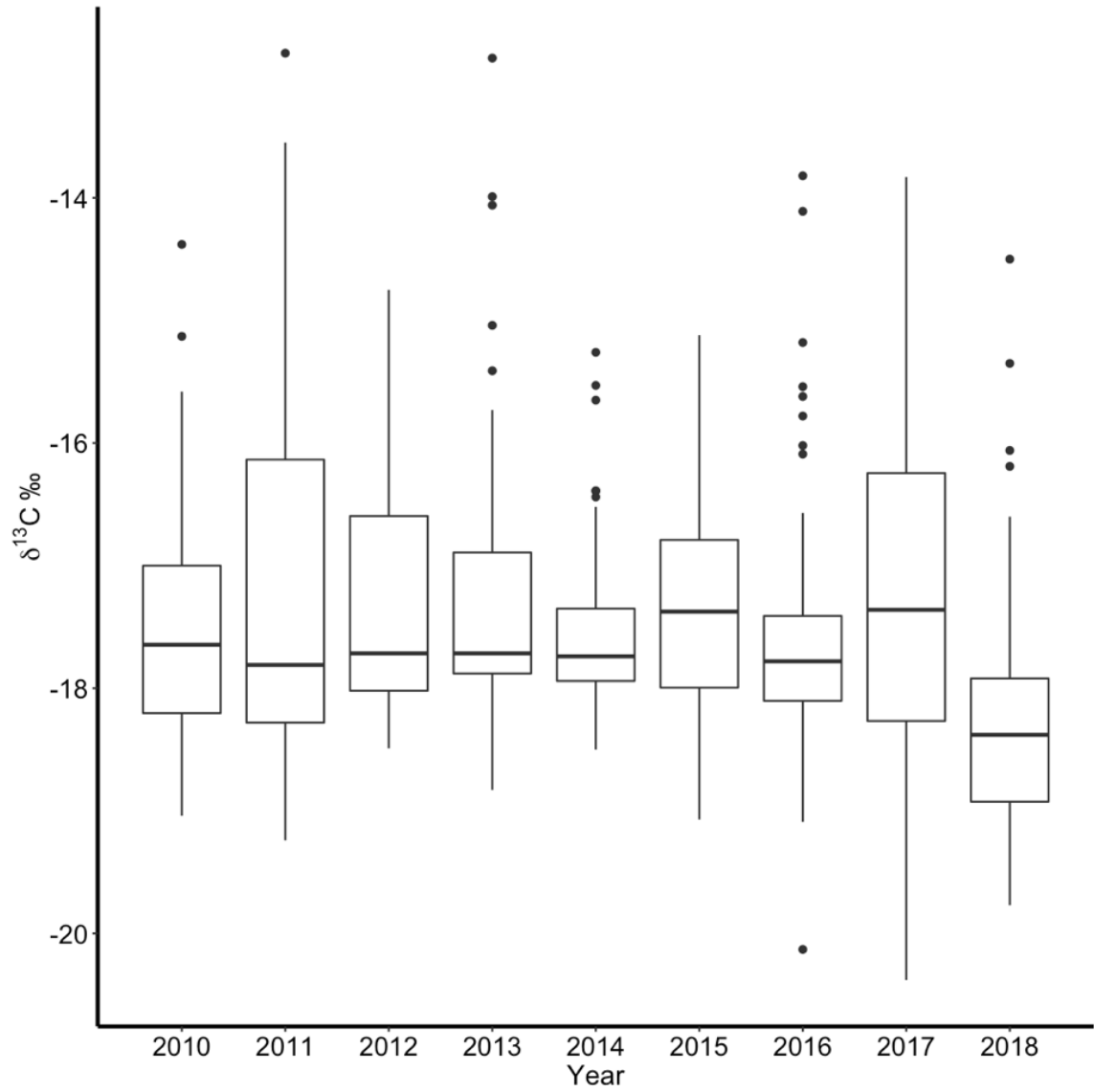


Figure 2.3 - Boxplot of inter-annual variation in plasma $\delta^{13}\text{C}$ values of female eiders nesting at Mitivik Island, Nunavut, Canada. High $\delta^{13}\text{C}$ values represent an inshore benthic diet, while a low $\delta^{13}\text{C}$ value represent an offshore pelagic diet.

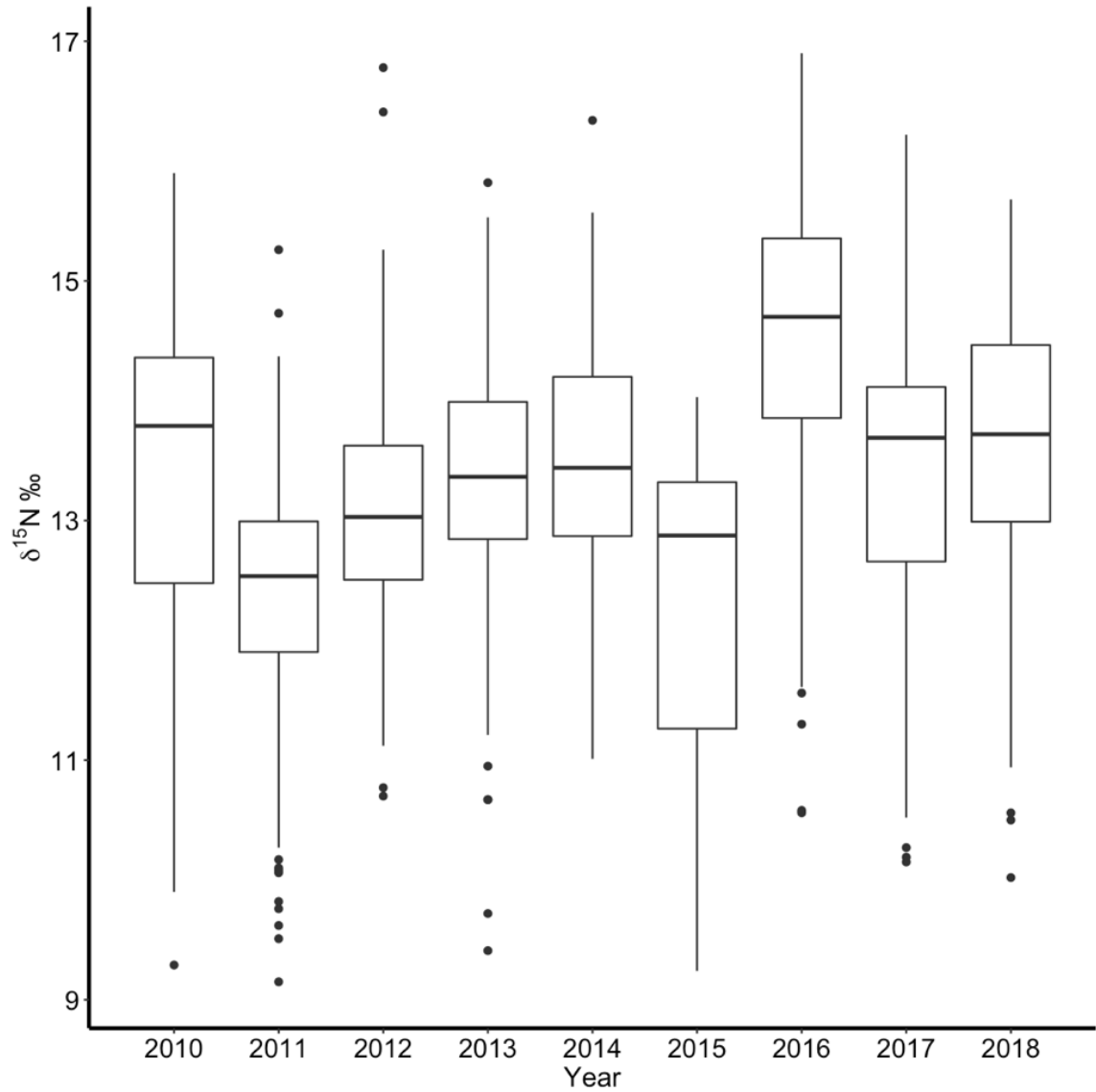


Figure 2.4 - Boxplot of inter-annual variation in plasma $\delta^{15}\text{N}$ values of female eiders nesting at Mitivik Island, Nunavut, Canada. High $\delta^{15}\text{N}$ values represent a higher trophic diet, compared to low $\delta^{15}\text{N}$ values.

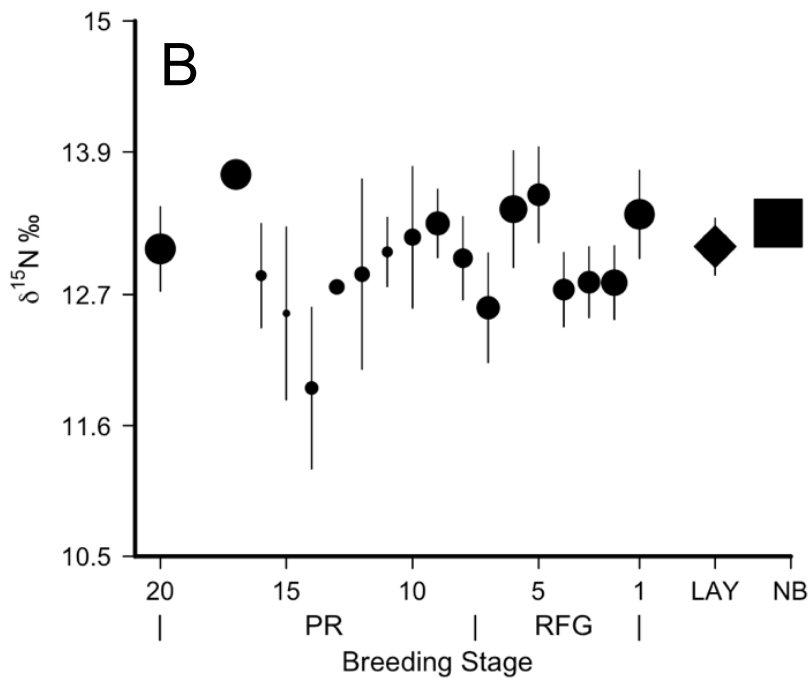
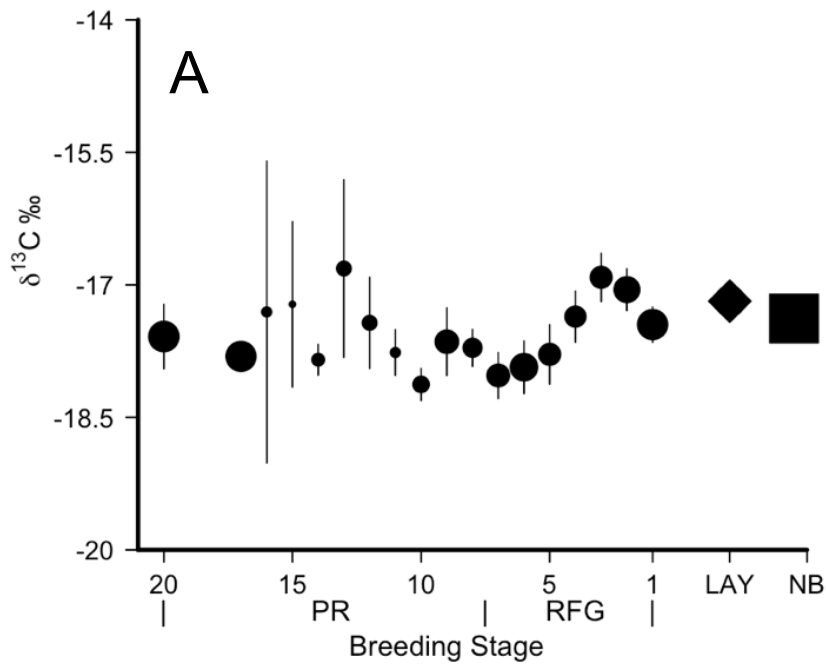


Figure 2.5 - Variation in plasma $\delta^{13}\text{C}$ (A), and $\delta^{15}\text{N}$ (B) values across breeding stages of female eiders nesting on Mitivik Island, Nunavut, Canada. Values are represented as mean \pm SEM provided for each day during pre-breeding (black circle), rapid follicle growth (black square), and laying (black triangle).

Chapter 3 :

Investigating resiliency to climate change in an Arctic seabird using inter-colony isotopic niche variation

Introduction

Over the past decade dramatic changes in environmental conditions have occurred globally including substantial increases in annual ambient temperature, as well as significant changes in oceanic conditions (e.g., decreased pH, increased temperature) (IPCC, 2018). Although these changes have caused a myriad of direct and indirect effects on organisms, a primary focus in ecology has been to quantify the ability of organisms to successfully time and complete key fitness-related life-history stages in the midst of these environmental changes (Root et al., 2003; Stearns, 1989). A suite of studies across a diversity of taxa have consistently demonstrated that the annual abundance and phenology of prey emergence is constantly changing, the severity of which varies spatially (Boggs, 1992; Durant et al., 2007; Post & Forchhammer, 2008; Visser et al., 1998). While we can generally appreciate that these environmentally-driven changes in prey dynamics are driven by human-induced climate change (Karl & Trenberth, 2003; Orłowsky & Seneviratne, 2012; Parmesan, 2006; Parmesan & Yohe, 2003), it is yet still unclear whether all organisms that are being affected have the ability to keep pace with this degree of change (Cohen et al., 2018).

Arctic ecosystems are particularly susceptible to the impacts of climate change due to multiple abiotic and biotic factors (Descamps et al., 2017; Kwok & Rothrock, 2009; Screen & Simmonds, 2010). Moreover, as warming continues the usual reflective effects of ice and snow cover acting to send ultraviolet (UV) radiation back into the atmosphere are declining rapidly, causing increasingly rapid rises in ambient temperatures (i.e., at a rate 2-4% faster than anywhere else on Earth; Johannessen et al., 2004). As a result, the timing of Arctic sea-ice melt continues to advance (Kern et al., 2010; White et al., 2010) and sea-ice extent has already receded significantly (Comiso et al., 2008; Overlsand and Wang, 2010), resulting in several downstream impacts on marine wildlife (Doney et al., 2011; Hoegh-Guldberg & Bruno, 2010). Nonetheless, despite these dramatic changes it remains difficult to predict the relative vulnerability of different species and even populations to this degree of change (Huey et al., 2012; Pacifici et al., 2015). Importantly, we know little about how this degree of change will affect variation and abundance in the resources that form central constraints in the life history

investment decisions of organisms (Post & Forchhammer, 2008; Visser et al., 1998). Both theoretical and empirical information has suggested that species, populations and individuals with more generalized, flexible diets and foraging strategies are better able to withstand intra- and inter-annual variation in environmental conditions and as a result will be better equipped to invest in and successfully complete energetically demanding life history stages such as reproduction (Bolnick et al., 2003; Hamer et al., 2007; Hennin et al., 2015). As such, being able to quantify species- or even population-level foraging specialization could provide key information as to how sensitive we expect populations to be to environmentally-induced trophic disruptions (Post et al., 2009), and therefore their overall resiliency to climate change (Winder & Schindler, 2004).

One group of organisms that has mixed levels of foraging specialization, different fitness-related constraints associated with investing in reproduction, and are sensitive to climate-induced trophic responses, are Arctic seabirds (Grémillet & Boulinier, 2009). Seabirds have evolved to take advantage of abundant and predictable seasonal food sources at marine-terrestrial interfaces, and often forage on a large diversity of prey items (Barrett et al., 2007). Furthermore, due extensive evolutionary radiation within seabirds, there are multiple sub-species found across their range, all of which show substantial genetic and phenotypic variation (Friesen et al., 1996; Jouanin & Mougin, 1979; Nisbit et al., 2017; Wojczulanis-Jakubas et al., 2014). By virtue of their wide-ranging distribution, sub-species or populations are likely exposed to extremely different environmental conditions, driving variation in the differential impact of foraging decisions on key life-history decisions, and therefore fitness (Frederiksen et al., 2012; Gilchrist & Mallory, 2005; Stempniewicz et al., 2007). Within Arctic ecosystems we expect these sub-species or – populations to be differentially impacted by climate change since within the last decade lower trophic level Arctic prey organisms - such as bivalves (e.g., blue mussel (*Mytilus edulis*) and small fish (e.g., arctic cod (*Boreogadus saida*), capelin (*Mallotus villosus*)) that normally form the prey-base for many higher trophic order seabird species have shown significant population declines and range changes (Buren et al., 2019; Doney et al., 2012; Harley et al., 2006; Philippart et al., 2011). As a result, Arctic seabirds that depend on these organisms to fuel key life-history stages such as migration and reproduction (Sydemen et al., 2012) are also demonstrating similar population declines (Anderson et al., 2018; Frederiksen et al., 2016; Goutte et al., 2015; Perkins et al., 2018).

With the impact of climate change varying significantly across the Arctic (Anisimov et al., 2007), the ability to quantify variation in foraging strategies at both the intra- and inter-population levels of Arctic species is a vital first step to assessing their ability to adapt to their rapidly changing environment. Although previous studies in seabirds have demonstrated individual-level variation in foraging decisions (Elliott et al., 2008; Watauki et al., 2004; Woo et al., 2008), and individuals with highly flexible (i.e., more generalized) foraging strategies are predicted to possess greater potential adaptive capacity (Hamer et al., 2007; Ronconi & Burger, 2008), little is currently known about the variation in foraging strategies at the level of a species' range. To be able to estimate the resiliency of Arctic seabirds to climate change, we first require baseline information on how foraging strategies of seabirds vary across a wide geographic range (Moe et al., 2009), as well as information on whether this variation is related to variation in environmental conditions (Croxall et al., 2002). Nonetheless, finding effective, efficient and fairly non-invasive techniques for quantifying inter-population variance in trophic specialization, and therefore foraging strategies, is challenging (Boecklen et al., 2011; Hobson, 1999). In recent decades, the quantification of stable isotopes (i.e., nitrogen - $\delta^{15}\text{N}$ and carbon - $\delta^{13}\text{C}$) in seabird tissues has proven to be a novel, repeatable and fairly non-invasive technique to investigate foraging niche dynamics at multiple temporal and spatial scales (Herman et al., 2017; Hobson, 1999; Horswill et al., 2016; Le Bot et al., 2019; Pavia et al., 2013). Since information on isotopic niches can be used to infer foraging strategies, dynamics, and decisions (Newsome et al., 2007), as well as how the trophic dynamics of organisms are being impacted by climate change (Post et al., 2009), isotopes and the flexibility in isotopic niches are increasingly used to estimate resiliency to change across wide-ranging species (Layman et al., 2007; Munroe et al., 2015).

Here we use information on the foraging niche ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic dynamics) of pre-laying common eiders (*Somateria mollissima*, hereafter eider) collected from 8 distinct breeding colonies across the species' breeding range to assess the resiliency of common eiders to environmental change. Eiders make an excellent system to test these questions for several reasons. First, eiders are comprised of six subspecies which have been hypothesized to vary significantly between specialist and generalist diets (Goudie et al., 2000; Jónsson, personal communication) and, by proxy, foraging strategies and niche. Secondly, eiders are widely distributed across the northern hemisphere where a significant number of seabird species reside, and as such they are exposed to a substantial amount of variation in available prey. Therefore, eiders are a useful representative species for seabirds in general as they are exposed

to a suite of environmental and dietary variation. Finally, due to their wide distribution, environmental variation may impose colony or sub-species-specific constraints in acquiring and digesting food, which then may be exacerbated by climate change (Stempniewicz et al., 2007; Sydeman et al., 2015).

To begin answering our questions, we first examined inter-colony variation in both isotopic values (nitrogen - $\delta^{15}\text{N}$ and carbon - $\delta^{13}\text{C}$) and trophic position as a means of measuring the breadth of their isotopic niche and assess the level of specialization in foraging strategies across colonies (Newsome et al., 2009). Based on specialist versus generalist theory (Bearhop et al., 2004; Julliard et al., 2006; Martinez del Rio et al., 2009; Newsome et al., 2009), we predicted that the niche characteristics of colonies would vary significantly across the range of eiders (Horswill et al., 2016). This is because we expect not only that different populations may have evolved differential specializations to locally-available prey, but also that we expect the impacts of climate change to interact differentially across space and time as the associated responses of lower trophic organisms vary across the Northern Hemisphere. From a resiliency point of view, we-predicted that colonies with a larger breadth of intra-population isotopic variation would possess a wider breadth of foraging strategies (generalist strategy) and would therefore be more resilient to constraints generated by resource limitation (i.e., variable distribution and quantity of prey). Next, to assess whether variation in environmental conditions influences isotopic niche dynamics, and therefore the relative risk of a given colony to the effects of climate change (Becker & Beissinger, 2006; Jaeger et al., 2010), we used variation in sea-surface temperatures (SST; an environmental variable which has previously been shown to influence seabird foraging and reproduction) (Paiva et al., 2013) to predict variation in isotopic niche dynamics. Given that warmer sea surface temperatures have been shown to negatively impact the abundance and distribution of key prey items for eiders (Beukema et al., 2005), we predicted that the specific sea surface temperatures that eiders experience at arrival on their own breeding grounds would negatively impact (i.e., restrict) their isotopic niche (Cherel et al., 2006). Again, we expect that colonies with a more generalist foraging niche to be more resilient to changes in localized environmental conditions, which may be driving prey distribution due to climate change, as these colonies should be able to locate and take advantage of a wider array of prey resources (Pavia et al., 2013). Finally, we propose a novel, qualitative method of assessing population-level foraging specialization built on three criteria from previous specialization theory (Bearhop et al., 2004; Julliard et al., 2006; Martinez del Rio et al., 2009;

Newsome et al., 2009). First, specialist colonies lack dispersal ability, and therefore will have a narrower breadth of $\delta^{13}\text{C}$ values. Second, specialist colonies will have a less diverse diet, and will likely have a narrower breadth of $\delta^{15}\text{N}$ values. Finally, specialist colonies will respond strongly to environmental variation and are less likely to adapt successfully to novel conditions. Overall, our aim of this study was to provide a biologically relevant and analytically efficient means to help conservation ecologists and wildlife managers predict the resilience of this species to climate change across its range, with the goal of extending this framework to other at-risk species and systems.

Methods

Study sites and blood sample collection

We collected blood samples of pre-breeding and nesting (i.e., incubating) eider females from 8 colonies across their breeding range in 2018 (Table 1, Fig. 1). At each study colony, colony-relevant methods were used to capture females, which was largely dependent on their breeding stage at capture. At Mitivik Island, Nunavut, Canada we caught pre-laying females at arrival from wintering grounds using large flight-nets. Within 3 minutes of a female hitting the flight net, females were extracted, and blood sampled to obtain baseline blood samples to eliminate any effects of capture stress (Hennin et al., 2015, Hobson et al., 1992). At all other colonies, females were captured on their nest during the incubation period using a bownet trap or noose-pole.

At each study location, we collected between 200-1000uL blood samples from individuals via the tarsal vein using a 23G thin-wall, 1-inch (c.25-mm) needle attached to a heparinized 1-mL syringe. Samples were then transferred to heparinized collection tubes and kept cool ($\sim 10\text{ }^{\circ}\text{C}$), and within 8 hours of collection, samples were centrifuged at 10,000 rpm for 10 minutes to separate the plasma and red blood cell fractions. Plasma was decanted into a separate cryovial, and both plasma and red blood cell samples were then stored at -20°C until further analysis.

Environmental indices

Sea surface temperature (SST) is a commonly used proxy for localized environmental conditions across our sampling locations, and representative of the environmental condition's eiders are directly exposed to while foraging during the pre-breeding period (Pavia et al., 2013). We obtained SST data from the National Oceanic and Atmospheric Administration (NOAA -

www.ncei.noaa.gov/erddap) (Table 2). Since eider breeding (i.e., laying) phenology varies across their range and our sites, we first calculated the mean laying date for each colony and then considered the month (i.e., 30 days) prior to that date as the “pre-breeding period” based on previous research (Hennin et al. 2015). Using this month time frame for each pre-breeding period, we then calculated the average sea surface temperature (AVG), the standard error of the mean (SEM), and the percent coefficient of variation (%CV) for SST for each colony as a means of generating a relative metric for variation in SST that could be compared across colonies.

Stable isotope analysis

Stable isotopes fractionate and turnover at different rates in different body tissues. Plasma samples have a turnover rate of 3 days (Hahn et al., 2012; Hobson & Clark, 1993) and red blood cells at a rate of 2-3 weeks (Hobson & Clark, 1993). Therefore, we were able to obtain pre-breeding isotopic niche estimates by analysing plasma samples collected from pre-laying eiders at Mitivik Island, and red blood cells from incubating females at all other sampling locations (Table 1). Stable Isotope analyses were based on previously validated techniques (see Hobson & Clark, 1992 for details). All samples were freeze dried until achieving a constant mass (roughly 72 hours). We then ground freeze dried samples into a fine, homogenized powder using a metal spatula. Red blood cells were not lipid extracted, as there are no lipids present (Hobson 1992), however, plasma samples were lipid extracted using a 2:1 chloroform:methanol solution (based on Bligh and Dyer, 1959). We added 1.9 mL of chloroform:methanol solution to 100 μ L of each freeze-dried plasma sample and incubated them at 30 °C for 24 hours. Samples were then centrifuged at 15000 rpm for 10 minutes. Using a p1000 pipette, we removed the lipid solution, reserving the plasma pellet. The plasma pellet was then washed once more with an additional 1.9 mL of chloroform:methanol solution, centrifuged at 15000 rpm for 10 minutes, and lipid solution was removed, leaving only the plasma pellet. Samples were left open for 24 hours in fume hood, allowing any remaining chloroform:methanol solution to evaporate.

Using a fine-scale 4-digit balance, 0.3-0.5 mg of each plasma and red blood cell sample was weighed into individual tin-capsules for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. Analysis of plasma isotopes were conducted at the using continuous-flow isotope-ratio mass spectrometry (CFIRMS) at the Environment Canada Stable Isotope Hydrology and Ecology Research Laboratory in Saskatoon, Saskatchewan. All red blood cell samples were prepared and analysed at La Rochelle Université,

France and measured for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ by mass spectrometry at the Littoral Environment et Sociétés (LIENSs) Stable Isotope platform. Both plasma and red blood cell samples were then combusted using a Eurovector 3000 (Milan, Italy) elemental analyzer, resulting in the production of CO_2 and N_2 analyte gases, which were separated by gas chromatograph and introduced into a NU Horizon (Nu Instruments, Wrexham, UK) triple-collector isotope-ratio mass-spectrometer via an open slit, then compared to a pure CO_2 or N_2 reference gas. Ratios of the stable forms of nitrogen ($^{15}\text{N}/^{14}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$) were expressed in delta notation (δ), as parts per thousand deviation from the primary standards: atmospheric nitrogen and Vienna Pee Dee Belemnite (VDPB) carbonate standards, respectively.

Isotopes are commonly used as both a spatial and temporal marker of dietary incorporation (Bearhop et al., 2004; Boecklen et al., 2011), largely due to our knowledge of the turnover rates of metabolically active tissues. Since turnover rates are specific to tissues, and vary with body size, it is important to use turnover rate values, termed trophic discrimination factors (TDF) (Bond & Diamond, 2011; Caut et al., 2009). We used red blood cell and plasma TDF values ($\delta^{15}\text{N}_{\text{eiderTDF}}$) from spectacled eiders (*Somateria fischeri*), a similar sized, and closely related species to common eider, as there is currently no common eider specific TDF value (Federer et al., 2010).

Stable isotopes naturally vary across the globe, providing an isotopic map (isoscape) of expected low-trophic (“baseline”) values (Bowen et al., 2009). Temperate isoscapes are well established in the literature, but isoscapes are much less pronounced in the Arctic, making it challenging to obtain the baseline isotopic values needed to compare isotopic groups (i.e., colonies, populations, species) across a wide geographical range (Bowen, 2010; Hobson, 1999a; Hobson et al., 2012; Jaeger et al., 2010). To account for baseline variation, we collected recent $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of known eider prey from the literature (Table 3). These values were then applied to the raw $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ eider values measures in our samples to correct our values and more accurately compare isotopic values of eiders across our colonies. To correct our raw values, we subtracted the baseline value from prey ($\delta^{13}\text{C}_{\text{base}}$ and $\delta^{15}\text{N}_{\text{base}}$) from the eider value ($\delta^{13}\text{C}_{\text{eider}}$ and $\delta^{15}\text{N}_{\text{eider}}$), giving us standardized values to compare across colonies ($\delta^{13}\text{C}_{\text{corr}}$ and $\delta^{15}\text{N}_{\text{corr}}$). Baseline values were also used to calculate the trophic position (TP) of each colony (Vander Zanden et al., 1997; Vander Zanden & Ramussen, 1999):

$$\text{TP} = ((\delta^{15}\text{N}_{\text{eider}} - \delta^{15}\text{N}_{\text{base}}) / \delta^{15}\text{N}_{\text{eiderTDF}}) + \text{TP}_{\text{base}}$$

Where TP_{base} is the trophic position of the baseline values, and a TP of 2 (a widely accepted value to use, and consistent with eider prey) was used.

We calculated average $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values using the corrected values for each location to accurately compare niche dynamics across colonies. Finally, we calculated the percentage of the coefficient of variation (%CV) in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, which allowed us to better understand inter-colony isotopic variation (Table 4).

Calculation and interpretation of niche dynamics

We used the SIBER package in R to calculate and compare the niche characteristics of each colony of eiders, using baseline corrected values (Jackson et al., 2011; R Core Team 2014; Table 5). One of these measurements is the 40% Standard Ellipse Area (SEA_c) corrected for small sample size. This metric captures 40% of individuals in the colony based on the bivariate normal distributions and provides information on the distribution of individuals within a foraging niche (Jackson et al., 2011). In addition, we calculated Layman metrics, including the range of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and the mean next nearest distance (MNND), which is a metric of the Euclidean distance between two isotopic points (Layman et al., 2007). These variables have been previously used to infer and compare foraging decisions (Herman et al., 2017; Le Bot et al., 2019), and dietary specialization (Newsome et al., 2007). To test these criteria, we first conducted a principal component analysis to collapse down our related isotopic metrics (average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, %CV $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, SEA_c , range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and MNND). We then examined whether environmental conditions (average SST and %CV SST) could predict variation in isotopic metrics (Table 6). The PCA identified 3 principal components (PC), explaining 49.4, 22.0, and 18.0% of variance in our isotopic metrics, with eigenvalues of 3.95, 1.76, and 1.44, respectively. SEA_c , range of $\delta^{15}\text{N}$, and range of $\delta^{13}\text{C}$ were all positively loaded on the first principle component (with correlation values of 0.47, 0.46, and 0.46, respectively), representing a metric of *isotopic niche breadth*. On to the second principal component, %CV $\delta^{13}\text{C}$ and AVG $\delta^{15}\text{N}$, were positively loaded (correlation values of 0.50 and 0.65, respectively), and %CV $\delta^{15}\text{N}$ was negatively loaded (-0.39), representing a metric of *trophic position*. Finally, %CV $\delta^{13}\text{C}$ and MNND both positively loaded onto the third principle component (correlation values of 0.68 and 0.47, respectively), representing a metric of *spatial foraging location*. The residuals from our PC groups were extracted to test for predictive relationships between isotopic metrics and SST metrics (AVG and %CV SST).

Statistical analyses

Our four goals for statistical analyses were to: (1) quantify variation in inter-colony isotopic values (Table 4); (2) calculate and compare the trophic position of eiders across colonies (Table 4); (3) test the relationship between isotopic niche metrics and colony location as a means of assessing latitudinal/longitudinal gradients (Table 1, 4); and (4) examine whether environmental variables could predict population-level variation in isotopic niche metrics (Table 5). To quantify variation in $\delta^{13}\text{C}_{\text{corr}}$ and $\delta^{15}\text{N}_{\text{corr}}$ (hereafter $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) across breeding colonies we first ran a MANOVA on our corrected isotopic values. We then ran two, one-way ANOVAs to test for variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ across locations, followed by a Tukey-HSD post-hoc test to identify where specific differences among colonies existed. Secondly, to assess inter-colony variation in trophic position (TP) we ran a one-way ANOVA, followed by a Tukey-HSD post-hoc test. Third, to assess whether colony location could predict variation in isotopic metrics, we ran two ANCOVAs including isotopic PC scores as dependent variables and the latitude and longitude of each location and independent variables. Finally, to determine whether inter-colony variation in isotopic metrics can be predicted by broad scale environmental metrics, we ran ANCOVAs with isotopic PC scores as our dependent variables and environmental PC scores related to sea surface temperature as our independent variables. All of our data met the assumptions of a given parametric test. All analyses were conducted in JMP version 14.1.0 (SAS).

Results

Inter-colony variation in isotopic values

Examining $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ together, we detected significant inter-colony variation in isotopic signatures of pre-breeding eiders (MANOVA Wilk's Lambda, $F_{14,364}=26.2$, $p<0.0001$, Fig. 2). We also detected significant variation in $\delta^{15}\text{N}$ (one-way ANOVA, $F_{7,183}=23.0$, $p<0.0001$), trophic position (one-way ANOVA, $F_{7,183}=19.3$, $p<0.0001$, Fig. 3), and $\delta^{13}\text{C}$ across colonies (one-way ANOVA, $F_{7,183}=29.8$, $p<0.0001$, Fig. 4). Post-hoc analyses revealed a diversity of complex inter-colony differences for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and trophic position (Fig. 3,4).

Spatial predictors of isotopic variation

Amongst the variables we used to represent spatial variation (i.e., latitudinal and longitudinal), only a handful significantly predicted variation in isotopic metrics. The range of ^{13}C values were marginally significantly different across colonies ($F_{2,5}=4.43$, $p=0.08$), and by latitude ($F_{1,1}=8.44$,

p=0.03), but not longitude ($F_{1,1}=0.21$, $p=0.67$; Table 7). We found that next neighbor distance differed significantly by colony ($F_{2,5}=8.61$, $p=0.02$), and with latitude ($F_{1,1}=17.20$, $p=0.01$), but not longitude ($F_{1,1}=2.81$, $p=0.15$). Finally, we found a significant difference in trophic positions (PCISO2) across colonies ($F_{2,5}=4.24$, $p=0.08$), driven by longitude ($F_{1,1}=3.08$, $p=0.04$) across colonies, but there were no differences in latitude across colonies ($F_{1,1}=3.08$, $p=0.14$).

Inter-colony variation in environmental variables

We found that average sea surface temperature differed significantly by colony ($F_{2,5}=9.45$, $p=0.02$), as well as across latitude ($F_{1,1}=8.56$, $p=0.03$) and longitude ($F_{1,1}=16.5$, $p=0.01$) (Table 7). However, while there was a marginally significant difference in the percent coefficient of variation (%CV) for SST across longitude ($F_{1,1}=5.10$, $p=0.07$), there were no differences between colonies ($F_{2,5}=2.98$, $p=0.14$) or across latitudes ($F_{1,1}=2.85$, $p=0.15$).

Relationship between isotopic niche and environmental variables

A significant, positive relationship was detected between average sea surface temperature (AVG SST) and trophic position (PCISO2; $F_{1,1}=13.1$, $p=0.02$) (Table 8). However, no other significant relationships were detected between isotopic niche variables and environmental variables (Table 8).

Discussion

To date, few studies have managed to successfully quantify dietary markers across the range of Arctic seabirds, many of which have pan-Arctic distributions (Dean et al., 2015; Herman et al., 2017; Votier et al., 2010). As a result, it is now critical to broadly assess the resiliency of seabirds to environmental changes to determine which populations or species are most at-risk from climate change. Using an international dataset collected from 8 breeding colonies of common eiders we aimed to use inter-colony variation in isotopic niche variables to begin estimating the resiliency of this species to climate change. First, we found significant inter-colony variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (corrected for baseline variation in prey $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values). These stable isotopes provide information on spatial and trophic foraging decisions, and the degree of foraging specialization (Bearhop et al., 2004; Newsome et al., 2007) and therefore their ability to overcome foraging constraints associated with climate change (Hamer et al., 2007). Second, we found mixed relationships between isotopic metrics and colony location (i.e., latitude and longitude), suggesting that foraging decisions are highly variable across the range of eiders.

Third, we found that eider isotopic signatures were generally not related with variation in localized environmental conditions. Together, these results suggest that certain eiders colonies may be more flexible in adjusting their diet and niche to respond to changes in prey composition and distributions relative to other colonies. Following a discussion of the implications of these results in more detail, we combine our results to propose a novel method of interpreting the degree of isotopic variation across colonies, in terms of foraging specialists versus generalists, as a means of helping to predict the resiliency of different eider breeding populations and other Arctic seabird species to the ongoing effects of climate change.

Inter-colony variation in isotopic niches

Little is currently known about the degree of variation in foraging decisions and isotopic niche across colonies of seabird species, especially common eiders. Nonetheless, given that the impacts of climate change on resource availability and diversity, and fitness related metrics (i.e., breeding) are inconsistent across broad spatial scales this is a critical variable to assess in the context of a changing Arctic. Interpreting only one year of isotope data, as we have here, can be challenging, and inferences from inter-colony variation should be made with caution. For example, the ability to accurately compare isotopic values across geographically distinct colonies hinges on the ability to correct a consumer's isotopic signature for baseline isotopic variation (Kline et al., 1993; Kling et al., 1992). Isotopic signatures of low trophic species naturally fluctuate between years, reflected in geographical isoscapes, which can be reflected in the isotopic signature of consumers, such as eiders (Cabana & Ramussen, 1996; Mehl et al., 2005). Isoscapes are less pronounced in the Arctic, making it challenging to understand what is driving baseline isotopic variation (Ainley et al., 2006; Moody et al., 2012; Schell et al., 1998). However, given the number and diversity of locations of colonies that we were able to sample, paired with our use of literature-derived baseline values to account for as much baseline variation as possible, strengthens our ability to interpret our data with confidence. As such, our results suggest that eiders do indeed have varied foraging strategies across their range which is corroborated by the variation in environmental variables quantified from our colonies. Additionally, our international collaborators have provided qualitative confirmation of our trophic position results for locations. For instance, the Faroe Island colony (i.e., *S.m. faeroeensis*) were believed to target only lower trophic organisms, such as amphipods (*Gammarus* sp.) despite having a relatively diverse prey selection (Jónsson, personal communication). Based on

our stable isotope results, *S.m. faeroeensis* indeed appears to forage a full trophic level lower compared to other eider colonies (Fig. 2,3), suggesting they forage predominantly on prey such as amphipods. In contrast, the Mitivik Island colony appears to incorporate more benthic, macroinvertebrate prey in their diets, resulting in a higher trophic level for the colony overall. These results are corroborated with isotopic studies of eider tissue and egg components conducted at this site (Sénéchal et al., 2011).

It is certainly possible other factors beyond prey distribution and choice may influence inter-colony isotopic variation, including the extreme variation in eider life history events and phenology that occurs across their range (Goudie et al., 2000). Some of the breeding colonies we sampled are migratory, while others are year-round residents, which likely generates inter-colony variation in energetic constraints and demands prior to breeding. Stress and energetic management are two important factors to account for because they can impact isotopic signatures (Sears et al., 2009; Williams et al., 2007). Previous studies have shown that metabolically active tissues are sensitive to the effects of stress and become increasingly enriched isotopically during these times (Hobson et al., 1993). As such, the energetic demand of migration and variation in exposure to extreme environmental conditions (Arctic versus Temperate conditions) across the annual cycle, particularly during the pre-breeding stage we focus on in this study, may explain some of the isotopic enrichment detected here.

Environmental variation weakly relates to inter-colony variation in isotopic niches

Climate change poses many risks to Arctic wildlife, either indirectly through trophic disruptions (Rosenblatt & Schmitz, 2016), or through direct interactions between an individual's physiology and localized environmental conditions (Doney et al., 2012; Grémillet & Boulinier, 2009). It is likely that a latitudinally- or longitudinally-based gradient in environmental conditions may be responsible for variation in the isotopic signatures across breeding colonies (Yurkowski et al., 2016). We confirmed that average sea surface temperature significantly related to both latitude and longitude, demonstrating a stronger relationship with longitude and that many isotopic metrics also differed by both latitude and longitude. Considering the role sea surface plays in influencing prey species distribution and abundance (Arula et al., 2014), it is likely that sea surface temperature also plays an important role in affecting variation in foraging conditions and therefore isotopic niche. In agreement with this, we found that colonies in warmer locations

(i.e., John's Island, Canada, Kirkjubøhólmur, Faroe Islands, Breiðafjörður, Iceland, and Grindøya, Norway) appeared to forage in larger, low trophic, niches compared to colonies in colder locations such as Kongsfjorden, Norway, Mitivik Island, Canada, and Tern Island, Canada, which forage within a higher trophic level and smaller niche. This is consistent with other studies which have found that broad-scale temperature patterns are able to predict isotopic metrics (Barnes et al., 2007).

Even so, based on our data there does not appear to be a clear gradient in environmental and weather patterns. For example, Kongsfjorden, Norway was the most northern colony sampled, but it has relatively warmer environmental conditions (i.e., sea surface temperature and ambient temperature) than some more southern Arctic colonies, such as Tern Island, Mitivik Island, Onega Bay, and Iceland (Table 2, Fig. 1) (Descamps et al., 2017; Svendsen et al., 2002). This supports previous research in which many of the high-Arctic areas experience milder conditions, compared to lower latitude locations in the spring (Johannessen et al., 2004; Wassmann et al., 2010). Therefore rather than solely gradients in climate, it may be that Arctic oceanic patterns and currents likely play a role in generating some of the complexity in the relationship between geographic location and isotopic niche.

Using isotopic niche specialization to predict resiliency across colonies

The term isotopic niche has only been present in the literature for roughly 15 years and it provides a framework for isotopic ecology (Newsome et al., 2007); however has yet to be implemented to predict resiliency of species or populations to climate change. Isotopic niche, or isotopic specialization, is related to the realized degree of dietary and foraging specialization or generality (Bearhop et al., 2004). Within the isotopic niche framework, a generalist species can either be made up of either a wide distribution of individually specialized populations, or by all populations sharing a similar degree of generalized diet (Yurkowski et al., 2016). The ability to quantify the apparent foraging generalization of a species across its range is critical given that we expect it may be the mechanism underlying species resiliency; specialist populations to be at greater risk to the effects of rapid environmental change compared to generalist, more flexible populations (Terraube et al., 2011). According to specialization theory (Bearhop et al., 2004; Julliard et al., 2006; Martinez del Rio et al., 2009; Newsome et al., 2009), we identified and quantified three criteria related to population-level foraging specialization. The criteria for defining a specialist colony were: 1) a narrower breadth of $\delta^{13}\text{C}$ values (less dispersal), 2) a

narrower breadth of $\delta^{15}\text{N}$ values (less diverse diet), and 3) strong responses to environmental variation. In addition to being considered specialists, colonies that meet these criteria and are thought to have less dietary flexibility, be less resilient, and more likely to be impacted by climate change.

Previous studies suggest that as a species, eiders have a largely specialized diet consisting largely of mollusks (i.e., blue mussels (*Mytilus edulis*), limpets (*Acmea testudinalis*), clams (*Histella arctica*)) (Bustness & Erikstad, 1988; Lovvorn et al., 2003; Merkel et al., 2007). Indeed, the morphology and phenology of eiders have evolved to take advantage of abundant mollusks across their range (Goudie et al., 2000). However, given the variation in environmental conditions across the range of eiders and the role environmental variation plays in modulating prey quality and diversity, significant inter-colony differences in the degree of diet specialization would be somewhat unsurprising. Indeed, there was significant variation in the breadth of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across our sampled colonies, and some colonies therefore fulfill the first two criteria of the definition of a “specialist” colony, while others do not. For instance, the Tern Island colony located in Nunavut, Canada had the smallest standard ellipse areas (SEAc; assessing breadth of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and it also experiences extensive sea-ice distribution (Saucier et al., 2004), which likely restricts the available foraging locations for birds at this colony during the pre-breeding period. Comparatively, John’s Island located off the southern coast of Nova Scotia, Canada in the warmer Atlantic Ocean had one of the largest isotopic niches of all the colonies, in terms of breadth of $\delta^{13}\text{C}$ values, likely because there were more available foraging areas allowing for greater dispersal. Within this framework, we would therefore predict John’s Island (SEAc = 3.78, range ^{13}C = 5.61, range ^{15}N = 3.03) to be more resilient to effects of climate change than Tern Island (SEAc = 0.44, range of ^{13}C = 1.89, range of ^{15}N = 1.89). Our third and final criteria indicating that a colony was “specialist” was that it shows strong responses to environmental variation. We found that colony-wide trophic position was highest for colonies foraging in colder temperatures (based on sea surface temperature), which is also associated with increased spatial foraging variation. For example, Mitivik Island is situated in the Canadian Arctic, as such is exposed to cold sea surface temperature (Table 2) and has a high trophic position (Table 4). As such, environmental conditions do seem to drive trophic dynamics and foraging decisions to all sampled colonies of eiders, indicating a degree of specialization species-wide for these criteria.

Taking these three criteria together, there is strong support that some colonies of eiders could be considered specialists, and others generalists. As such, climate change may pose key fitness-related downstream constraints which modulate life history investment unequally across the distribution of common eiders. However based on these results as a whole, common eiders would be considered a generalist species, and therefore likely to be quite resilient to environmental changes resulting from climate change. It will be critical to assess moving forward is whether colonies are considered specialists because of prey selection, or whether they are specialists due to ice-restrictions influencing available foraging areas. Although extremely challenging, future studies would benefit from quantifying prey abundances at each site in conjunction with ice imagery to determine the underlying mechanism driving specialization across these colonies. While additional studies quantifying the foraging and breeding responses of birds to environmental variation will be necessary to confirm these predictions, our study nonetheless provides the first internationally-coordinated application of quantitative isotopic techniques across a large spatial scale estimate foraging specialization and therefore the expected resiliency to climate change.

Conclusions and future directions

Tracking inter-colony variation in key fitness-related decisions across a widely dispersed species is challenging (Cristofari et al., 2016; Younger et al., 2016; Welker et al., 1997). This is especially challenging in species with pan-Arctic distributions (Gilchrist, 1999; Hansen et al., 2012; Yurkowski et al., 2016), as the impacts of climate change, and associated environmental conditions and constraints are highly variable across the Arctic, making it challenging to model the responses of Arctic species to environmental variables and constraints (Henry and Molau, 1997). It has therefore been challenging to develop a framework by which we can estimate how the dietary decisions of sensitive Arctic organisms will ultimately impact fitness and population resiliency within the ongoing effects of climate change. Using a unique, international dataset, we were able to quantify the degree of inter-colony isotopic niche variation in wild-living common eiders. Our work suggests that niche characteristics vary across the range of this seabird species, which may be driven by a combination of environmental factors including local temperatures and oceanic currents. Our results linking trophic position and variation in average SST provide further evidence that seabird foraging decisions are modulated by localized impacts of environmental conditions. These effects, coupled with the significant inter-colony variation in

isotopic niche metrics, suggest that common eider colonies differ in their resiliency across their range, making it important to consider population-level responses when considering species-level resiliency. Considering that colonies with a larger breadth of isotopic signatures are predicted to be more resilient to environmental changes due to climate change, our data suggest that eider colonies will differ substantially in their resiliency, but at the population level will be able to successfully cope with projected environmental change. Although extremely challenging, future studies would benefit from collect multi-year datasets from the same sampling locations and if possible the same individuals to combine isotopic metrics with key breeding parameters, and thereby assess resiliency. This type of sampling approach will provide the information necessary data to make stronger quantifications of isotopic specialization and therefore more robust predictive models of population resiliency.

Acknowledgments

We thank the 2018 Mitivik Island field crews for data collection and I. Butler and R. Kelly for data organization. We thank all collaborators who assisted in sample collection, and also the lab technicians at Littoral Environment et Sociétés (La Rochelle Université, LIENSs). We also thank the Natural Sciences and Engineering Research Council of Canada, Environment and Climate Change Canada, Canada Research Chairs Program, Northern Scientific Training Program, the Nunavut Wildlife Management Board, Polar Continental Shelf Project, and the Canadian Network of Centres of Excellence (ArcticNet), and Polar Knowledge Canada for logistical support and research or personal funding. Animal care approval for this project was granted through the University of Windsor Committee for Animal Care (AUPP #11-06; Reproductive Strategies of Arctic-Breeding Common Eiders) and ECCC Animal Care (EC-PN-15-026).

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Table 3.1 – Summary of common eider colonies sampled for stable isotopic analysis. Eiders have an expansive range, as such samples from multiple independent colonies provides a metric of population-level resiliency. We used red blood cells (RBC) for eiders sampled while incubating their nest, and plasma for eiders that were sampled during the pre-breeding period to assess pre-breeding isotopic signatures.

Location	Sub-species	Lat	Long	Colony	Tissue
Kongsfjorden, Norway	<i>S. m. mollissima</i>	78.918	11.910	2000	RBC
Grindoya, Norway	<i>S. m. mollissima</i>	69.633	18.844	150	RBC
Tern Island, Canada	<i>S. m. borealis</i>	69.547	-80.812	1000	RBC
Breiðafjörður, Iceland	<i>S. m. borealis</i>	65.078	-22.736	300	RBC
Oneaga Bay, Russia	<i>S. m. mollissima</i>	65.048	35.774	150	RBC
Mitivik Bay Island, Canada	<i>S. m. borealis</i>	64.029	-81.789	1000	Plasma
Kirkjubøhólmur, Faroe Islands	<i>S. m. faeroeensis</i>	61.950	-6.799	80	RBC
John’s Island, Canada	<i>S. m. dresserii</i>	43.645	-66.041	500	RBC

Table 3.2 – Summary of average and percent coefficient variation in inter-colony sea surface temperature (SST) for the relative pre-laying month for each common eider colony. The breeding phenology of eiders varies across their range, with certain colonies laying earlier than other. As such, average values (AVG) and percentage of coefficient of variation (%CV) include SSTs for the relative month leading up to average colony lay dates.

Location	Lay Month	AVG	<u>%CV</u>
Kongsfjorden, Norway	<u>May</u>	1.10	65.04
Grindoya, Norway	<u>May</u>	5.99	12.55
Tern Island, Canada	<u>June</u>	0.12	366.99
Breiðafjörður, Iceland	<u>May</u>	6.34	17.23
Oneaga Bay, Russia	<u>May</u>	3.02	53.82
Mitivik Bay Island, Canada	<u>June</u>	0.57	39.86
Kirkjubøhólmur, Faroe Islands	<u>May</u>	7.98	4.73
John’s Island, Canada	<u>April</u>	4.35	16.67

Table 3.3 – Average prey isotopic signatures were collected from the literature to correct common eider isotopic values in order to be able to compare inter-colony isotopic niche. Prey isotopic values (also referred to as baseline) vary across the globe, thereby making untreated isotopic values collected from multiple source locations non-comparable.

Location	Prey Type	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Source
Kongsfjorden, Norway	<i>Hiatella artica</i>	-20.30	6.90	Vieweg et al. 2012
Grindoya, Norway	<i>Hiatella artica</i>	-19.32	7.26	Fredriksen 2003
Tern Island, Canada	<i>Hiatella artica</i>	-18.22	8.64	Sénéchal et al. 2011
Breiðafjörður, Iceland	<i>Mya edulis</i>	-19.60	7.40	Sara et al. 2007
Oneaga Bay, Russia	<i>Styela rustica</i>	-21.60	6.49	Yakovis et al. 2012
Mitivik Island, Canada	<i>Hiatella artica</i>	-18.22	8.64	Sénéchal et al. 2011
Kirkjubøhólmur, Faroes	<i>Mytilus edulis</i>	-19.20	8.41	Bustamante, unpublished
John's Island, Canada	<i>Mytilus edulis</i>	-19.99	7.17	English et al. 2015

Table 3.4 – Summary of mean \pm standard error of mean, percent coefficient of variation (%CV) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ raw values, and average trophic position (TP) of common eiders nesting across 8 colonies. Prey values (Table 3) are applied to these values in order to make inter-colony comparisons. These values are for both breeding and non-breeding eiders, depending on sampling method.

Location	AVG $\delta^{13}\text{C}$	%CV $\delta^{13}\text{C}$	AVG $\delta^{15}\text{N}$	%CV $\delta^{15}\text{N}$	TP
Kongsfjorden, Norway	-18.42 \pm 0.21	4.61	11.76 \pm 0.25	8.52	3.2
Grindoya, Norway	-17.80 \pm 0.14	3.21	11.13 \pm 0.10	3.82	3.0
Tern Island, Canada	-18.83 \pm 0.06	1.65	12.37 \pm 0.11	4.21	2.9
Breiðafjörður, Iceland	-17.77 \pm 0.19	5.19	11.58 \pm 0.22	8.97	3.0
Oneaga Bay, Russia	-19.42 \pm 0.16	3.98	10.15 \pm 0.09	4.33	2.9
Mitivik Island, Canada	-18.16 \pm 0.15	6.01	13.51 \pm 0.18	9.59	3.0
Kirkjubøhólmur, Faroe Islands	-18.55 \pm 0.36	7.75	10.08 \pm 0.24	9.65	2.4
John's Island, Canada	-16.88 \pm 0.35	9.05	12.04 \pm 0.18	6.35	3.0

Table 3.5 – Summary of inter-colony common eider stable isotopic metrics calculated using SIBER. Isotopic metrics, standard ellipse area corrected for small sample size (SEAc), mean next neighbor distance (MNND), range of $\delta^{13}\text{C}$ values, and range of $\delta^{15}\text{N}$ range, characterize foraging dynamics. All metrics are calculated using corrected $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, thereby are comparable across colonies.

Location	SEAc	MNND	$\delta^{13}\text{C}$ range	$\delta^{15}\text{N}$ range
Kongsfjorden, Norway	2	0.40	3	3.43
Grindoya, Norway	1	0.29	2	1.49
Tern Island, Canada	0	0.16	1	1.89
Breiðafjörður, Iceland	3	0.53	3	3.90
Oneaga Bay, Russia	1	0.29	3	1.78
Mitivik Bay Island, Canada	4	0.33	5	5.66
Kirkjubøhólmur, Faroe Islands	3	0.41	5	3.61
John's Island, Canada	4	0.57	6	3.03

Table 3.6 – List of principal component correlation values based on common eider plasma and red blood cell isotopic metrics. Bold values reflect metrics which significantly loaded and included in the principal component.

Variable	Principal component		
	1	2	3
AVG $\delta^{13}\text{C}$	-0.124	-0.201	0.676
%CV $\delta^{13}\text{C}$	0.326	0.498	-0.184
AVG $\delta^{15}\text{N}$	-0.091	0.653	0.353
%CV $\delta^{15}\text{N}$	0.332	-0.389	-0.321
SEAc	0.469	0.053	0.224
Range $\delta^{15}\text{N}$	0.458	0.245	-0.067
Range $\delta^{13}\text{C}$	0.463	-0.117	0.103
NND	0.340	-0.240	0.466
Eigenvalue	3.951	1.762	1.440
Cumulative variance explained	49.384	22.027	18.001

Table 3.7 – Regression analysis between isotopic metrics and principal component residuals as dependent variables, and latitude and longitude and independent variables. Bold p-values reflect a significant (or marginally significant at the $p = 0.1$ level) relationship between dependent and independent variables.

	Variable	Latitude		Longitude	
		F _{1,1}	p	F _{1,1}	p
Isotopic Metrics	AVG $\delta^{13}\text{C}$	0.29	0.61	4.82	0.08
	%CV $\delta^{13}\text{C}$	0.05	0.83	1.55	0.27
	AVG $\delta^{15}\text{N}$	0.85	0.40	1.63	0.26
	%CV $\delta^{15}\text{N}$	0.51	0.50	1.18	0.33
	SEAc	2.92	0.15	0.08	0.78
	$\delta^{13}\text{C}$ range	8.44	0.03	0.21	0.67
	$\delta^{15}\text{N}$ range	0.29	0.61	0.27	0.62
	NND	17.20	0.01	2.81	0.15
	ISOPC1	2.45	0.18	0.01	0.92
	ISOPC2	3.08	0.14	7.87	0.04
ISOPC3	1.30	0.31	1.00	0.36	
Environmental Metrics	AVG SST	8.56	0.03	16.51	0.01
	%CV SST	2.85	0.15	5.10	0.07

Table 3.8 – Regression analysis between residual PC scores and sea surface temperature (both average (AVG) and percent of coefficient of variation (%CV)). Bold values indicate a significant result.

Variable	AVG SST		%CV SST	
	F _{1,1}	p	F _{1,1}	p
PC1	0	0.99	0.94	0.38
PC2	13.1	0.02	2.19	0.2
PC3	0.14	0.72	2.49	0.18

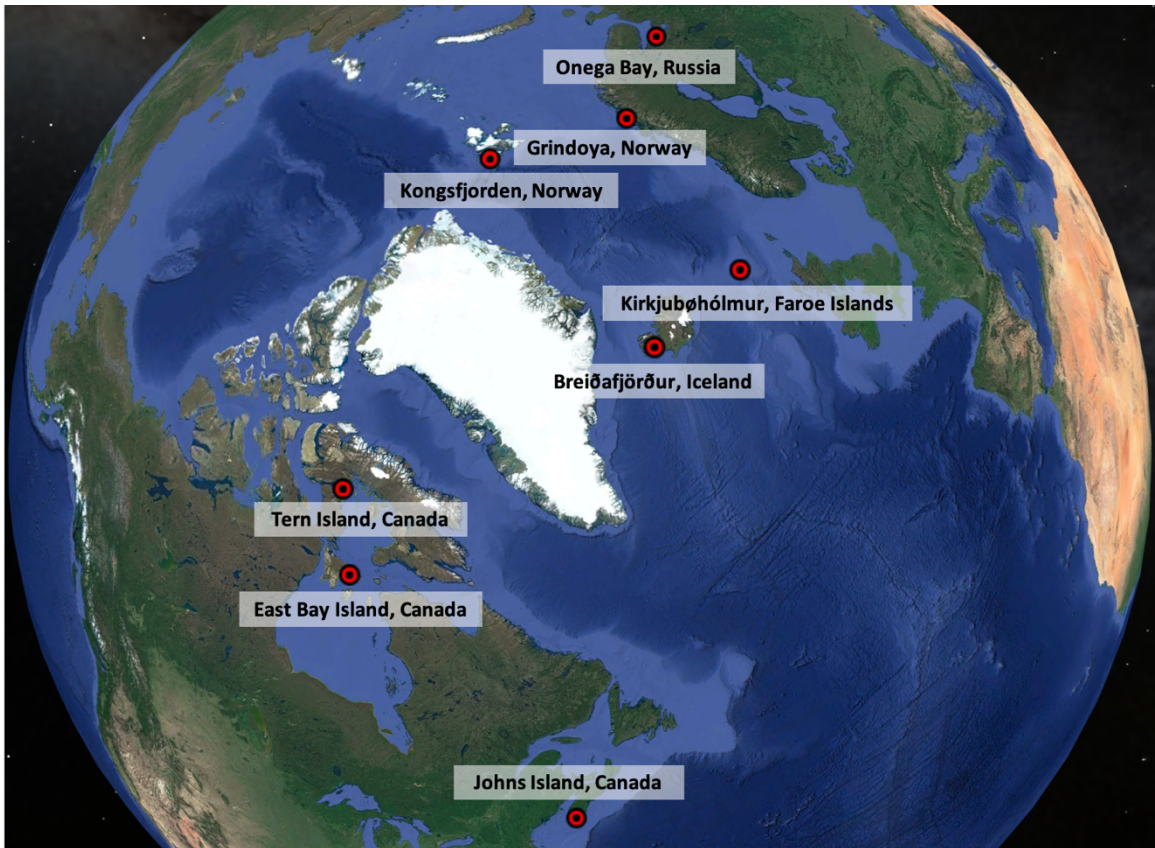


Figure 3.1 – Map of 8 breeding common eider colonies. Each location was sampled during the pre-breeding or breeding period.

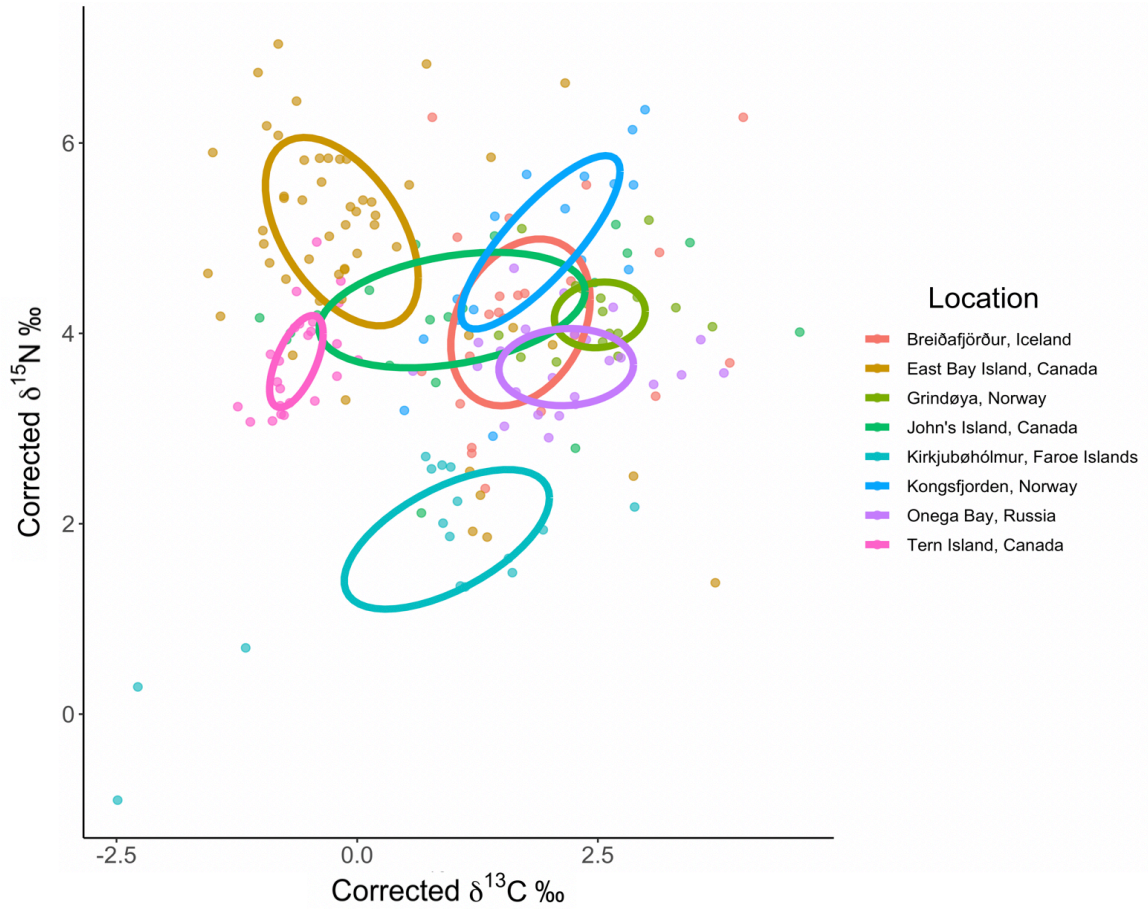


Figure 3.2 – Inter-colony variation in isotopic niche of eiders nesting at 8 different breeding colonies. Each colour is an independent colony. Ellipses represent 40% of the individuals' isotopic signatures within each year. 40% ellipses are used to represent the placement of birds within each colony in isotopic space and compare placement among years. Isotopic values are corrected for baseline variation in prey isotopic signatures (i.e., $\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{prey}}$).

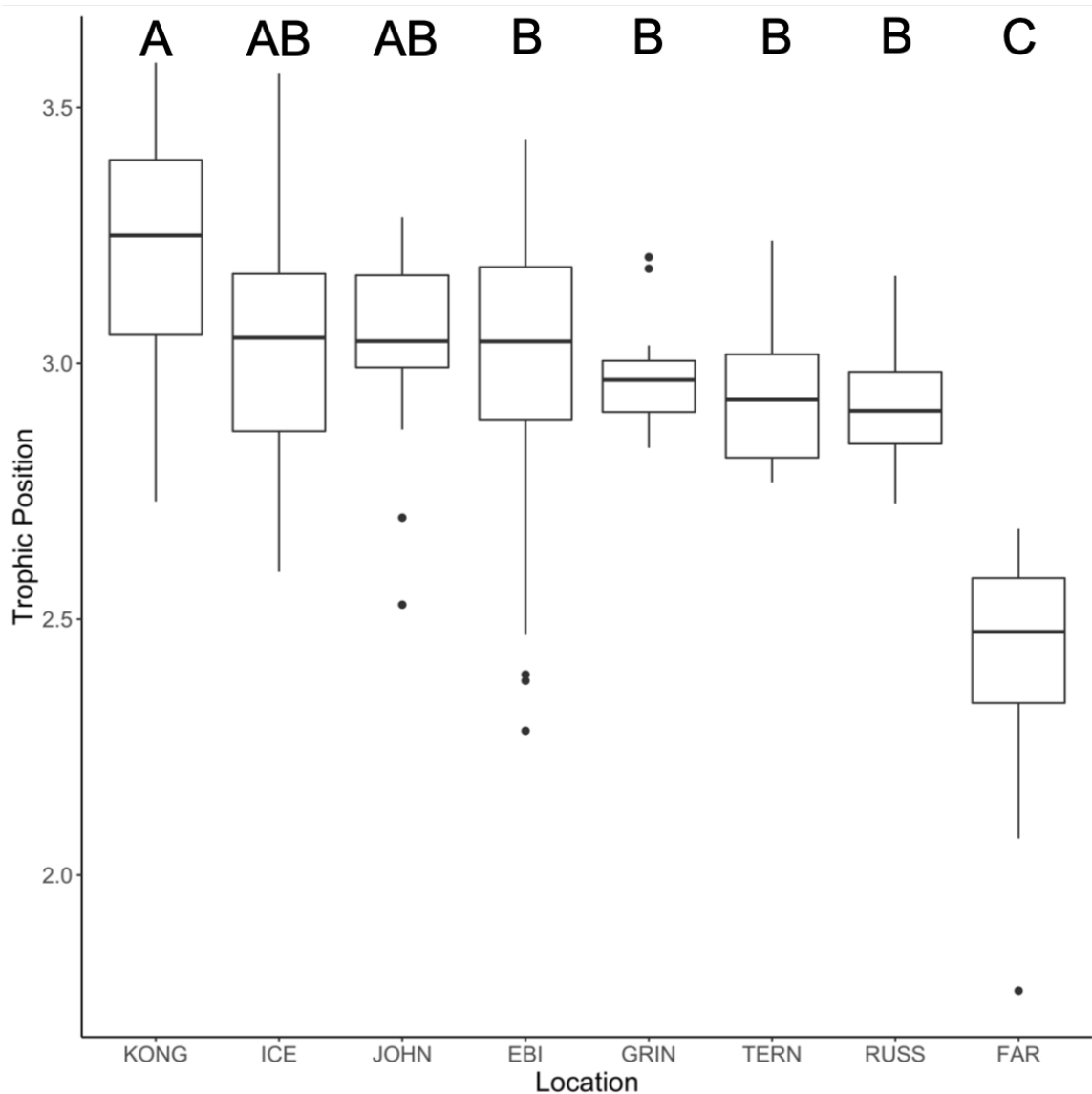


Figure 3.3 – Inter-colony variation in trophic position, with tukey-HSD groups listed above each colony. SPIT = *Kongsfjorden, Norway*; GRIN = *Grindoya, Norway*; RUSS = *Oneaga Bay, Russia*; ICE = *Breiðafjörður, Iceland*; MI = *Mitivik Island, Canada*; JOHN = *Johns Island, Canada*; TERN = *Tern Island, Canada*; FAR = *Kirkjubøhólmur, Faroe Islands*. Different letters above boxplots represent distinct groups based on the out of variance in trophic position. Groups with two letters were described as in between two groups. See methods for description of trophic position calculation.

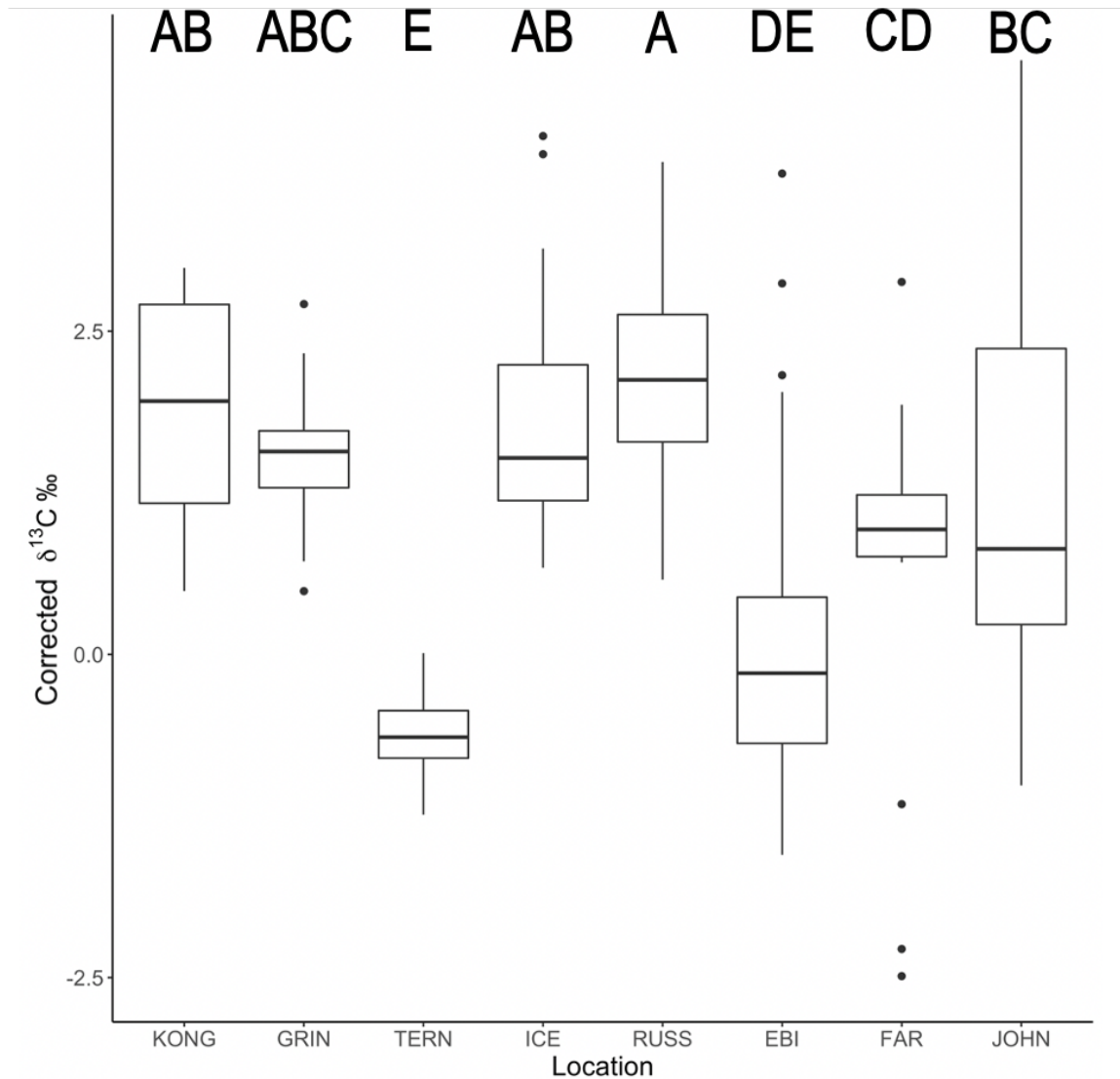


Figure 3.4 – Inter-colony variation in $\delta^{13}\text{C}_{\text{corr}}$ values, which have been corrected by baseline prey values to make comparable across colonies. See table 3 for further information on prey values, and methods for information on correcting values. SPIT = *Kongsfjorden, Norway*; GRIN = *Grindoya, Norway*; RUSS = *Oneaga Bay, Russia*; ICE = *Breiðafjörður, Iceland*; MI = *Mitivik Island, Canada*; JOHN = *Johns Island, Canada*; TERN = *Tern Island, Canada*; FAR = *Kirkjubøhólmur, Faroe Islands*.

Chapter 4 :

A novel application of stable isotopes: using isotopic variation to link environmental conditions, breeding parameters, and resiliency to change

The ability to locate resources in a rapidly changing environment is one of the largest constraints organisms currently face (Newton, 1998; Stephens & Krebs, 1986). Understanding how the foraging flexibility of organisms responds to environmental variation to impact key life history investment decisions may provide key information on species resiliency to climate change (Oliver et al., 2015). In this thesis I proposed a novel and non-invasive method of using isotopic foraging niche as a means of predicting resiliency to environmental change in a model Arctic seabird. Specifically, I aimed to quantify the degree of pre-breeding isotopic variation across multiple scales, using a diving Arctic seaduck (common eider - *Somateria mollissima*, hereafter eiders), as a useful general model for Arctic seabirds (Goudie et al. 2000). In Chapter 2 my goal was to: i) quantify variation in isotopic niche between breeding stages and years, ii) link inter-annual variation in isotopic niche to variation in environmental conditions, and iii) determine whether broad-scale variation in isotopic niche during breeding predicted investment in a number of breeding decisions known to impact fitness. First, I found that isotopic values varied significantly across years and across multiple, successive pre-breeding stages, providing evidence that female eiders modulate their diet to overcome constraints associated with resource limitation and environmental conditions (i.e., ice cover) during an energetically demanding life history stage (Hennin et al., 2015). Further, I found that isotopic metrics were able to predict variation in the ability to invest in reproduction, with certain foraging decisions being associated with a higher average population-level breeding propensity. There was also a shift in foraging decisions throughout the pre-breeding season, specifically an increase in $\delta^{13}\text{C}$ at the onset of rapid follicle production. Variation in $\delta^{13}\text{C}$ was associated with spatial foraging dynamics (Hobson & Clark, 1992a), and my results indicated that females move closer inshore once they near laying. Finally, I generally found that isotopic variation could not be strongly explained by variation in two relevant, broad-scale environmental metrics (i.e., NAO, mean ambient temperatures). Building off of these results, my primary goal for Chapter 3 was to use an international dataset to: i) explore inter-colony variation in isotopic niche, ii) quantify the inter-annual trophic position of eiders, and iii) determine whether localized environmental conditions predicted variation in isotopic niche. I found that isotopic niche and trophic position varied significantly across breeding colonies of eiders, providing evidence for mixed foraging

strategies across eider populations. Further, I found that trophic position, but not other isotopic metrics, were significantly related to variation in sea surface temperature (SST). It is likely that a relationship between isotopic metrics and sea-ice dynamics would provide a stronger result which would be the next step to pursue. Collectively, the results of this thesis provide important context into predicting the ability of seabirds to adaptively respond to variation in environmental conditions through shifts in their trophic dynamics and as such, their ability to modulate their foraging decisions to meet the energetic demands associated with reproduction. These results also provide a fairly non-invasive alternative method to better predict population resiliency to climate change based upon quantifying population-level foraging decisions, which is a known constraint affecting the energetics and functioning of organisms (Bolnick et al., 2003).

Interpreting a novel application of stable isotopes

Resource accrual is critical for successfully investing in reproduction, with the conditions that organisms are exposed to during the pre-breeding period often posing fitness-related constraints (Newton, 1998; Stephens & Krebs, 1986). As such, foraging flexibility – the ability to switch between a suite of foraging strategies depending on resource availability – is a phenotypic response of organisms to match key breeding decisions to trophic dynamics and the environmental conditions which link them (Kassen, 2002; Ryall & Fahrig, 2006). With the current rate of climate change, it is important to determine how and why these linkages might become disrupted, and if organisms possess the breadth of decisions required to accrue the required resources under this amount of change (Hamer et al., 2007). The ability to quantify the degree of foraging flexibility across relevant spatial and temporal scales provides important information on the ability of organisms to overcome fitness-related constraints (Ronconi & Burger, 2008). However, there are many gaps in our current understanding of what influences organismal foraging flexibility and how and why this flexibility influences breeding investment (Love et al., 2014). My thesis aims to help fill some of these gaps, by investigating: 1) isotopic variation across multiple spatiotemporal scales, 2) the roles of resource acquisition in modulating reproductive investment, 3) the relationship between environmental conditions and isotopic niche, and 4) whether we can use stable isotopes to predict resiliency to climate change.

Spatiotemporal isotopic variation

Arctic seabirds are a group of diverse organisms that use multiple different foraging strategies to invest in reproduction (Ricklefs, 1983). For example, common eider are a species that depend on resources to meet the demands of multiple stages of reproduction: from reaching a minimum body condition threshold to invest in reproduction (Legagneux et al., 2016; Hennin et al., 2015), to fueling the actual production of eggs (Erikstad et al., 1998; Robertson & Cooke, 1993), and then depending on stored resources to fuel a 24-day incubation period (Sénéchal et al., 2011). As such, resource limitation poses severe fitness-related constraints in this species. Changes in the need for different resources are represented in the pre-breeding isotopic signatures of eiders, specifically high $\delta^{15}\text{N}$ and lower $\delta^{13}\text{C}$ during pre-reproductive investment (Chapter 2). As the breeding season progresses, changes in $\delta^{13}\text{C}$ indicate that eiders also begin to forage closer to their breeding colony (Chapter 2). No study to our knowledge has been able to track foraging decisions, by means of stable isotope analysis, from breeding investment to the onset of egg laying in any seabird. These new results provide evidence that seabirds have the ability to match their energetic demand to environmental conditions, which may be limiting resource abundance.

Annual shifts in trophic dynamics are becoming increasingly common (Post et al., 2009), with many higher order organisms struggling to keep-pace with the current rate of change (Hansen et al., 2013). With this, temporal variation in higher order foraging decisions provides a key snapshot into food web resiliency as a whole (Hobson et al., 1994; Horswill et al., 2016). However, being able to collect and then quantify this type of information within and across years and populations is often very challenging. Seabirds, as a comparative model group, show a wide breadth in species-specific foraging flexibility. For instance, results from Chapter 2 suggest that common eider show significant flexibility in isotopic values across successive pre-breeding stages, which provides further evidence that this species may be highly flexible in their foraging decisions in response to the varying energetic demands of specific life stages. Recent work has also demonstrated that other seabird species show similar levels of inter-annual responses to resource demography (Le Bot et al., 2019). As such, it will be important to continue investigating the inter-specific variation in foraging flexibility in relation to investment decisions as a means of informing conservation-based management decisions.

All species possess a certain level of adaptive capacity, often by means of phenotypic flexibility (i.e., shifting the expression of phenotypes to match environmental conditions and phenology), to overcome constraints associated with increased environmental variability (Sauve et al., 2019). However, since the impacts of climate change are not specific to one region, they are causing increased levels of localized environmental variation (IPCC, 2018). In turn, certain populations of wide-ranging species may be better able to overcome the constraints associated with localized conditions, and the impacts of climate change as a whole (Møller et al., 2008). However, the degree to which different populations vary in traits such as their foraging flexibility across the range of many species is widely unknown and challenging to quantify. With this, even ‘snapshots’ of how variable different populations are in their foraging decisions can provide key baseline context for improving our understanding of how populations will respond to further change. For example, results from Chapter 3 suggest that common eider show significant inter-colony variation in their foraging decisions, and importantly, that specific eider colonies appear to be foraging at completely different trophic levels. These data further support and are consistent with other wide-ranging seabird species, which also appear to show colony-specific foraging decisions (Herman et al., 2017; Votier et al., 2010).

Life history investment modulated through foraging decisions

One of the most energetically demanding life history stages is reproduction (Hennin et al., 2015, 2016, 2018), and results from Chapter 2 confirm that multiple foraging strategies may be required to overcome stage-specific constraints leading up to being able to successfully invest in reproduction. It is generally accepted that organisms with a generalist foraging strategy will be better equipped to overcome resource-based constraints to successfully invest in reproduction, regardless of the associated environmental conditions (Bolnick et al., 2013). For example, during resource poor years, some seabird species have been shown to flexibly increase their foraging rate to offset the reduced energy gain per prey item (Burger & Piatt, 1990; Litzow & Piatt, 2003). In order to successfully invest in reproduction during these poor prey years, individuals must work harder, expending more energy, which in itself can have fitness-related consequences (Ronconi & Burger, 2008). Since selection in longer lived organisms favours breeding only when conditions are optimal (Wooler et al., 1992), and there is less evolutionary cost to forgoing reproduction in these species, we would expect a strong link between foraging decisions and the ability to invest in breeding in a given year (i.e., breeding propensity). Results from Chapter 2

confirm this, where the probability of investing in reproduction was highest in female eiders which had both an inshore, small niche diet and shifted niche across breeding stages. Inter-breeding-stage trends provide evidence that optimal breeding phenology decisions are contingent on specific foraging decisions, likely those that enable birds to overcome the energetic demand associated with breeding. Overall, these results suggest that the foraging strategies of breeding female eiders are very complex, with females needing to make multiple flexible foraging decisions in order to successfully meet the energetic demands of successive reproductive stages and investment in laying.

Flexible foraging in response to broad- and fine-scale environmental variation

Environmental conditions pose both direct and indirect constraints to organisms across the globe (Belyea & Lancaster, 1999). One important aspect of this is the impact of environmental conditions on trophic dynamics (Wassmann et al., 2011). For lower trophic organisms, these constraints are more direct, as low trophic species depend on specific environmental conditions to breed compared to higher trophic organisms (Cloern & Jassby, 2008). It is challenging to understand these dynamics, as there are multiple environmental conditions which organisms are exposed to and depend upon to invest in life history stages. This is particularly true for marine organisms, as they persist or depend on the ocean throughout their life, and the ocean has shown to be significantly sensitive to the impacts of climate change (Brierly & Kingsford, 2009). Indeed, environmental conditions can also pose multiple constraints, many of which may be synergistic in their impacts on all orders of organisms (Sydeman et al., 2012). Nonetheless, we expect that the ability to switch foraging strategies depending on the environmental conditions an individual is exposed to will be under increased selection with increased levels of environmental variability (Réale et al., 2003). Results from Chapters 2 and 3 indicate that both inter-annual and inter-colony trophic dynamics in female common eiders are significantly related to localized sea surface temperature during the pre-breeding period. These results therefore provide good evidence that the localized environmental conditions that eiders face on their breeding grounds may significantly influence the proximate foraging decisions that ultimately shape their overall reproductive investment decisions.

A novel technique estimating resiliency through stable isotope analysis

Investigating the response of organisms to climate change is challenging, as the impacts of climate change pose direct and indirect impacts on multiple life history stages (Sydeman et al.,

2012), modulating the key fitness-related decisions that higher order species make (Charman et al., 2008). Indeed, the ability to locate resources in a rapidly changing environment is becoming increasingly challenging for organisms and poses downstream constraints on investment in life history stages (Boggs, 1992; Newton, 1998; Stephens & Krebs, 1986). As such, it is more crucial than ever to determine how species living and breeding in habitats like the Arctic, which is showing amplified rates of environmental change, will respond to current and future change (Cohen et al., 2014). To begin this daunting process, I used this thesis to propose a novel method of quantifying foraging flexibility during breeding, and within and across populations, as a means of predicting resiliency to climate change in common eiders. As a starting point, one of Chapter 2's central objectives to achieve our overall goal was to use eiders as a model to investigate relationships between environmental conditions and the ability of organisms to locate sufficient resources, which then modulates the ability of these organisms to invest in reproduction. These relationships can be broad, such as the impact of wide-ranging environmental indices (i.e., North Atlantic Oscillation) on breeding propensity (Descamps et al., 2010), or more localized, such as more fine-scale environmental conditions (i.e., local sea ice dynamics, Jean-Gagnon et al., 2018) impacting reproductive costs and constraints (Hepp et al., 2015). Chapter 3 simultaneously sought to both refine and broaden these questions by showing that variation in localized environmental conditions, such as sea surface temperature (SST) at the breeding colony, can provide a window into key trophic dynamics across broadly-distributed populations. Taken together, these results provide key evidence that some organisms possess enough phenotypic flexibility to cope with highly variable environmental conditions through modulating their foraging decisions, and still be able to invest in reproduction. However, across the range of species, certain locations may be under greater stress from climate change, and therefore lack the resiliency to overcome these constraints.

Environmental constraints driving foraging decisions

Environmental conditions are a significant constraint driving life history decisions, and also limiting the ability of organisms to invest in reproduction (Boggs, 1992; Daunt et al., 2006; Drent and Daan, 1980). Climate change is associated with many global trophic disruptions (Edwards & Richardson, 2004; Hjort, 1914), and must be considered when predicting the resiliency of organisms. Indeed, the impacts of climate change are highly varied across the globe, and even across different regions, such as the Arctic (IPCC, 2018). We proposed the use of a stable isotope

analysis in a model seabird organism, across multiple spatiotemporal scales, as a means of predicting resiliency to climate change. In this thesis, I used two scales of variation to test for isotopic variation as a proxy for foraging dynamics: 1) temporal (Chapter 2), and 2) spatial (Chapter 3). As such, relationships between environmental conditions (e.g., inter-annual and inter-colony) and isotopic metrics therefore represent responses of organisms to changes in conditions. These responses are important to understand, as they provide a window into the ability to shift fitness-related foraging decisions, and organismal resiliency (Oliver et al., 2015). We found that trophic dynamics of eiders, specifically their trophic position, were most strongly related to environmental conditions (Chapter 2). However, we did not find strong relationships between $\delta^{13}\text{C}$ and environmental conditions. This is surprising, as $\delta^{13}\text{C}$ values represent spatial foraging dynamics (Hobson & Clark, 1992a), which are certainly constrained by environmental conditions (i.e., sea ice dynamics). There are a few possible explanations for this, which could provide important context for further applications. First, it is possible that the model organism we chose, common eider, may possess higher adaptive capacity than expected, and may be able to overcome many of the associated changes in environmental conditions. The results presented in this thesis support the idea of eiders having a generalist diet overall (Chapter 2), with significant inter-colony variation in trophic dynamics being detected (Chapter 3). With this, I expect that specialized foraging organisms, or specialized individuals within a population (e.g., ringed seals, Yurkowski et al., 2016) may lack the required foraging flexibility to keep pace with environmental change.

Another possible explanation is that the environmental indices I selected – relative ambient temperature, North Atlantic Oscillation, and relative sea surface temperature – were not strong enough predictors of the actual environmental conditions which drive the foraging decisions being made by eiders, and by extension possibly other marine organisms. For example, previous research has shown that the ability of eiders to invest in reproduction is contingent on meeting a threshold body condition (Sénéchal et al. 2010; Legagneux et al., 2016), and doing so appears highly constrained by sea-ice dynamics (Jean-Gangon et al., 2018). For this thesis, we were unable to include sea-ice dynamics, and instead related sea surface temperature to inter-colony isotopic niche variation (Chapter 3). Our finding that the breadth of inter-colony niche varies significantly with localized sea surface temperature suggest that eiders flexibly adjust fitness-related foraging decisions in response to environmental constraints. This provides

evidence that, as a species, eiders may be resilient to climate change; although certain colonies may be under greater climate-induced pressure, and may lack the required resiliency to persist.

Modulating foraging decisions across multiple temporal scales

The isotopic signature of a high-trophic organism is contingent on lower order trophic interactions, specifically which primary producers are fueling the trophic dynamics (Yamamuro et al., 1995). As such, similar food webs fueled by different primary producers will cause bottom-up isotopic variation, as primary producers often vary significantly in their isotopic routing (Hanson et al., 2010). For example, climate change has resulted in baseline changes in Arctic primary producers, from phytoplankton-based to ice-algal-based (Gosselin et al., 1997; Kohlbach et al., 2016). This can have significant ecological implications, as many Arctic organisms have evolutionarily timed their life history stages to match the emergence of phytoplankton, not ice-algae (Ramírez et al., 2017). It is possible to infer which primary producer is fueling the food-web by measuring $\delta^{13}\text{C}$ in consumers, as ice-algae has higher overall $\delta^{13}\text{C}$ values compared to phytoplankton, and since carbon trophic enrichment is negligible (Budge et al., 2008). Our finding in Chapter 2 that the $\delta^{13}\text{C}$ values of female pre-breeding eiders decrease with relative arrival date, where early arriving individuals forage closer to shore, is likely associated with sea-ice dynamics and ice-bound primary producers. For many other species and systems, this trophic shift has resulted in reduced prey biomass, and fewer adults successfully rearing offspring (Burthe et al., 2012). Interestingly, we found that eiders with high $\delta^{13}\text{C}$ values (associated with inshore foraging, or ice-algae based food webs) are more likely to breed than eiders with low $\delta^{13}\text{C}$ values (i.e., birds associated with offshore foraging, or phytoplankton-based food webs). In terms of resiliency, these results support the idea that eiders possess sufficient foraging flexibility to overcome key fitness-related trophic shifts related to climate change to invest in reproduction, regardless of the environmental conditions. Combining all of this information suggests that foraging decisions are indeed modulated by environmental conditions (i.e., sea ice dynamics), which pose downstream constraints on reproductive investment, and that the resiliency of organisms likely vary across multiple scales (both temporal and spatial).

Future directions and conclusions

Quantifying foraging flexibility and the degree of foraging specialization in species is challenging (Bolnick et al., 2003, Bearhop et al., 2004), as it requires the collecting of repeated samples from individuals over time. Further, with the increased ecological pressure from climate change,

shifts in trophic dynamics have led to increased egg predation in seabird colonies by novel predators (Drent & Prop, 2008; Iverson et al., 2014). Three of the biggest gaps I was unable to examine with my thesis were: 1) whether variation in isotopic niche (i.e., foraging decisions) predicts variation in fitness (e.g., breeding success – the ability to hatch ducklings) either within or across colonies to quantitatively assess impacts of foraging on resiliency; 2) relating individual variation in isotopic variables to breeding parameters; and 3) quantifying intra-individual variation in foraging flexibility over time. With regards to quantifying breeding success, collecting data on hatching success at the Mitivik Island (focal) breeding colony is now very difficult given the fact that very few ducklings survive due to ongoing polar bear predation (Dey et al., 2017). We are therefore currently limited to investigating variation in isotopic niche across the pre-breeding period and using it to predict the ability to invest in reproduction. The ability to apply this framework to a system where offspring survival is high would provide additional, highly informative context. At the inter-colony level, many of the collaborative teams that I collaborated with do not have the capacity to follow females to the end of incubation to estimate breeding success. As such, both at the within- and between-colony levels, it is still currently very difficult to quantitatively use variation in isotopes to assess how variation in foraging flexibility ultimately impacts population resiliency in this species. Secondly, although I was able to relate mean isotopic values to mean breeding parameters, I was unable to relate individual-based variation in isotopes to their breeding parameters, largely because broad-scale metrics like NAO are consistent across all individuals, making it statistically challenging to test this at the individual level. However, based on the amount of variation in ^{13}C and ^{15}N values across individuals, it is likely that there are indeed individuals with specialist and generalist foraging strategies within the colony. To test this idea, future studies may be able to take advantage of high quality tracking data throughout the pre-breeding period to relate isotopic niche to spatial use of habitat and potential restrictions on foraging areas (i.e., ice cover) to verify some of these relationships, particularly with regards to inshore and offshore foraging. Although challenging, by synchronously collecting these data, we would be able to assess the presence of true specialists and generalists within a colony or population. Finally, collecting intra-individual data across years is very challenging in many systems, especially with seabirds such as eiders, making it difficult to determine whether individuals show inter-annual flexibility in the foraging strategies. Although eiders show a high degree of nest-site fidelity, we have little control over which individuals are captured, as we catch and recapture eiders entirely

haphazardly. Further, it is important to minimize human influence on seabird colonies to prevent depredation from other nearby predatory nesters and to minimize additional stressors during an already challenging time, as such capturing eiders on their nest at the focal colony at MI is not possible. Other systems, specifically other pelagic seabirds (e.g., thick-billed murre, black-legged kittiwake) may be better suited to assess intra-individual foraging flexibility because they appear to be more tolerant of human disturbance and easier to recapture. Comparing intra- and inter-individual, as well as inter-colony, flexibility will be key to uncover additional scales of resiliency.

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