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

Kyle J. L. Parkinson1,5 · Holly L. Hennin2 · H. Grant Gilchrist2 · Keith A. Hobson3,4 · Nigel E. Hussey1 · Oliver P. Love1

Received: 5 October 2021 / Accepted: 20 September 2022 © Crown 2022

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 δ13C and δ15N 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...
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 sea ice 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. 2018). Specifically, the combination of stable isotope measurements of carbon (δ 13C), which provides information on basal sources reflective of habitat use (i.e., inshore vs. offshore, see Sénéchal et al. 2011), and nitrogen (δ 15N), 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 in 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 $\delta^{15}$N values and higher $\delta^{13}$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 interannual 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 sea ice 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 x 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-scope scopes from three 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 interannual 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 μL 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 chloroform: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 δ13C and δ15N 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 N2 and CO2 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 (δ13C = −20.18, δ15N = +14.31%, respectively) and PRGgel (δ13C = −13.64, δ15N = +5.07%, respectively). Within-run (n = 5) precisions as determined from both reference and sample duplicate analyses were ±0.1% for both δ13C and δ15N.

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 (SEAc), X range (i.e., maximum range of δ13C) and Y range (i.e., maximum range of δ15N) (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

| 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 δ13C          | 0.29675                    | −0.58426               | 0.19752      |
|           | %CV δ13C          | −0.42799                   | 0.08641                | −0.13040     |
|           | AVG δ15N          | −0.35635                   | 0.21296                | 0.01793      |
|           | CV δ15N           | 0.30971                    | 0.36609                | 0.44129      |
| Eigenvale |                  | 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               |
| Eigenvale |                  | 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 δ¹⁵N and δ¹³C values at the colony-level, we ran a MANCOVA (with δ¹⁵N and δ¹³C 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., δ¹⁵N: trophic position; δ¹³C: spatial foraging), we followed the MANCOVA with two separate one-way ANCOVAs for δ¹⁵N and δ¹³C 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 fine-scale, breeding-stage specific changes in foraging strategies via variation in δ¹³C and δ¹⁵N, we conducted break-point analyses. This analysis identifies sudden and significant positive or negative changes in the data set (Muggeo 2003) through estimating break-points by iteratively fitting a model with a linear predictor. For each iteration, a standard linear model is fitted, and the break-point value is updated until convergence occurs. We performed break point analyses for both δ¹³C and δ¹⁵N 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 δ¹⁵N and δ¹³C (Table 2; Figs. 1, 2, 3). ANCOVAs examining the two isotopes separately, revealed that only δ¹⁵N showed significant year- and breeding-stage effects (with no year by stage interaction). Variation in δ¹³C was negatively correlated with capture date, with earlier arriving females having higher δ¹³C values (Table 3).

Fine-scale changes in isotopic values across breeding stages

While δ¹⁵N 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 δ¹³C, 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 δ¹³C 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 δ¹³C 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).
Oecologia

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 to respond to current and projected environmental change. We found significant variation in their δ¹⁵N 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, δ¹⁵N 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

Table 2 Summary of MANCOVA and ANCOVA analyses examining predictors of variance in plasma δ¹³C and δ¹⁵N values in female common eiders breeding at the East Bay Island, Nunavut, Canada

| Analysis          | Variable                  | F    | df     | p       |
|-------------------|---------------------------|------|--------|---------|
| MANCOVA (δ¹⁵N and δ¹³C) | 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 (δ¹⁵N)     | 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 (δ¹³C)     | 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.
an increase in δ13C 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., δ13C). 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 δ15N related to breeding stage would indicate adjustments in foraging strategies to the changing energetic demands.
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 sea ice 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, Whitman et al. 2020). Combining compound-specific stable isotope analyses of individual amino acids and spatial tracking will provide future opportunities to investigate colony-level resilience to changes in prey availability predicted by climate change.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s00442-022-05267-9.

**Acknowledgements** We thank the 2010–2018 East Bay Island field crews for data collection, and I. Butler and R. Kelly for data management. 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 Knowledge Canada, the Polar Continental Shelf Program, Oceans North, and the ArcticNet Canadian Network of Centres of Excellence for financial support. Animal care approval for this project was granted through both the University of Windsor Committee for Animal Care (AUPP #11-06 and #19-06; Reproductive Strategies of Arctic-Breeding Common Eiders) and ECCC Animal Care (EC-PN-15-026).

**Author contribution statement** KJLP, HLH, HGG, and OPL: conceived the research ideas and collected the data. KJLP, KAH, and OPL: analyzed the data. KJLP, HLH, KAH, and OPL: wrote the manuscript. All authors contributed to editing the manuscript. HGG and OPL: provided funding for the research.

**Declarations**

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

**References**

Alatalo RV (1982) Evidence of interspecific competition among European tit spp.: a review. Ann Zool Fenn 19:309–317

Bearhop S, Adams CE, Waldron S, Fuller RA, MacLeod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. J Anim Ecol 73:1007–1012
Becker BH, Zachariah Peery M, Beissinger SR (2007) Ocean climate and prey availability affect the trophic level and reproductive success of the marbled murrelet, an endangered seabird. Mar Ecol Prog Ser 329:267–279

Bligh EG, Dyer WJ (1959) A rapid method of total lipid extraction and purification. Can J Biochem Physiol 37:911–917

Boecklen WJ, Yarnes CT, Cook BC, James AC (2011) On the use of stable isotopes in trophic ecology. Annu Rev Ecol Evol Syst 42:411–440

Boggs CL (1992) Resource allocation: Exploring connections between foraging and life history. Funct Ecol 6(5):508–518

Bolnick DI, Svannbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. Am Nat 161:1–28

Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. Nature 441:81–83

Bottitta GE, Nol E, Gilchrist HG (2003) Effects or experimental manipulation of incubation length on behaviour and body mass of common eiders in the Canadian Arctic. Waterbirds 26:100–107

Chesson PL (1986) Environmental variation and the coexistence of species. In: Diamond J, Case TJ (eds) Community Ecology. Harper and Row, New York

Comiso JC, Parkinson CL, Gersten R, Stock L (2008) Accelerated decline in the Arctic sea ice cover. Geophys Res Lett 35:1–6

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mis-match hypothesis. Adv Mar Biol 26:249–293

Deforges J, Outridge P, Hobson KA, Heide-Jørgensen MP (2021) Anthropogenic and climatic drivers of long-term changes of mercury and feeding ecology in Arctic Beluga (Delphinapterus leucas) populations. Environ Sci Technol 56(1):271–281

Descamps S, Yoccoz NG, Gaillard J, Gilchrist HG, Erikstad KE, Hansen SA, Cazelles B, Forbes MR, Bøttør J (2010) Detecting population heterogeneity in effects of North Atlantic oscillations on seabird body condition: get into the rhythm. Oikos 119:1526–1536

Descamps S, Bøttør J, Love OP, Gilchrist HG (2011a) Individual optimization of reproduction in a long-lived migratory bird: a test of the condition-dependent model of laying date and clutch size. Funct Ecol 25:671–681

Descamps S, Forbes MR, Gilchrist HG, Love OP, Bøttør J (2011b) Avian cholera, post-hatching survival and selection on hatch characteristics in a long-lived bird. J Avian Biol 42:39–48

Descamps S, Aars J, Fuglei E, Koivus KM, Lydersen C, Pavlova O, Pedersen AØ, Ravolainen V, Strøm H (2017) Climate change impacts on wildlife in a high Arctic archipelago – Svalbard, Norway. Glob Change Biol 23:490–502

Forero MG, Hobson KA, Bortolotti GR, Donáz AA, Bertellotti M, Blanco G (2002) Food resource utilisation by the Magellanic penguin evaluated through stable isotope analysis: segregation by sex and age and influence on offspring quality. Mar Ecol Prog Ser 234:289–299

González-Medina E, Castillo-Guerrero JA, Herza ZS, Fernández G (2018) High quality diet improves lipid metabolic profile and breeding performance in the blue-footed booby, a long-lived seabird. PLoS One 13(2):e0193136

Guéry L, Descamps S, Pradel R, Hansen SA, Erikstad KE, Gabrielsen GW, Gilchrist HG, Bøttør J (2017) Hidden survival heterogeneity of three common eider populations in response to climate fluctuations. J Anim Ecol 86:683–693

Guéry L, Descamps S, Hodges KI, Pradel R, Moe B, Hanssen SA, Erikstad KE, Gabrielsen GW, Gilchrist HG, Jenouvrier S, Bøttør J (2019) Winter extratropical cyclone influence on seabird survival: variation between and within common eider populations. Mar Ecol Prog Ser 627:155–170

Hahn S, Hoye BJ, Korthals H, Klüssmann M (2012) From food to offspring: tissue specific discrimination and turn-over of stable isotopes in herbivorous waterbirds and other avian foraging guilds. PLoS One 7:1–6

Hallett TB, Coulson T, Pilkington JG, Clutton-Brock TH, Pemberton JM, Grenfell BT (2004) Why large-scale climate indices seem to predict ecological processes better than local weather. Nature 430:71–75

Hennin HL, Legagneux P, Bøttør J, Williams TD, Gilchrist HG, Bøttør TM, Love OP (2015) Pre-breeding energetic management in a mixed-strategy breeder. Oecologia 177:235–243

Hennin HL, Bøttør J, Legagneux P, Gilchrist HG, Williams TD, Love OP (2016a) Energetic physiology mediates individual optimization of breeding phenology in a migratory arctic seabird. Am Nat 188:434–445

Hennin HL, Wells-Berlin AM, Love OP (2016b) Baseline glucocorticoids are drivers of body mass gain in a diving seabird. Ecol Evol 6:1702–1711

Hennin HL, Dey CJ, Bøttør J, Gilchrist HG, Legagneux P, Williams TD, Love OP (2018) Higher rates of prebreeding condition gain positively impact clutch size: a mechanistic test of the condition-dependent individual optimization model. Funct Ecol 32:2019–2028

Hennin HL, Legagneux P, Gilchrist HG, Bøttør J, McMurty JP, Love OP (2019) Plasma mammalian leptin analogue predicts reproductive phenology, but not reproductive output in a capital-income breeding seabird. Ecol Evol 9:1512–1522

Herman RW, Valls FCL, Hart T, Petry MV, Trivelpeix WZ, Polito MJ (2017) Seasonal consistency and individual variation in foraging strategies differ among and within Pygoscelis penguin species in the Antarctic peninsula region. Mar Biol 164:115

Hobson KA (1999a) Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120:314–326

Hobson KA (2006) Using stable isotopes to quantitatively track endogenous and exogenous nutrient allocations to eggs of birds that travel to breed. Ardea 94(3):359–369

Hobson KA, Clark RG (1992a) Assessing avian diets using stable isotopes I: turnover of 813C in tissues. Condor 94:181–188

Hobson KA, Clark RG (1992b) Assessing avian diets using stable isotopes II: factors influencing diet-tissue fractionation. The Condor 94:189–197

Hobson KA, Clark RG (1993) Turnover of 813C in cellular and plasma fractions of blood: implications for non-destructive sampling in avian dietary studies. Auk 110:638–641

Hobson KA, Alisauskas RT, Clark RG (1993) Stable-Nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. Condor 95:388–394

Hobson KA, Jaatinen K, Öst M (2015) Differential contributions of endogenous and exogenous nutrients to egg components in wild Baltic common eiders (Somateria mollissima): a test of alternative stable isotope approaches. Auk 132(2):624–633

Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the worlds marine ecosystems. Science 328:1523–1528

Hutchinson GE (1957) Concluding remarks: cold spring harbor symposium. Quant Biol 22:415–427

Intergovernmental Panel on Climate Change (2018) Global warming of 1.5°C, an IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. IPCC, Geneva

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER—stable isotope bayesian ellipses in R. J Anim Ecol 80:595–602

Jean-Gagnon F, Legagneux P, Gilchrist G, Bélanger S, Love OP, Bøttør J (2018) The impact of sea ice conditions on breeding....
decisions is modulated by body condition in an Arctic partial capital breeder. Oecologia 186:1–10
Johannessen OM, Bengtsson L, Miles MW, Kuzmina SI, Semenov VA, Alekseev GH, Nagurnyi AP, Zakharov VF, Bobylev LP, Pettersson LH, Hasselmann K, Cattle HP (2004) Arctic climate change: observed and modelled temperature and sea-ice variability. Tellus 56:328–341
Jones DO, Yool A, Wei C, Henson SA, Ruhl HA, Watson RA, Gehlen M (2014) Global reductions in seabird biomass in response to climate change. Glob Change Biol 20:1861–1872
Kitaysky AS, Piatt JF, Hatch SA, Kitaiskaia EV, Benowitz-Fredricks ZM, Shultz MT, Wingfield JC (2010) Food availability and population processes: severity of nutritional stress during reproduction predicts survival of long-lived seabirds. Funct Ecol 24:625–637
Kovacs KM, Lydersen C, Overland JE, Moore SE (2011) Impacts of changing sea-ice conditions on Arctic marine mammals. Mar Biodivers 41:181–194
Legagneux P, Hennin HL, Gilchrist HG, Williams TD, Love OP, Béty J (2016) Unpredictable perturbation reduces breeding propensity regardless of pre-laying reproductive readiness in a partial capital breeder. J Avian Biol 47:880–886
Leibold MA (1996) The niche concept revisited: mechanistic models and community context. Ecology 76(5):1371–1382
Lepage D, Gauthier G, Menu S (2000) Reproductive consequences of egg-laying decisions in snow geese. J Anim Ecol 69:414–427
Love OP, Gilchrist HG, Descamps S, Semeniuk CAD, Bêty J (2010) Pre-laying climate cues can time reproduction to optimally match offsprings hatching and ice conditions in an Arctic marine bird. Oecologia 164:277–286
Mancinelli G, Vizzini S (2015) Assessing anthropogenic pressures on coastal marine ecosystems using stable CNS isotopes: State of the art, knowledge gaps, and community-scale perspectives. Estuarine Coast Shelf Sci 156:195–204
Matich P, Shipley ON, Weideli OC (2021) Quantifying spatial variation in isotopic baselines reveals size-based feeding in a model estuarine predator: implications for trophic studies in dynamic ecosystems. Mar Biol 168:108–120
McNamara JM, Houston AI (1996) State-dependent life histories. Nature 380:215–221
Meier WN, Hovelsrud GK, van Oort BEH, Key JR, Kovacs KM, Michel C, Haas C, Granskg MA, Gerland S, Perovich DK, Makshtas A, Reist JD (2014a) Arctic sea ice in transformation: a review of recent observed changes and impacts on biology and human activity. Rev Geophys 51:185–217
Meier WN, Hovelsrud GK, van Oort BEH, Key JR, Kovacs KM, Michel C, Haas C, Granskg MA, Gerland S, Perovich DK, Makshtas A, Reist JD (2014b) Arctic sea ice transformation: a review of recent observed changes and impacts on biology and human activity. Rev Geophys 51:185–217
Moreno R, Jover L, Munilla I, Velando A, Sanpera C (2010) A three-isotope approach to disentangling the diet of a generalist consumer: the yellow-legged gull in northwest Spain. Mar Biol 157:545–553
Mosbech A, Gilchrist HG, Merkel F, Sonne C, Flagstad A, Nyegaard H (2006) Year round movements of northern common eiders Somateria mollissima borealis breeding in Arctic Canada and West Greenland followed by satellite telemetry. Ardea 94:651–665
Muggeo VMR (2003) Estimating regression models with unknown break-points. Stat Med 22:3055–3071
Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. Front Ecol Environ 5:429–436
Newton I (1998) Population limitation in birds. Academic Press, London
Paiva VH, Geraldes P, Marques V, Rodriguez R, Garthe S, Ramos JA (2013) Effects of environmental variability on different trophic levels of the North Atlantic food web. Mar Ecol Prog Ser 477:15–28
Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Ann Rev Ecol Syst 18:293–320
Pethybridge H, Choy CA, Logan JM, Allain V, Lorrain A, Bodin N, Somes CJ, Young J, Ménard F, Langlais C, Duffy L, Hobday AJ, Kuhnert P, Fry B, Menkes C, Olson RJ (2017) A global meta-analysis of marine predator nitrogen stable isotopes: relationships between trophic structure and environmental conditions. Glob Ecol Biogeogr 27:1043–1055
Polito MJ, Trivelpiece WZ, Patterson WP, Karpovsky NJ, Reiss CS, Emslie SD (2015) Contrasting specialist and generalist patterns facilitate foraging niche partitioning in sympatric populations of Pygoscelis penguins. Mar Ecol Prog Ser 519:221–237
R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
Reusch TBB, Chapman ARO (1995) Strom effects on eelgrass (Zostera marina L.) and blue mussel (Mytilus edulis L.) beds. J Exp Mar Biol Ecol 192:257–271
Romero LM, Reed JM (2005) Collecting baseline corticosterone samples in the field: is under 3 min good enough? Comp Biochem Physiol 140:73–79
Rutschmann A, Miles DB, Le Galliard J-F, Richard M, Mouherat S, Sinervo B, Clabort J (2016) Climate and habitat interact to shape the thermal reaction norms of breeding phenology across lizard populations. J Anim Ecol 85:457–466
Seamom JO, Adler GH (1996) Population performance of generalist- and specialist rodents along habitat gradients. Can J Zool 74:1130–1139
Sénéchal É, Béty J, Gilchrist HG, Hobson KA, Jamieson SE (2011) Do purely capital layers exist among flying birds? Evidence of exogenous contribution to arctic-nesting common eider eggs. Oecologia 165:593–604
Seyboth E, Groch KR, Rosa LD, Reid K, Flores PAC, Secchi ER (2016) Southern right whale (Eubalaena australis) reproductive success is influenced by krill (Euphausia superba) density and climate. Nature 6:1–8
Steenweg RJ, Crossin GT, Kyser TK, Merkel FR, Gilchrist HG, Hennin HL, Robertson GF, Provenerch JF, Flemming JM, Love OP (2017) Stable isotopes can be used to infer the overwintering locations of prebreeding marine birds in the Canadian Arctic. Ecol Evol 7(21):8742–8752
Stenseth NC, Ottersen G, Hurrell JW, Mysterud A, Lima M, Chan KS, Yoccoz NG, Ádlandsvik B (2003) Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. Proc R Soc Lond 270:2087–2096
Stephens WD, Krebs RJ (1986) Foraging theory. Princeton University Press, Princeton (NJ)
Tylanakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. Ecol Lett 11:1351–1363
Vanderklift MA, Ponsard S (2003) Sources of variation in consumer-diet δ15N enrichment: a meta-analysis. Oecologia 136:169–182
Vandermeer JH (1972) Niche theory. Ann Rev Ecol Syst 3:107–132
Vézina F, Salvante KG (2010) Behavioural and physiological flexibility are used by birds to manage energy and support investment in the early stages of reproduction. Curt Zool 56:767–792
Vézina F, Williams TD (2003) Plasticity in body condition in breeding birds: what drives the metabolic cost of egg production? Physiol Biochem Zool 76:716–730
Walther G, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin J-M, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389–395
Ward EJ, Holmes EE, Balcomb KC (2009) Quantifying the effects of prey abundance on killer whale reproduction. Can J Fish Aquat Sci 46:632–640

Wassmann P, Duarte CM, Agusti S, Sejr MK (2011) Footprints of climate change in the Arctic marine ecosystem. Glob Change Biol 17:1235–1249

Whiteman J, Newsome S, Bustamante P, Cherel Y, Hobson KA (2020) Quantifying capital vs income breeding: new promise with stable isotope measurements of individual amino acids. J Anim Ecol 2020(00):1–11

Williams TD (2012a) Chapter 2: The hormonal and physiological control of egg production Physiological adaptations for breeding birds. Princeton University Press, Princeton, pp 8–51

Williams TD (2012b) Physiological adaptations for breeding birds. Princeton University Press, Princeton, New Jersey, USA

Yukowski DJ, Richardson ES, Lunn NJ, Muir DCG, Johnson AC, Derocher AE, Ehrman AD, Houde M, Young BG, Debets CD, Sciullo L, Thiemann AD, Ferguson SH (2020) Contrasting temporal patterns of mercury, niche dynamics, and body fat indices of polar bears and ringed seals in a melting icescape. Environ Sci Technol 54(5):2780–2789

Zhang S, Ma Z, Choi C, Melville DS, Zhao T, Bai Q, Liu W, Chan Y, van Gils JA, Piersma T (2019) Morphological and digestive adjustments buffer performance: how staging shorebirds cope with severe food declines. Ecol Evol 9(7):3868–3878