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GLOBAL CHANGE ECOLOGY – ORIGINAL RESEARCH

Breeding stage and tissue isotopic consistency suggests colony-level flexibility in niche breadth of an Arctic marine bird

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Abstract
Organisms must overcome environmental limitations to optimize their investment in life history stages to maximize fitness. Human-induced climate change is generating increasingly variable environmental conditions, impacting the demography of prey items and, therefore, the ability of consumers to successfully access resources to fuel reproduction. While climate change effects are especially pronounced in the Arctic, it is unknown whether organisms can adjust foraging decisions to match such changes. We used a 9-year blood plasma δ^{13}C and δ^{15}N data set from over 700 pre-breeding Arctic common eiders (*Somateria mollissima*) to assess breeding-stage and inter-annual variation in isotopic niche, and whether inferred trophic flexibility was related to colony-level breeding parameters and environmental variation. Eider blood isotope values varied both across years and breeding stages, and combined with only weak relationships between isotopic metrics and environmental conditions suggests that pre-breeding eiders can make flexible foraging decisions to overcome constraints imposed by local abiotic conditions. From an investment perspective, an inshore, smaller isotopic niche predicted a greater probability to invest in reproduction, but was not related to laying phenology. Proximately, our results provide evidence that eiders breeding in the Arctic can alter their diet at the onset of reproductive investment to overcome increases in the energetic demand of egg production. Ultimately, Arctic pre-breeding common eiders may have the stage- and year-related foraging flexibility to respond to abiotic variation to reproduce successfully.

Keywords Isotopic niche · Foraging flexibility · Phenology · Trophic interactions · Reproductive investment · Adaptive capacity · Carbon-13 · Nitrogen-15

Introduction

Investment in various life history stages is significantly influenced by an individual's ability to obtain dietary resources and optimally allocate them to meet the energetic demands of the associated life history (McNamara and Houston 1996). Consequently, resource limitation is one of the strongest constraints influencing the ability of an individual to optimize foraging decisions to maximize fitness (Stephens and Krebs 1986; Newton 1998). Since the quality and quantity of available dietary resources can be influenced by variability in the surrounding environment, variation in environmental conditions can play an important role in shaping the relationship between resource acquisition, fitness, and population demography (Boggs 1992). However, as climate change continues to generate increases in mean annual temperatures and variability in climatic conditions (IPCC 2018), animals are expected to be increasingly impacted by

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mounting instability in resource availability (Cushing 1990; Tylianakis et al. 2008).

Relative to other temperate and tropical ecosystems, the Arctic is experiencing amplified rates of climate change (Wassmann et al. 2011), which is reducing seaice extent (Johannessen et al. 2004; Comiso et al. 2008; Hoegh-Guldberg and Bruno 2010; Ciancio et al. 2016), leading to bottom-up trophic disruptions (Wassmann et al. 2011; Boeitus et al. 2013; Jones et al. 2014; Meier et al. 2014a, b). As such, many key prey sources are declining or their distributions are shifting (Both et al. 2006), complicating species' ability to acquire resources and their ability to optimize investment decisions in energetically demanding life history stages, such as reproduction (Ward et al. 2009; Seyboth et al. 2016). Whether Arctic species have the required adaptive capacity to be flexible enough to optimize breeding decisions to proximately keep pace with the current rate of environmental change has, therefore, become an important topic of investigation (Kovacs et al. 2011; Moore and Huntington 2011; Descamps et al. 2017).

Determining the downstream influence of environmental variation on reproductive investment first requires consideration of which prey items organisms consume to fuel reproduction (Walther et al. 2002; Rutschmann et al. 2016). The use of tissue stable isotope measurements to represent foraging niche is well-established in several taxa (Bearhop et al. 2004) and is increasingly used to assess individual- and population-level responses to rapid environmental change (Dawson and Siegwolf 2011; Mancinelli and Vizzini 2015; Pethybridge et al. 2017). Specifically, the combination of stable isotope measurements of carbon ($\delta^{13}C$), which provides information on basal sources reflective of habitat use (i.e., inshore vs. offshore, see Sénéchal et al. 2011), and nitrogen ($\delta^{15}N$), which allows relative estimation of trophic level (Peterson and Fry 1987), provides a non-lethal method of quantifying isotopic niche (Newsome et al. 2007; Matich et al. 2021). Quantifying isotopic niche space or volume can provide insight on the degree of trophic specialization (Seamon and Adler 1996), where groups with larger isotopic niches are predicted to have more diverse diets (i.e., more generalist; Moreno et al. 2010). The degree of trophic specialization can then be used to predict how resilient organisms or populations will be to further environmental change (Polito et al. 2015). For example, groups with a more generalist isotopic niche might be expected to be more successful investing in reproduction, regardless of environmentally induced trophic disruptions because of their greater dietary flexibility (Seamon and Adler 1996). Furthermore, isotopic niche provides a useful tool to assess shifts in community-wide trophic dynamics in response to environmental change (Hobson and Clark 1992a, b, 1999; Newsome et al. 2007; Herman et al. 2017), and insight into how foraging decisions might affect key fitness-related decisions (Hutchinson 1957; Vandermeer 1972; Alatalo 1982; Bolnick et al. 2003). Finally, quantification of isotopic niche also provides a testable framework in which to investigate how environmental variability mediates trophic dynamics and ultimately influences reproductive investment decisions (Chesson 1986; Leibold 1996). Nonetheless, this framework relies on several assumptions (Matich et al. 2021) and a primary assumption is that baseline isotope values remain constant or are accounted for through periods of investigation. However, of the multi-year isotopic studies conducted in the Arctic, none have identified significant inter-annual variation in baseline values (Yurkowski et al. 2020; Deforges et al. 2021). In addition, tracing nutrients isotopically during reproduction is complex and depends on the degree to which birds may be income or capital breeders (Hobson 2006; Hobson et al. 2015, Whiteman et al. 2020). Even considering these caveats, establishing temporal variability in the isotopic niches of populations can be a useful tool for examining the influence of environmental change in polar regions which are historically relatively slow to change over time compared to more southern regions (Yurkowski et al. 2020).

Female common eiders (*Somateria mollissima*) make an ideal study species to test these linkages given that a key environmental factor limiting Arctic-nesting eiders is sea ice cover, particularly during spring migration and the pre-laying period which can restrict access to foraging grounds of this diving seabird (Jean-Gagnon et al. 2018). In addition, female eiders must meet a minimum body condition threshold to invest in reproduction (Hennin et al. 2016a, b), and their ability to do so is influenced by access to resources just prior to breeding (Love et al. 2010; Jean-Gagnon et al. 2018). This is an important consideration because female eiders that can fatten more quickly lay earlier (Hennin et al. 2019), invest in larger clutches (Descamps et al. 2011a; Hennin et al. 2018) and ultimately recruit more ducklings into the breeding colony (Love et al. 2010; Descamps et al. 2011b). Since Arctic-breeding eiders do not migrate with substantial fat stores and instead rely on lipid and protein sources consumed on the breeding grounds to produce their eggs (Sénéchal et al. 2011), and prey items used during egg formation differ in nutritional value (Paiva et al. 2013), the ability to access nutritious prey close to eiders breeding grounds likely influences breeding decisions and outcomes (e.g., Kitaysky et al. 2010), especially under climatically unpredictable conditions (Barbraud et al. 2012). Assessing the isotopic niche sampled before laying may help to provide a general snapshot of female foraging prior to and during laying, acting as an important potential predictor of variation in reproductive investment (Sénéchal et al. 2011).

Here we use a 9-consecutive-year (2010–2018) isotopic data set collected from over 700 Arctic-nesting female common eiders (hereafter eiders) to investigate the linkages between environmental variability, variation in important breeding metrics, and temporal variation in isotopic niche at an Arctic-breeding colony. Specifically, our first objective was to quantify variation in isotopic niche across breeding stages and years. Given the nutritional demands of egg formation (Descamps et al. 2010; Love et al. 2010; Sénéchal et al. 2011; Hennin et al. 2015, 2016a, b, 2018, 2019) and presence of seaice being a major constraint to pre-breeding fattening in female eiders, we predicted that as birds approached laying, they would have higher δ^{15}N values and higher δ^{13}C values as birds targeted higher trophic level prey (Forero et al. 2002; Becker et al. 2007; González-Medina et al. 2018) found closer to shore, respectively. Likewise, given the energetic demands of initiating and fueling egg formation, we predicted that in years when the colony exhibited a larger isotopic niche (more generalized foraging strategy) more birds would have greater access to a diversity of resources, and, therefore, be able to fatten more quickly, generating shorter mean delays before laying, earlier mean laying dates, and higher colony-level breeding propensity (Love et al. 2010; Descamps et al. 2011a; Hennin et al. 2015, 2016a, b, 2018). Finally, we predicted significant inter-annual variation in isotopic niches, driven by inter-annual variation in environmental conditions and trophic dynamics. Considering the highly variable sea ice conditions during the pre-breeding period (Love et al. 2010; Jean-Gagnon et al. 2018), and that local environmental conditions can influence both seabird foraging behavior (Hobson 1999; Paiva et al. 2013) and seaice conditions (Meier et al. 2014a, b), our second objective was to examine whether broad-scale environmental conditions explained inter-annual variation in isotopic niche. We predicted that in years with warmer winters, warmer springs, and higher overall ambient temperatures (as indicated by the North Atlantic Oscillation [NAO] index), there ought to be a greater degree of open water and, therefore, a wider variety of possible prey items available to eiders, resulting in a broader colony-wide isotopic niche.

Methods

Study species and breeding parameters

From 2010 to 2018, we undertook sampling at the largest and longest continually monitored colony of common eiders in the eastern Canadian Arctic, at East Bay Island (EBI), which is found within in the Qaqsauqtuuq Migratory Bird Sanctuary, Nunavut, Canada (64°02′N, 81°47′W). EBI is a small (800 m × 400 m), low lying island (< 8 m elevation). Females breeding at this colony migrate from their wintering grounds off the western coast of Greenland and the northern coast of Newfoundland and Labrador, Canada in May (Mosbech et al. 2006; Steenweg et al. 2017), arrive at EBI in early to mid-June, and lay their eggs in mid-June to early July (Hennin et al. 2015; Jean-Gagnon et al. 2018). Using flight nets, we captured female common eiders as they flew over the colony in mid-June, coinciding with their timing of arrival at the breeding grounds (Descamps et al. 2010; see Supplementary Materials Table S1).

After capture, females were blood sampled within 3 min of capture (Romero and Reed 2005) from the tarsal vein using a 1-mL heparinized syringe and 23G thin-wall, 0.5-inch needle (see Hennin et al. 2015, 2016a, b for details). Plasma was separated from red blood cells, and both components were frozen at − 20 °C. After sampling, females were banded with a metal band and alpha-numeric Darvic bands, then affixed with a unique combination of colored and shaped nasal tag plastic discs using UV degradable monofilament. Females were identified within the breeding colony by their nasal tags using spotting-scopes from seven permanent blinds positioned around the periphery of the island. By observing the females and their associated behaviors, we obtained: breeding propensity (probability of breeding) and lay date (and, therefore, the interval in days between capture at the colony and laying). From these data, we assigned reproductive stage to all birds as either laying (LAY), rapid follicle growth (RFG), pre-recruiting (PR), and non-breeding (NB) (see Hennin et al. 2015 for details; see Supplementary Material). Laying and incubating females were determined based on careful observations from blinds and monitoring of nests, along with noting the presence of an egg in the oviduct at capture. All work was approved by the animal care committees of the University of Windsor (AUPP 11-06 and 19-11) and Environment and Climate Change Canada (EC-PN-15-026).

Environmental indices

We selected climate variables predictive of the storm activity and ice conditions eiders face during the pre-breeding period (see Supplementary Materials Table S2). The North Atlantic Oscillation (NAO) index was used as a proxy for inter-annual variation in environmental conditions, as it impacts a wide area across the Northern Atlantic Ocean. The relationship between temporal variation in NAO values and energetic constraints has been demonstrated in multiple seabird species (Stenseth et al. 2003; Hallett et al. 2004; Sandvik and Erikstad 2008), including eiders (Descamps et al. 2010; Guéry et al. 2017, 2019). We calculated the average winter NAO (December–March), which directly impacts the body condition of female eiders (Descamps et al. 2010) and the average spring NAO (April–July; pre-breeding conditions for eiders at EBI). All NAO values were obtained from the National Weather Service (https://www.cpc.ncep.noaa.gov/). As a proxy for localized environmental conditions at the breeding grounds, we used air temperature (Ta) measured at the Coral Harbour Airport Weather Station (70 km from the breeding colony). We first calculated the mean Ta for each individual on the dates that coincided with the isotopic half-life of plasma (i.e., air temperature roughly 3 days prior to sample collection; Hobson and Clark 1993; Hahn et al. 2012). This value was then averaged across all the individuals in the colony for each year.

Stable isotope analysis and niche metrics

Female eiders caught during their arrival period at EBI ranged in body mass from 1.5 to 2 kg (Hennin et al. 2015), making the use of plasma (with a half-life of approximately 3 days; Hobson and Clark 1992a, b; Hahn et al. 2012) appropriate to assess the most recent isotopic niche space occupied by these individuals (Supplementary Materials Table S3). We freeze-dried 100 uL of plasma from each individual until achieving a constant mass (minimum of 78 h). All samples were then ground into a homogenized, fine powder using a metal spatula. Since plasma is often high in lipids we then lipid extracted all plasma samples using a 2:1 choloroform:methanol solution (Bligh and Dyer 1959). We weighed between 0.3 and 0.5 mg of each sample, using a four-digit balance (Sartorius AG, Model CP2P, Gottingen, Germany), into individual 3.5 × 5 mm tin capsules for δ^{13}C and δ^{15}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. Encapsulated plasma was combusted at 1030 °C in a Carlo Erba NA1500 or Eurovector 3000 elemental analyser. The resulting N_2 and CO_2 were separated chromatographically and introduced to an Elementar Isoprime or a Nu Instruments Horizon isotope ratio mass spectrometer. We used two reference materials to normalize the results to VPDB and AIR: BWBIII keratin (δ^{13}C = − 20.18, δ^{15}N = +14.31%, respectively) and PRCgel (δ^{13}C = − 13.64, δ^{15}N = +5.07%, respectively). Within-run ($n = 5$) precisions as determined from both reference and sample duplicate analyses were ± 0.1% for both δ^{13}C and δ^{15}N.

We used a bivariate approach to calculate isotopic niche size for each year and each breeding stage within the SIBER package (Jackson et al. 2011) in R (R Core Team 2014, Version 4.0.3). Calculated niche metrics included: mean next-neighbor distance (MNND), standard ellipse area (SEA$_C$), X range (i.e., maximum range of δ^{13}C) and Y range (i.e., maximum range of δ^{15}N) (see Supplementary Material Table S3). We then ran a principal component analysis (PCA) to collapse down our eight isotopic metrics and four environmental metrics. This generated three principal components for isotopic metrics, and three principal components for environmental metrics used for further analysis (Table 1, see Supplementary Materials).

Table 1 List of principal component correlation values based on plasma isotopic metrics derived from bulk d15N and d13C values of female common eiders breeding at the East Bay Island, Nunavut, Canada and environmental metrics (see Methods for details)

Group	Variable	ISOPC1 (Spatial Foraging)	ISOPC2 (Niche Breadth)	ISOPC3 (TP)
Isotopic	Y Range	0.20201	**0.51061**	**– 0.57323**
	X Range	**0.45855**	0.13017	– 0.12389
	MNND	– 0.17996	**0.40414**	**0.63032**
	SEAc	**0.47159**	0.1755	0.08766
	AVG δ^{13}C	0.29675	**– 0.58426**	0.19752
	%CV δ^{13}C	**– 0.42799**	0.08641	– 0.13040
	AVG δ^{15}N	– 0.35635	0.21296	0.01793
	CV δ^{15}N	0.30971	0.36609	**0.44129**
Eigenvalue		3.7445	1.4859	1.2791
Cum. Percent		46.806	18.574	15.989

Group	Variable	ENVPC1 (Spring)	ENVPC2 (NAO)
Environment	S NAO	**0.6001**	**– 0.53296**
	W NAO	0.35475	**0.84569**
	Ta	**– 0.71696**	– 0.02764
Eigenvalue		1.1305	1.0078
Cum. Percent		37.685	33.592

Bold values indicate statistically significant relationships at the alpha level of 0.05

Statistical analyses

We had four goals in our statistical analyses, namely, examining whether: (1) isotopic niche at the colony-level varied across years, and (2) breeding stages, and whether inter-annual variation in isotopic metrics (3) predicted variation in key breeding parameters (Table S1), and (4) was related to inter-annual variation in environmental indices (winter NAO, spring NAO; pre-breeding Ta PC groups; Table S2).

First, to assess annual variation in $\delta^{15}N$ and $\delta^{13}C$ values at the colony-level, we ran a MANCOVA (with $\delta^{15}N$ and $\delta^{13}C$ as dependent variables) using our 9-year data set for common eider females including year, breeding stage, the interaction between year and breeding stage, body mass, and relative capture date as independent variables. Since each isotope represents different trophic dynamics (i.e., $\delta^{15}N$: trophic position; $\delta^{13}C$: spatial foraging), we followed the MANCOVA with two separate one-way ANCOVAs for $\delta^{15}N$ and $\delta^{13}C$ to disentangle the effects of our independent variables on each of our isotopic metrics (dependent variables). In the ANCOVAs, we included year, breeding stage, the interaction between year and breeding stage, body mass, and relative capture date as independent variables. Second, to examine finer-scale, breeding-stage specific changes in foraging strategies via variation in $\delta^{13}C$ and $\delta^{15}N$, we conducted break-point analyses. This analysis identifies sudden and significant positive or negative changes in the data set (Muggeo 2003) through estimating 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 convergence occurs. We performed break point analyses for both $\delta^{13}C$ and $\delta^{15}N$ separately including the delay before laying as an independent variable using the Segmented R package (Muggeo 2003; R Core Team 2014). Third, we ran an ANCOVA to test whether mean inter-annual isotopic metrics (i.e., ISOPC1 (Spatial Foraging Breadth), ISOPC2 (Niche Breadth), and ISOPC3 (Trophic Position) predicted variation in colony mean capture dates and breeding parameters by including colony mean breeding parameters as dependent variables (i.e., breeding propensity, the delay between capture at the colony and laying, and relative lay date). Finally, to determine whether inter-annual variation in isotopic metrics could be predicted by inter-annual variation in environmental traits, we ran separate ANCOVAs with the isotopic PC scores as our dependent variables (ISOPC1, ISOPC2, and ISOPC3) and the environmental PC scores (ENVPC1 and ENVPC2) as our independent variables. All our analyses met the assumptions of a parametric test. All statistical tests were run using JMP (Version 14.1.0 SAS) unless otherwise stated.

Results

Inter-annual and breeding stage variation in isotopic values

The MANCOVA analysis detected a significant interaction between year and breeding stage in predicting variation in female eider plasma $\delta^{15}N$ and $\delta^{13}C$ (Table 2; Figs. 1, 2, 3). ANCOVAs examining the two isotopes separately, revealed that only $\delta^{15}N$ showed significant year- and breeding-stage effects (with no year by stage interaction). Variation in $\delta^{13}C$ was negatively correlated with capture date, with earlier arriving females having higher $\delta^{13}C$ values (Table 3).

Fine-scale changes in isotopic values across breeding stages

While $\delta^{15}N$ values were relatively consistent throughout the pre-laying period, breakpoint analyses detected a significant increase approximately 2 days prior to laying (breakpoint value: 1.8 ± 5.4 days, Fig. 3b). A breakpoint was also detected for $\delta^{13}C$, where values were relatively consistent across the pre-laying period, until 7.4 days prior to laying. This occurred at approximately the initiation of the rapid follicle growth (RFG) stage, when $\delta^{13}C$ values began increasing significantly (breakpoint value: 7.4 ± 2.5 days, Fig. 3a).

Using isotopic metrics to predict breeding parameters

There was a significant negative relationship between ISOPC2 (Niche Breadth) and breeding propensity (one-way ANCOVA: $F_{1,7} = 15.37$, $p = 0.01$, $w = 0.60$ Table 4). We found that females that foraged more inshore (higher $\delta^{13}C$ values) and within a narrower niche had a higher probability of breeding. However, we found no other significant relationships between colony-level isotopic metrics and capture or breeding parameters (Table 4).

Climate and isotopic metrics

We found a significant negative relationship between ENVPC2 (North Atlantic Oscillation values) and ISOPC3 (Trophic Position) (ANCOVA, $F_{1,1} = 8.26$, $p = 0.03$, $w = 0$), suggesting that milder spring environmental conditions were associated with more variable trophic position. However, we did not detect any other relationships between environmental variables and isotopic metrics (Table 3).

Table 2 Summary of MANCOVA and ANCOVA analyses examining predictors of variance in plasma δ^{13}C and δ^{15}N values in female common eiders breeding at the East Bay Island, Nunavut, Canada

Analysis	Variable	*F*	df	*p*
MANCOVA (δ^{15}N and δ^{13}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 capture date	19.50	2, 599	**0.0001**
	Body mass	0.50	2, 599	0.61
ANCOVA (δ^{15}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 capture date	1.41	1, 1	0.23
	Body mass	0.13	1, 1	0.71
ANCOVA (δ^{13}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 capture date	27.00	1, 1	**0.0001**
	Body mass	0.51	1, 1	0.47

Bold values indicate statistically significant relationships

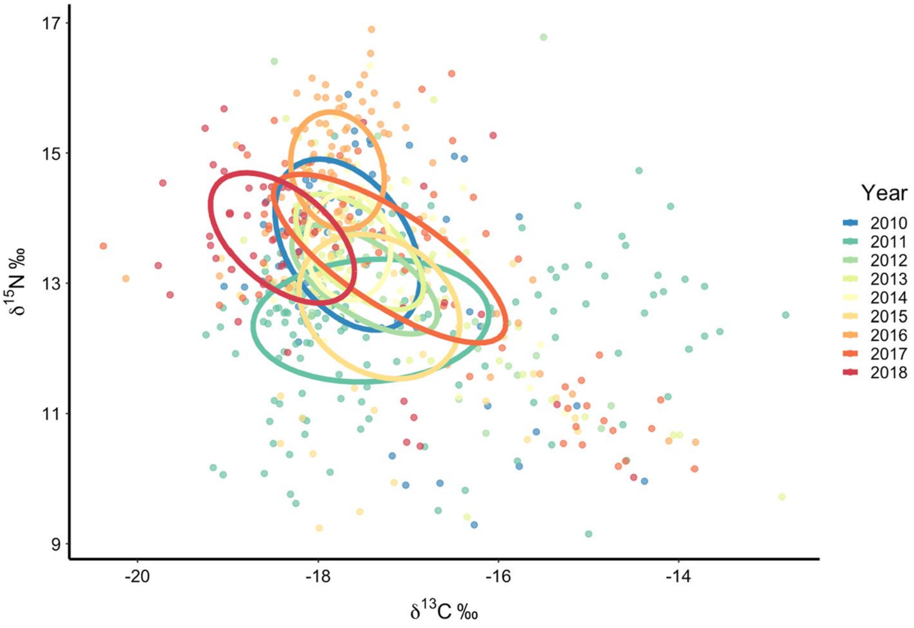

Fig. 1 Inter-annual variation in plasma isotopic niche of eiders nesting at East Bay Island, NU, Canada. Each color indicates a different year. Ellipses represent 40% of the individuals' isotopic values that comprise the sampled population within each year. Ellipses are used to represent the placement of birds within each year in isotopic space and compare placement among years

Discussion

Using a 9-consecutive-year data set we asked whether information on annual- and reproductive stage-based variation in isotopic niche dynamics helps to predict whether a breeding colony of eiders has the foraging flexibility respond to current and projected environmental change. We found significant variation in their δ^{15}N values across years, individuals, and breeding stages suggesting that either access to prey or selective choice to forage at certain trophic levels differs across breeding stages. Regardless, δ^{15}N values significantly increased 2–3 days prior to laying, suggesting the increased energetic demand of ovarian follicle production during the rapid follicle growth period may drive a change in trophic decisions and/or that internal nutrient mobilizations associated with egg formation occurred (Whiteman et al. 2020). We also detected

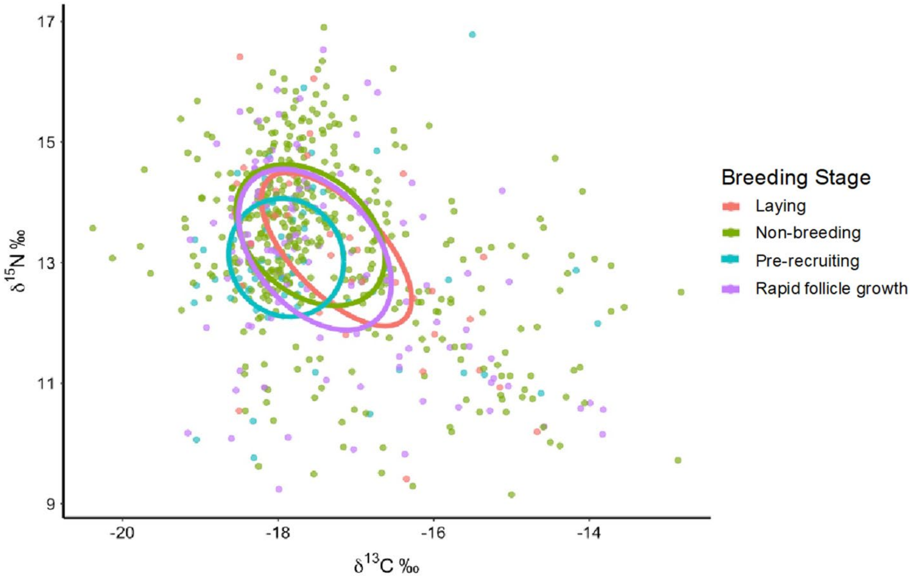

Fig. 2 Breeding stage-related variation in plasma isotopic niche of eiders nesting at East Bay Island, NU, Canada. PR (green line; pre-recruiting), shows 40% of the individuals which started laying at least 8-day post-capture; RFG (blue line; rapid follicle growth), is characterized by birds that are delayed between 8 and 1 days before breeding and Lay (red line; laying or incubating) is the 40% ellipse of birds during laying or incubation the same day of capture

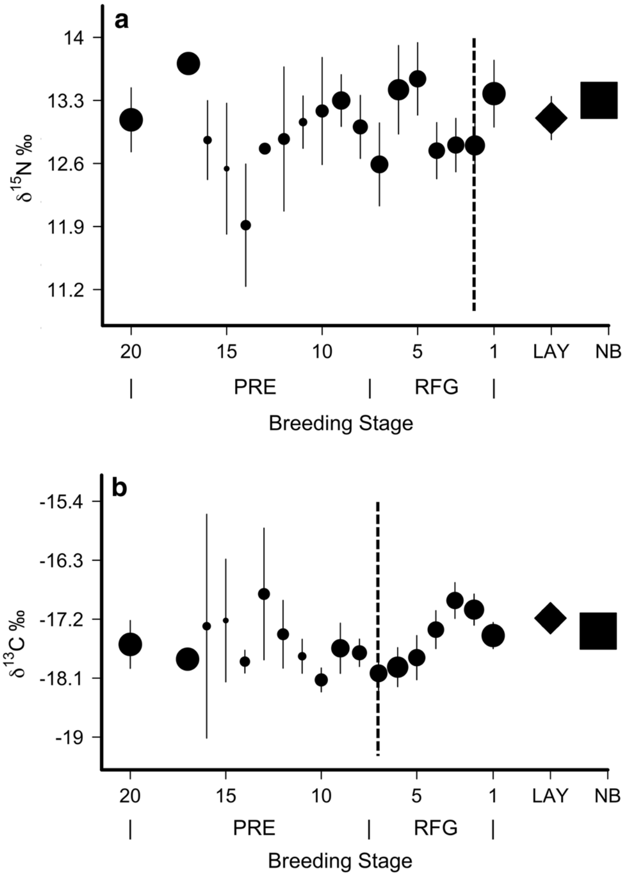

Fig. 3 Variation in plasma $\delta^{13}C$ (A), and $\delta^{15}N$ (B) values across breeding stages of female eiders nesting on East Bay Island. Values are represented as mean ± SEM provided for each day during pre-breeding (black circle), rapid follicle growth (black square), and laying (black triangle). The size of the data points represents the sample size. Dashed, vertical lines represent statistically significant change in $\delta^{13}C$ and $\delta^{15}N$ values detected from breakpoint analyses

an increase in $\delta^{13}C$ as birds transitioned from the pre-breeding to the rapid follicle recruitment stage. This shift could similarly be associated with diet shifts and/or internal isotopic processes associated with nutrient mobilization to developing eggs. Assuming a dietary effect, this, combined with our result indicating isotopic niche breadth (more inshore, narrow niche) positively predicted breeding propensity, suggests that eiders may shift foraging locations inshore to respond to the increased energetic demand of the reproductive organ load. We also found that isotopic niche breadth (more inshore, narrow niche) positively predicted breeding propensity, although not laying date. Furthermore, we found that breeding birds tended to feed more benthically when producing eggs. Despite these linkages to breeding investment, we detected significant relationships between environmental conditions and trophic dynamics, but not spatial foraging indices (i.e., $\delta^{13}C$). Our results suggest that common eiders may use flexible foraging strategies to overcome environmental constraints to invest in reproduction. Considering the rapid and substantial changes occurring in Arctic marine ecosystems, these findings provide a first step toward bridging key mechanistic gaps in determining how large-scale environmental processes proximately impact the foraging decisions and physiology of female eiders expected to influence colony-level resiliency.

Links between isotopic niche variation and breeding investment decisions

Given the energetic demands leading up to laying (Sénéchal et al. 2011; Hennin et al. 2015), we predicted that shifts in $\delta^{15}N$ related to breeding stage would indicate adjustments in foraging strategies to the changing energetic demands

Table 3 Summary of ANCOVA analyses using environmental metrics [ENVPC1 (Spring Weather); and ENVPC2 (NAO)] to predict variation in plasma isotopic metrics [ISOPC1 (Spatial Foraging Location); ISOPC2 (Niche Breadth); and ISOPC3 (Trophic Position)] in female common eiders breeding at the East Bay Island, Nunavut, Canada

Variable	ISOPC1			ISOPC2			ISOPC3		
	R^2	$F_{2,6}$	p	R^2	$F_{2,6}$	p	R^2	$F_{2,6}$	p
Full 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**

*Marginal significance (see results)

Bold values indicate statistically significant relationships

Table 4 Summary of ANCOVA analyses between breeding parameters [relative capture date (RAD); percent breeding propensity (BP); delay before laying (delay); relative lay date (RLD)] and isotopic metrics [ISOPC1 (Spatial Foraging Location); ISOPC2 (Niche Breadth); and ISOPC3 (Trophic Position)]

PC	RAD			BP			Delay			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	0.3	0.84	0.53	0.7	4.48	**0.07***	0	0.02	1.00	0.2	0.51	0.70
ISO1	–	0.16	0.70	–	0.62	0.47	–	0.03	0.87	–	0.01	0.91
ISO2	–	1.57	0.27	–	12.67	**0.02**	–	0.00	0.97	–	1.25	0.31
ISO3	–	0.79	0.42	–	0.15	0.72	–	0.02	0.91	–	0.25	0.64

*Marginal significance (see results)

of breeding. We found that δ^{15}N was indeed higher during the pre-recruiting and RFG stages compared to the laying stage (Table 2; Figs. 2, 3b). Interestingly, we did not find any changes in δ^{15}N either between pre-recruitment stage, despite birds needing to gain significant body fat (i.e., body mass of 500–750 g) to invest in breeding, and initiation of rapid follicle growth (although see details below for changes in δ^{13}C values). However, we detected a significant breakpoint, and the highest δ^{15}N values, nearly 2 days prior to laying (i.e., during RFG). This coincides with the most energetically demanding rapid follicle growth (RFG) stage of reproduction (see Hennin et al. 2015). This suggests that females may shift their prey consumption to match the energetic requirements of completing the RFG stage and then laying. We suggest that combined, these results provide evidence that females make biologically relevant trophic decisions to fuel the energetic costs of flight and diving while carrying the additional weight of developing yolks and their supporting reproductive tissues (see Vézina and Williams 2002; Vézina and Salvante 2010; reviewed in Williams 2012a, b). We acknowledge, however, that it is plausible that isotopic effects of RFG may have led to these switches in δ^{15}N values. Previous work on species relying on some degree of capital (i.e., stored) resources to fuel egg production have indicated that δ^{15}N fractionation can increase in tandem with the increased energetic demand associated with egg production via protein catabolism (Hobson et al. 1993; Vanderklift and Ponsard 2003). It is, therefore, important to note that previous work at EBI has shown that pre-breeding eiders rely heavily on income-based resources to fuel egg production (Sénéchal et al. 2011) and only enter a fasting (protein catabolism) state during incubation (Bottitta et al 2003). As such, we would expect minimal impact of fractionation on stable isotope values in plasma due to fasting or rapid follicle growth in our focal birds. Nevertheless, we acknowledge that such processes require further examination in Arctic-breeding female eiders.

We found that birds captured earlier (presumably also representing earlier-arriving birds) foraged closer to shore in agreement with our predictions. This could be the result of birds needing to forage at the mouths of rivers as freshwater inflow into the bay begins to open up small areas of open water prior to marine ice off, where birds can access resources (Jean-Gagnon et al. 2018). We also detected a significant breakpoint in δ^{13}C values in which females moved to forage at more inshore locations as they transitioned into the RFG period. This suggests that when females are under significant energetic demands at the onset of ovarian follicle recruitment, they may switch from foraging on offshore benthic macroinvertebrates, to prey with lower digestive and foraging energetic costs, such as amphipods (*Gammarus* spp.). This trophic switch may be driven by a variety of non-exclusive reasons, including fueling the growth of reproductive organs and follicles. Amphipods are an eider prey species found more inshore near the surface of the water (Sénéchal et al. 2011). They require less metabolic energy and time to digest compared to hard-shelled benthic prey (e.g., blue mussels, sea urchins) (Zhang et al. 2019) while simultaneously reducing the energetic costs of diving as females become more buoyant, as they continuously accumulate needed fat stores for reproduction (Sénéchal et al. 2011). Conserving fat stores for their upcoming incubation fast is critical. Foraging on amphipods close to the colony may reduce the costs of commuting and foraging, and may be an important energy-conserving strategy.

Interestingly, we found that an inshore, smaller isotopic niche, predicted higher breeding propensity (Table 4; Figs. 1, 3a). Previous studies have demonstrated that in years with later ice breakup, females were less likely to breed (Jean-Gagnon et al. 2018). In addition, previous research at EBI has shown that unpredictable food shortages during the RFG stage reduce the probability that an individual breeds, regardless of reproductive readiness (Legagneux et al. 2016), suggesting that reproductive decisions are highly responsive to environmentally driven changes in resource availability typically related to ice cover and access to prey (see below). Considering the short Arctic breeding season (Lepage et al. 2000) and the role that ice dynamics play in impacting the decision to breed (Jean-Gagnon et al. 2018), the relationship between breeding propensity and isotopic niche may only be evident in years with the greatest environmental, and therefore, energetic constraints and may only impact individuals with lower body condition.

Lack of a relationship between environmental conditions and isotope values

We predicted that in years with milder winters, milder springs, and higher overall ambient temperatures, there would be more open water and a wider variety and quantity of prey items available, resulting in a broader colony-based isotopic niche. In contrast, we only detected a significant, negative relationship between trophic position (ISOPC3) and pre-breeding NAO (ENVPC2) (Table 3). In years with higher winter storm activity and milder springs at EBI (i.e., breeding grounds), females had a greater range and variance in $\delta^{15}N$ values on breeding grounds, potentially related to accessing resources from multiple trophic levels. In years with harsh winter conditions, mussel beds and other prey sources may be depleted due to the increased storm activity on wintering grounds (Reusch and Chapman 1995). Consequently, eiders may employ a more generalist foraging strategy upon arrival to breeding areas to compensate for diminished abundance of preferred prey during winter, explaining the higher MNND values calculated during these conditions. Similarly, we predicted that $\delta^{13}C$ would also be strongly related to environmental indices, but this relationship was not observed (Table 3). This was surprising considering that eiders are known to adjust their foraging areas based on extent of sea ice (Jean-Gagnon et al. 2018), and given the impacts of environmental conditions on regional seaice dynamics near the nesting colony; although we are still learning about benthic–pelagic coupling in the marine system. However, since variation in $\delta^{13}C$ is largely driven by input from primary producers, it is possible that the lack of diversity of primary production around the nesting colony in EBI, consistent with the circumpolar Arctic (Ramírez et al. 2017), limits our ability to detect a relationship between $\delta^{13}C$ and environmental conditions. Thus, the ability to apply bulk stable isotopes in this context could be constrained by the biogeochemical processes of isotopic incorporation (see Boecklen et al. 2011, Whiteman et al. 2020). Combining compound-specific stable isotope analyses of individual amino acids and spatial tracking will provide future opportunities to investigate colony-level resiliency to changes in prey availability predicted by climate change.

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Declarations

Conflict of interest The authors have not disclosed any competing interests.

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