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Article title/Titill greinar: Do foraging ecology and contaminants interactively predict parenting hormone levels in common eider?

Published in/Útgáfurit: General and Comparative Endocrinology

Publication year/Útgáfuár: 2023

DOI (krækja í greinina hjá útgefanda): <https://doi.org/10.1016/j.ygcen.2023.114261>

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Document version/Útgáfa greinar: Post-print, samþykkt ritrýnt handrit

Please cite the published version: Vinsamlega vísið til útgefna greinarinnar:

Smith, R. A., Fort, J., Legagneux, P., Chastel, O., Mallory, M. L., Bustamante, P., Danielsen, J., Hanssen, S. A., Jónsson, J. E., Magnúsdóttir, E., Moe, B., Parenteau, C., Parkinson, K. J. L., Parsons, G. J., Tertitski, G., & Love, O. P. (2023). Do foraging ecology and contaminants interactively predict parenting hormone levels in common eider? *General and Comparative Endocrinology*, 337, Article 114261. <https://doi.org/10.1016/j.ygcen.2023.114261>

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Science of the Total Environment

Environmental and life-history factors influence inter-colony multidimensional niche metrics of a breeding Arctic marine bird --Manuscript Draft--

Manuscript Number:	STOTEN-D-21-07959R2
Article Type:	Research Paper
Keywords:	Stable isotopes; carbon-13; nitrogen-15; THg; Climate change; common eider
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Abstract:	<p>Human industrialization has resulted in rapid climate change, leading to wide-scale environmental shifts. These shifts can modify food web dynamics by altering the abundance and distribution of primary producers (ice algae and phytoplankton), as well as animals at higher trophic levels. Methylmercury (MeHg) is a neuro-endocrine disrupting compound which biomagnifies in animals as a function of prey choice, and as such bioavailability is affected by altered food web dynamics and adds an important risk-based dimension in studies of foraging ecology. Multidimensional niche dynamics (MDND; $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, THg; total mercury) were determined among breeding common eider (<i>Somateria mollissima</i>) ducks sampled from 10 breeding colonies distributed across the circumpolar Arctic and subarctic. Results showed high variation in MDND among colonies as indicated by niche size and ranges in $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and THg values in relation to spatial differences in primary production inferred from sea-ice presence and colony migratory status. Colonies with higher sea-ice cover during the pre-incubation period had higher median colony THg, $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$. Individuals at migratory colonies had relatively higher THg and $\delta^{15}\text{N}$, and lower $\delta^{13}\text{C}$, suggesting a higher trophic position and a greater reliance on phytoplankton-</p>

	<p>based prey. It was concluded that variation in MDND exists amongst eider colonies which influenced individual blood THg concentrations. Further exploration of spatial ecotoxicology and MDND at each individual site is important to examine the relationships between anthropogenic activities, foraging behaviour, and the related risks of contaminant exposure at even low, sub-lethal concentrations that may contribute to deleterious effects on population stability over time. Overall, multidimensional niche analysis that incorporates multiple isotopic and contaminant metrics could help identify those populations at risk to rapidly altered food web dynamics.</p>
Response to Reviewers:	See 'Response to Reviewers' document for responses to Editor comments.

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Environmental and life-history factors influence inter-colony multidimensional niche metrics of a breeding Arctic marine bird

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Keywords

Stable isotopes; carbon-13; nitrogen-15; THg; climate change; common eider

Reviewers/Editor comments:

Please find attached your paper with some minor comments that need to be addressed. Please check your tense throughout the paper and remove pronouns.

Author Response: Thank you very much to the Editor for their time spent revising the manuscript. I've accepted all suggested changes and ensured that past tense is used throughout the paper. Further, pronouns of 'we' and 'our' have been removed from the paper.

1 **Environmental and life-history factors influence inter-colony multidimensional niche**
2 **metrics of a breeding Arctic marine bird**

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30 **Abstract**

31 Human industrialization has resulted in rapid climate change, leading to wide-scale
32 environmental shifts. These shifts can modify food web dynamics by altering the abundance and
33 distribution of primary producers (ice algae and phytoplankton), as well as animals at higher
34 trophic levels. Methylmercury (MeHg) is a neuro-endocrine disrupting compound which
35 biomagnifies in animals as a function of prey choice, and as such bioavailability is affected by
36 altered food web dynamics and adds an important risk-based dimension in studies of foraging
37 ecology. Multidimensional niche dynamics (MDND; $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, THg; total mercury) were
38 determined among breeding common eider (*Somateria mollissima*) ducks sampled from 10
39 breeding colonies distributed across the circumpolar Arctic and subarctic. Results showed high
40 variation in MDND among colonies as indicated by niche size and ranges in $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and THg
41 values in relation to spatial differences in primary production inferred from sea-ice presence and
42 colony migratory status. Colonies with higher sea-ice cover during the pre-incubation period had
43 higher median colony THg, $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$. Individuals at migratory colonies had relatively
44 higher THg and $\delta^{15}\text{N}$, and lower $\delta^{13}\text{C}$, suggesting a higher trophic position and a greater reliance
45 on phytoplankton-based prey. It was concluded that variation in MDND exists amongst eider
46 colonies which influenced individual blood THg concentrations. Further exploration of spatial
47 ecotoxicology and MDND at each individual site is important to examine the relationships
48 between anthropogenic activities, foraging behaviour, and the related risks of contaminant
49 exposure at even low, sub-lethal concentrations that may contribute to deleterious effects on
50 population stability over time. Overall, multidimensional niche analysis that incorporates
51 multiple isotopic and contaminant metrics could help identify those populations at risk to rapidly
52 altered food web dynamics.

53 **Highlights**

- 54 1. Common eider colonies vary in their 3-dimensional ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$, THg) niche size
55 2. Colonies with higher sea-ice cover had higher $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and THg
56 3. Colonies considered migratory had higher median $\delta^{15}\text{N}$ and THg, but lower $\delta^{13}\text{C}$
57 4. Individuals with lower $\delta^{13}\text{C}$ and higher trophic positions had higher THg

58

59 **Graphical Abstract**



Migratory Colonies **↑ Sea-Ice Cover**



↑ $\delta^{15}\text{N}$
↑ THg
↓ $\delta^{13}\text{C}$



↑ $\delta^{15}\text{N}$
↑ THg
↑ $\delta^{13}\text{C}$

60

61 **1. Introduction**

62 Global anthropogenic activity has resulted in environmental shifts within Arctic systems
63 including rising air and ocean temperatures (Zhang 2005; Screen and Simmonds 2010; Najafi et
64 al. 2015), changes in wind and ocean circulation (Timmermans et al. 2011), and a dramatic
65 modification of sea-ice cover in marine systems (Johannessen et al. 2004; Hoegh-Guldberg and
66 Bruno 2010; IPCC 2019). These multiple stressors generate cumulative effects which have direct
67 and indirect influences on biological systems, ultimately having the potential to affect food web
68 characteristics including prey availability and selection (Vasseur and McCann 2005; Frederiksen
69 et al. 2006; Parmesan 2006). Arctic marine food-webs have been particularly impacted, leading
70 to abiotic shifts resulting in alterations of prey abundance and availability which have modified
71 the foraging niche of higher trophic-level organisms (Moline et al. 2008; Pecuchet et al. 2020).

72 The foraging niche of an organism includes both dietary and environmental components,
73 and therefore has been used to discern both trophic roles by consumers and changes in their
74 resource use (Newsome et al. 2007). Studies examining foraging niche size (the spatial and
75 trophic-level range at which a group forages) have been used to investigate the effect of
76 phenological changes in primary production on predators (Rabosky 2009). In polar regions,
77 changes in the abundance, distribution, and phenology of primary producers such as
78 phytoplankton and ice-algae can have effects on higher trophic-level wildlife (Frederiksen et al.
79 2006; Kohlbach et al. 2016; Renaut et al. 2018; Lewis et al. 2020). Sympagic-pelagic-benthic
80 coupling drives energy flow between the surface and benthic habitats and provides a foundation
81 for Arctic ecosystem functioning involving benthic consumers, but is being decoupled due to
82 changing sea-ice dynamics (Søreide et al. 2012; Kohlbach et al. 2016; Yurkowski et al. 2020a).
83 These shifts can generate bottom-up effects on the foraging ecology of higher trophic species,

84 especially those that rely on consuming resources that inhabit the sea floor (Leu et al. 2011; Post
85 et al. 2013; Post 2017; Cusset et al. 2019).

86 A further consequence of changing marine ecosystems is shifts in wildlife exposure to
87 contaminants (Muir et al. 1999; Macdonald et al. 2005; Stern et al. 2012). It is well established
88 that Arctic marine food webs are influenced by long-range transport of contaminants (Macdonald
89 et al. 2000; Braune et al. 2005; Kirk et al. 2012). On top of this, melting of the cryosphere is
90 releasing stored contaminants from years of higher contaminant output into the current system
91 (Rydberg et al. 2010; Schuster et al. 2018; Hawkings et al. 2021). Methylmercury (MeHg) is a
92 biologically converted form of mercury (Hg) and is a contaminant of concern due to its high
93 bioavailability in organic tissues and toxic effects at even low, sub-lethal concentrations (Wiener
94 et al. 2003; Whitney and Cristol 2017; Evers 2018). Uptake of MeHg into wildlife can disrupt
95 endocrine functioning, behaviour, and reproductive success (e.g., Cardona-Marek et al. 2009;
96 Chen and Hale 2010; Whitney and Cristol 2017). Specifically, reproductive effects in birds
97 include reduced clutch size, altered parental breeding behaviour and reduced hatching and
98 fledgling success (Braune et al. 2012; Tartu et al. 2013; Goutte et al. 2014; Hartman et al. 2019).

99 Climate change can affect the distribution and accumulation of Hg in Arctic ecosystems
100 (Stern et al. 2012; McKinney et al. 2015; Foster et al. 2019). Further, changes in Arctic food web
101 dynamics and trophic relationships may shift the flow of Hg between organisms (Braune et al.
102 2014). To study this, stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) are tracers that can
103 provide time-integrated information on habitat use and diet (Bearhop et al. 2006; Cherel and
104 Hobson 2007; Inger and Bearhop 2008). In coastal polar environments, $\delta^{13}\text{C}$ provides dietary
105 information on sources of primary productivity and foraging habitat, for example, between ^{13}C -
106 depleted phytoplankton-derived carbon and ^{13}C -enriched sea-ice derived carbon (Hobson et al.

107 2002; Kohlbach et al. 2016; Yurkowski et al. 2020a; Lewis et al. 2020). In addition, benthic or
108 nearshore environments with macroalgae are typically enriched in ^{13}C compared to pelagic or
109 offshore sources (Hobson and Welch 1992; Hobson et al. 1995; France 1995). Values of $\delta^{15}\text{N}$
110 indicates relative trophic level, with higher trophic levels associated with increased $\delta^{15}\text{N}$ values
111 (Hobson and Welch 1992). Thus, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values can help determine environmental and
112 dietary sources of Hg due to varying uptake with carbon-source and trophic level (Atwell et al.
113 1998; Cardona-Marek et al. 2009; Pomerleau et al. 2016; Carravieri et al. 2017). However, while
114 $\delta^{15}\text{N}$ values relate to Hg concentrations, high variability in Hg still occurs among individuals
115 despite similar $\delta^{15}\text{N}$ values (Atwell et al. 1998; Bearhop et al. 2000; DiMento et al. 2019).

116 While isotope biplots consisting of just $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ capture an incomplete portrayal of
117 ecological niche due to the inclusion of only two isotopic variables, a multidimensional niche,
118 including three or more total variables, can provide more information to assess foraging ecology,
119 albeit with greater complexity in interpretation (Swanson et al. 2015; Hobson et al. 2015;
120 O'Donovan et al. 2018). Therefore, including Hg in niche analyses along with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
121 provides a broader, risk-based method to quantify an individual and population's foraging
122 ecology and multidimensional niche dynamics (MDND; Yurkowski et al. 2020b). This analytical
123 approach, combining stable isotopes and contaminants, has been applied to multiple taxa
124 including mammals, fish, and reptiles (Guzzo et al. 2016; Jackson et al. 2016; Purwandana et al.
125 2016; Yurkowski et al. 2020b). However, a MDND approach to determine niche size has not
126 been investigated in seabirds despite them being considered sentinels of ecosystem change (Le
127 Bohec et al. 2013). Arctic seabirds demonstrate varying foraging specializations on a diversity of
128 prey items reflecting climate-induced trophic shifts and can inform spatial variation and temporal

129 changes in sea-ice and ocean dynamics that propagate up the food web, making them an ideal
130 model to research MDND (Pratte et al. 2019; Albert et al. 2020; Renedo et al. 2020).

131 An inter-colony and inter-individual approach was used to examine spatial variation in
132 the 3-dimensional niche of common eiders (*Somateria mollissima*, hereafter eiders). Eiders are a
133 long-lived, colonial-nesting marine bird with high site fidelity and widely dispersed breeding
134 populations across the Arctic. Across their range, eiders are likely exposed to diverse
135 environmental conditions that influence colony demographics at varying intensities that may
136 influence foraging decisions and, although typically at low concentrations in eiders, Hg exposure
137 (Mallory et al. 2004; 2017; Jónsson et al. 2013; Goudie et al. 2020; Noel et al. 2021). Eider prey
138 primarily includes a diversity of benthic invertebrates (e.g., urchins, mussels, and gastropods) as
139 well as pelagic macroinvertebrates to a lesser extent (e.g., amphipods; Sénéchal et al. 2011;
140 Kristjánsson et al. 2013; Waltho and Coulson 2015). The abundance and distribution of these
141 prey groups vary spatio-temporally and correlate with both predator Hg concentrations and
142 phenological shifts in primary production (Mouritsen et al. 2005; Barber et al. 2015; Fort et al.
143 2016; Savoy et al. 2017). Thus, examining $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and Hg niche dynamics of a costal,
144 primarily benthic-foraging species provides an avenue to investigate prey shifts and Hg exposure
145 (Sénéchal et al. 2011), as well as relative differences in ice algae and phytoplankton-based food
146 webs in relation to sea-ice cover (Søreide et al. 2012; Kohlbach et al. 2016).

147 A 3-dimensional approach combining $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and total Hg (THg) measurements
148 collected from individuals at 10 eider breeding colonies located across their circumpolar range
149 was used to evaluate variation in eider foraging ecology and Hg exposure. It was anticipated that
150 colonies would show differences in 3-dimensional niche size which were influenced by spatial
151 differences in primary productivity (i.e., sea-ice algae and phytoplankton) and migratory

152 behaviour. To examine these possible drivers of colony-level variation in niche size, colony sea-
153 ice cover was examined during a period reflecting periods of isotopic integration in blood.
154 Specifically, it was predicted that colonies with higher sea-ice cover would have smaller niche
155 sizes than those with no sea ice present due to more restricted foraging habitat and likely less
156 diverse prey availability (Yurkowski et al. 2016; Pratte et al. 2019). Niche size along with colony
157 migratory behaviour was also examined with a prediction that eiders from resident colonies
158 would have smaller niche sizes compared to migratory colonies, given that residents remain at
159 the same geographical location year-round and are likely exposed to a narrower range of
160 environmental conditions (Herrera 1978; Gómez et al. 2016).

161 Next, as individual values and colony ranges of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and THg provide important
162 and unique information about foraging ecology, these values were related to colony sea-ice cover
163 during the pre-breeding period when birds foraging at high rates to obtain body condition needed
164 to breed. It was predicted that colonies with higher sea-ice cover would have lower $\delta^{13}\text{C}$, $\delta^{15}\text{N}$
165 and THg ranges due to restricted foraging locations available because of higher sea-ice
166 concentrations. It was also predicted higher individual $\delta^{13}\text{C}$ related to ice algae presence, higher
167 THg due to greater environmental Hg via melting sea-ice, and higher $\delta^{15}\text{N}$ related to higher
168 trophic level foraging through reduced benthic access. Second, these metrics were related to
169 colony migratory status with the prediction that that migratory colonies would have wider $\delta^{13}\text{C}$,
170 $\delta^{15}\text{N}$ and THg ranges due to a presumed broader distribution and use of habitat. It was also
171 predicted that higher individual THg, $\delta^{15}\text{N}$ and lower $\delta^{13}\text{C}$ at migratory colonies due to foraging
172 in areas with greater year-round phytoplankton abundance.

173 Finally, the relationship between trophic position (the vertical placement of an individual
174 in the food-web based on prey and individual $\delta^{15}\text{N}$ values) and inter-individual $\delta^{13}\text{C}$ values on

175 THg concentrations was examined with a prediction that THg would increase with higher trophic
176 position due to the biomagnification of THg, and lower $\delta^{13}\text{C}$ values because of a greater
177 consumption of resources derived from phytoplankton (Atwell et al. 1998; McMahon et al. 2006;
178 Stern et al. 2012). Examination of 3-dimensional niche size among eider colonies allowed for
179 identification of key environmental and behavioural factors that may have influenced niche
180 dynamics. Furthermore, MDND can be used to infer colony-level variability in resource use and
181 overall niche diversity which allowed for broad predictions about flexibility and resiliency to
182 environmental change (Vander Zanden et al. 2010; Paredes et al. 2012; Smith and Reeves 2012;
183 Sydeman et al. 2012). As such, it was also considered how this measurement of niche size may
184 help predict the resiliency of eider colonies to environmental change.

185 **2. Methods**

186 ***2.1. Study sites and sample collection***

187 Whole blood samples were collected from pre-incubating or incubating eiders in 2018 at 10
188 breeding colonies (total number of individuals = 240) across the Arctic and subarctic (spanning a
189 longitude from -147.776 to 35.774 and latitude from 78.918 to 43.645; Figure 1, Table 1). Eiders
190 were captured using colony- and breeding stage-specific techniques. Pre-incubating eiders were
191 sampled at East Bay Island (within in the Qaqsauqtuuq (East Bay) Migratory Bird Sanctuary,
192 Nunavut, Canada), whereas incubating eiders were sampled at the other nine locations.

193 At East Bay Island, eiders were captured using large flight nets. Birds were collected
194 from the nets and a 1-mL tarsal blood sample was obtained from each female eider (Hennin et al.
195 2015). These samples were used for isotopic analyses and were collected using a 23G thin-wall,
196 1-inch needle attached to a sodium-heparinized 1 mL syringe (Lemons et al. 2012). After
197 transferring to a heparinized 1.5 mL Eppendorf tube, samples were kept cool ($\sim 10^\circ\text{C}$), and

198 within 8 h, were centrifuged at 10,000 rpm for 10 min to separate red blood cells (RBCs) and
199 plasma. Plasma was then transferred by pipetting into a separate cryovial and stored along with
200 RBC samples at -20°C until isotopic analysis. During the same capture period as the first sample,
201 a second blood sample of 1-mL was obtained from the jugular vein using 23G thin wall, 1-inch
202 needles attached to heparinized 3mL syringes to be used for Hg analysis. The whole blood
203 sample was placed in acid-rinsed cryovials and kept at ~10°C, and frozen within 6 hours of
204 collection until analysis.

205 At the other nine colonies, female eiders were captured on their nest during incubation
206 using either a bownet, noose pole or dogs (John's Island location only; Milton et al. 2016). The
207 specific incubation stage could not be determined at all sites or for all individuals and was
208 excluded from analysis. For most sites, a 200-1000 µL blood sample was collected from the
209 tarsal vein using a 23G thin-wall, 1-inch needle attached to a heparinized 1 mL syringe. At the
210 Alaskan site, up to 5mL of blood was collected from the jugular vein using a non-heparinized
211 syringe, while at the Icelandic site, blood was collected from the brachial vein. After collection,
212 samples were kept cool and transferred to heparinized 1.5mL cryovials. Generally, within 8-12 h
213 samples were centrifuged for 5-10 min to separate red blood cells (RBCs) and plasma. Plasma
214 was then placed into a separate cryovial and stored along with RBC samples at a minimum of -
215 20°C until analysis.

216 ***2.2. Stable isotope analysis***

217 Stable isotopes of elements turnover at different rates based on dietary composition, metabolic
218 rate and specific metabolic activity of the tissue, as well as individual body size and temperature
219 exposure (Hobson and Clark 1992; Carleton and Martinez del Rio 2005). While specific turnover
220 times have not been established for eiders, for avian blood components generally, plasma has a

221 faster turnover rate that reflects recent diet (days), while the turnover rate of RBCs is slower and
222 reflects diet over a longer period (weeks; Hobson and Clark 1992; Hahn et al. 2012; Barquete et
223 al. 2013). Further, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ usually have similar turnover times, hence are comparable
224 (Bearhop et al. 2002). Stable isotope ratios were measured in plasma of pre-incubating eiders at
225 East Bay Island, and in RBCs of incubating eiders at the other nine colonies. Therefore, despite
226 sampling colonies at different life history stages, by using tissues with relatively shorter (plasma)
227 and longer (RBC) turnover times for analysis, we were able to compare them within a similar
228 stage including the pre-incubation period while eiders are heavily foraging, either at resident
229 sites or in the last period of migration to build up stored resources for their incubation fast.

230 Samples were freeze-dried for approximately 72 h after collection. Samples were then
231 ground into a fine, homogenized powder using a metal spatula cleaned with acetone. Plasma
232 samples were then lipid extracted using a 2:1 chloroform:methanol solution (Søreide et al. 2006).
233 Specifically, 2:1 chloroform:methanol solution (1.9mL) was added to 100 μL of each plasma
234 sample, which were then placed in a water bath at 30°C for 24 h. Samples were then centrifuged
235 at 15,000 rpm for 10 min to separate the lipid solution from the plasma pellet. A p1000 pipette
236 was used to remove the lipid solution, leaving the plasma pellet behind. The pellet was washed
237 again with an additional 1.9 mL of the chloroform:methanol solution and centrifuged for a final
238 10 min at 15,000 rpm. The remaining lipid solution was removed, leaving only a plasma pellet.
239 Samples were left open in the fume hood for 24 h to allow for any remaining
240 chloroform:methanol solution to evaporate. Since RBCs have minimal lipids present, they did
241 not undergo lipid extraction (Hobson and Clark 1992).

242 Plasma and RBC samples were weighed into individual tin-capsules using a 4-digit
243 balance to obtain 0.3-0.5 mg of sample. Plasma samples were prepared at the University of

244 Windsor, and plasma stable isotopes were analysed at the Environment and Climate Change
245 Canada Stable Isotope Laboratory in Saskatoon, Saskatchewan, using continuous-flow isotope-
246 ratio mass spectrometry (CFIRMS; Harris et al. 1997). Samples were weighed into pre-
247 combusted tin capsules. Encapsulated plasma was combusted at 1030°C in a Carlo Erba NA1500
248 or Eurovector 3000 elemental analyser. The resulting N₂ and CO₂ were separated
249 chromatographically and introduced to an Elementar Isoprime or a Nu Instruments Horizon
250 isotope ratio mass spectrometer. Two reference materials were used to normalize the results to
251 VPDB and AIR: BWBIII keratin ($\delta^{13}\text{C} = -20.18$, $\delta^{15}\text{N} = +14.31$ ‰, respectively) and PRCgel
252 ($\delta^{13}\text{C} = -13.64$, $\delta^{15}\text{N} = +5.07$ ‰, respectively). Within run (n = 5) precisions as determined from
253 both reference and sample duplicate analyses were ± 0.1 ‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

254 The RBC samples were prepared for isotope analysis at La Rochelle University, France,
255 and were analysed at the LIENS Institute (La Rochelle, France) as detailed in Fort et al. (2014).
256 Plasma and RBC samples were combusted using a Eurovector 3000 (Milan, Italy) elemental
257 analyser which results in production of N₂ and CO₂ gases. These were separated by gas
258 chromatography and introduced into a NU Horizon (Nu Instruments, Wrexham, UK) triple-
259 collector isotope-ratio mass-spectrometer via an open split. Ratios of carbon (¹³C/¹²C) and
260 nitrogen (¹⁵N/¹⁴N) were expressed in typical delta notation (δ) as per mil (‰) deviation from the
261 primary standards (Vienna Pee Dee Belemnite (VDPB) and atmospheric nitrogen (AIR),
262 respectively). Replicate measurements (n = 20) per run of laboratory standards (USGS-61 and
263 USGS-62) indicated that the measurement accuracy was <0.2‰ for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values.

264 Baseline stable isotopes of Arctic marine food webs vary spatiotemporally, thus
265 measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of biota from different regions can only be compared if corrected
266 for such baseline variance (Bowen 2010; Hobson et al. 2012; de la Vega et al. 2019). Based on

267 previously published $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of known eider bivalve prey at the different breeding
268 sites, stable isotope data was corrected by subtracting baseline bivalve isotope values from the
269 eider tissue values to obtain “corrected” isotopic values (Table 2). However, THg values were
270 not corrected to baseline values. Additionally, we were unable to account for the potential impact
271 of incubation stage on $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ or Hg values. Both Hg and $\delta^{15}\text{N}$ values can be elevated in
272 blood due to mobilization of internal nutrient stores during the incubation fast (Hobson et al.
273 1993; Wayland et al. 2005). However, use of RBCs instead of plasma at all but one site (East
274 Bay Island) to determine incubating female $\delta^{15}\text{N}$ values minimized this effect (Cherel et al.
275 2005). Furthermore, sampling of eiders during incubation, when Hg is known to increase
276 (Wayland et al. 2005), lessens, but does not mitigate the potential bias of East Bay Island pre-
277 breeding eiders having elevated Hg relative to the other colonies, as the pre-breeding eiders have
278 not yet depurated Hg to their eggs during laying (Akearok et al. 2010). Hence, caution should be
279 taken when comparing Hg values between East Bay Island and the other nine colonies.

280 Diet-tissue isotopic discrimination factors allow modeling of isotopic trophic positions or
281 nutrient source tracing (e.g., Wolf et al. 2009; Federer et al. 2010; Bond and Diamond 2011).
282 Such factors have not been established for common eiders, so those reported by Federer et al.
283 (2010) for spectacled eider (*Somateria fischeri*) (plasma: +4.9‰; RBC: +4.0‰) were used.
284 Trophic position was calculated using baseline $\delta^{15}\text{N}$ bivalve values for the individual’s colony
285 ($\delta^{15}\text{N}_{\text{base}}$), discrimination factors from the respective tissue of spectacled eiders ($\delta^{15}\text{N}_{\text{TDF}}$; Federer
286 et al. 2010), trophic position (TP) of baseline prey values (TP_{base} ; value of 2 consistent with eider
287 prey), and the non-colony corrected $\delta^{15}\text{N}$ values for that individual eider ($\delta^{15}\text{N}_{\text{eider}}$; Hobson and
288 Welch 1992; Vander Zanden et al. 1997; Vander Zanden and Rasmussen 1999).

289
$$\text{TP} = ((\delta^{15}\text{N}_{\text{eider}} - \delta^{15}\text{N}_{\text{base}}) / \delta^{15}\text{N}_{\text{TDF}}) + \text{TP}_{\text{base}}$$

290 **2.3. THg analysis**

291 Whole blood collected at East Bay Island was sent to the Research and Productivity Council
292 (RPC) in New Brunswick, Canada for THg analysis. Each sample was prepared by microwave-
293 assisted digestion in nitric acid (SOP 4.M26). Mercury was then analysed by cold vapour atomic
294 absorption spectroscopy (AAS; SOP 4.M52 & SOP 4.M53) to obtain THg concentrations.
295 Quality assurance/control procedures included analysis of four reagent blanks as well as four
296 randomly selected duplicate samples. Previous quality assurance/control procedures using CRM
297 (certified reference materials) were conducted on common eider samples from East Bay in
298 previous sampling years (Provencher et al. 2016, 2017). Mercury concentrations were converted
299 from wet weight to dry weight for comparison with the other colonies following known
300 equations and moisture values for avian blood at 79% (Eagles-Smith et al. 2008).

301 For the remaining nine colonies, THg analyses were conducted at LIENSs Institute using
302 RBCs separated from plasma collected from incubating females. These eiders were captured
303 while incubating (Hanssen et al. 2002; Bottitta et al. 2003; Sénéchal et al. 2011), thus by
304 collecting and analysing RBCs alone, the timeframe which the RBCs represent (weeks) aligns
305 with the timeframe represented in the East Bay Island eiders (days) since whole blood has a
306 turnover rate approximately intermediate of plasma and RBC (Cherel et al. 2005). Therefore, this
307 provides justification for including the colony in our analysis despite potential differences in
308 physiology due to their reproductive stages. Freeze-dried blood was analysed using an Advanced
309 Hg Analyser spectrophotometer (Altec AMA 254). A quality control program included running
310 blanks prior to the analysis at the limit of detection of 0.05 ng of Hg. Certified reference
311 materials (DOLT-2 and TORT-2) were analysed every 15 samples (certified Hg concentrations:
312 $0.44 \pm 0.18 \mu\text{g/g dw}$ for DOLT-2 and $0.27 \pm 0.06 \mu\text{g/g dw}$ for TORT-2, measured

313 concentrations: 0.44 ± 0.01 $\mu\text{g/g dw}$ for DOLT-2 and 0.26 ± 0.01 $\mu\text{g/g dw}$ for TORT-2). Samples
314 were analyzed for THg since Hg exists as primarily MeHg in avian blood (near 1:1 ratio; Wiener
315 et al. 2003; Rimmer et al. 2005).

316 **2.4. Statistical analysis**

317 Colony 3-dimensional niche size (using THg, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and ranges along the THg, $\delta^{13}\text{C}$ and
318 $\delta^{15}\text{N}$ axes were determined for 10 eider colonies using the R package nicheROVER v1.0
319 (Swanson et al. 2015) in R version 3.6.2 (R Development Core Team). NicheROVER uses
320 Bayesian statistical methods to calculate a multidimensional niche region in multivariate space
321 that represents the spatial breadth and placement of a group's (i.e., colony's) niche in relation to
322 other groups, and infers the niche size of each group based on that group's individual values for
323 each dimension (Swanson et al. 2015). Since the variables are in different units ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$:
324 ‰ vs. THg: $\mu\text{g/g dw}$), all values were scaled and centred by subtracting the mean for each
325 variable and dividing it by the standard deviation, thereby standardizing all data. To determine if
326 there were any correlations among variables prior to analysis, independence was tested by
327 calculating Spearman's correlation coefficient between THg and colony-corrected $\delta^{15}\text{N}$ which
328 showed a significant but relatively weak correlation ($R=0.43$, $p<0.001$). Thus, THg and $\delta^{15}\text{N}$,
329 while related, do possess independent variation that allowed for inclusion of both metrics in our
330 analysis to account for spatial variation in THg concentrations. A 95% probability niche region
331 in multivariate space was calculated at 10,000 iterations using diffuse priors (Swanson et al.
332 2015; Yurkowski et al. 2020b). Additional script at 10,000 iterations was conducted to obtain
333 $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and THg ranges (difference between the highest and lowest values; Swanson et al.
334 2015; Yurkowski et al. 2020b). Three-dimensional models of the niche ranges were visualized

335 using the scatter3D function in the car package v.3.0-9 (Fox and Weisberg 2019) and the rgl
336 package v.0.100.54 (Adler and Murdoch 2017; see Supplemental Materials).

337 Primary migratory status of each colony, not including the potential for individual
338 variation, was determined by consulting previous studies (Schamel 1997; Bønløkke et al. 2006;
339 Hanssen et al. 2016; Steenweg et al. 2017; Mallory et al. 2020) and through spatial tracking data
340 collected by the SEATRACK program (<https://seapop.no/en/seatrack/>). Moreover, the proportion
341 of sea-ice cover surrounding each colony within a timeframe reflecting turnover rates of isotope
342 sampling was determined (plasma within a week of sampling, RBC within a month of sampling;
343 Hobson and Clark 1992; Barquete et al. 2013). Sea-ice cover was analyzed via a satellite image
344 of a 100 km area around each colony on a cloud-less day from NASA Worldview dataset
345 (EOSDIS, <https://worldview.earthdata.nasa.gov>). Land pixels were removed from the image
346 manually and the remaining pixels were categorized into two groups (open water or sea ice)
347 using a K-means clustering procedure via RGB values of the pixels
348 (<http://mkweb.bcgsc.ca/color-summarizer/>). The resulting proportion of pixels was used as a
349 proxy for the proportion of sea ice around the colony during the time of isotopic turnover for
350 each colony (Cusset et al. 2019).

351 A preliminary 2-tailed *t*-test was used to determine independence between colony sea-ice
352 cover and migratory behaviour, which were not significantly correlated ($t_5=2.11$, $p=0.09$).
353 Therefore, to determine sources of niche variation with sea ice cover, a general linear model
354 (GLM) was used to examine how log-transformed niche size varied by colony sea-ice cover.
355 Next, six GLMs were used to analyze the relationship between sea ice cover and colony $\delta^{15}\text{N}$,
356 log-transformed $\delta^{13}\text{C}$ and THg ranges, as well as median individual colony-corrected $\delta^{15}\text{N}$, and
357 log-transformed $\delta^{13}\text{C}$ and THg values for each of the 10 colonies. Median values were used to

358 avoid data skewed by high/low individual values within a mean and better represent general
359 colony values.

360 To examine variation in niche dynamics between migratory and resident colonies, a 2-
361 tailed *t*-test was conducted to analyze how log-transformed colony niche size varied with
362 migratory status (migratory or resident being the two groups). Following this, six 2-tailed *t*-tests
363 were used to analyze whether migratory status of a colony resulted in different colony $\delta^{15}\text{N}$, and
364 log-transformed $\delta^{13}\text{C}$ and THg ranges, as well as individual colony-corrected eider $\delta^{13}\text{C}$, $\delta^{15}\text{N}$
365 and log-transformed THg values.

366 Finally, a general linear mixed model (GLMM) was used to examine the relationship
367 between colony-corrected isotopes indicating carbon source ($\delta^{13}\text{C}$), trophic position of each
368 individual, and log-transformed THg. The model consisted of THg as the dependent variable,
369 with $\delta^{13}\text{C}$ and trophic position as independent variables, as well as colony as a random variable.
370 All models conducted throughout the study met statistical assumptions, and all log-
371 transformations were conducted using natural log.

372 **3. Results**

373 ***3.1. Niche size and underlying sources of variation***

374 Three-dimensional niche size was highly variable among colonies, ranging from 1.4 (Grindøya)
375 to 21.7 (Iceland), with an average niche size among all colonies of 9.2 ± 7.8 (Figure 2, see
376 Supplemental Materials). However, niche size was not correlated with colony sea ice cover ($t_8=-$
377 0.92 , $p=0.54$) or migratory status ($t_4=-0.61$, $p=0.57$). The Christiansø colony in Denmark had the
378 lowest colony-corrected $\delta^{13}\text{C}$ values, suggesting higher phytoplankton-derived carbon in their
379 diet, while the Alaskan colony had the highest colony-corrected $\delta^{13}\text{C}$ suggesting eiders were
380 feeding on prey reflecting more ice algae- or inshore-derived carbon (see Supplemental

381 Materials). The Alaskan colony also had the highest colony-corrected $\delta^{15}\text{N}$ values, with the
382 Faroe Islands having the lowest values, suggesting that Faroese eiders forage at lower trophic
383 levels, whereas the Alaskan eiders forage at higher trophic levels.

384 ***3.2. Relationship between colony migratory behaviour and sea-ice cover with isotopes and*** 385 ***THg***

386 Inter-colony variation in sea-ice presence was positively correlated with median eider THg
387 concentrations, as well as $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (Table 3). However, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, as well as THg
388 ranges did not vary with colony sea-ice cover (Table 3). Migratory colonies had higher
389 individual $\delta^{15}\text{N}$ and THg, as well as lower individual $\delta^{13}\text{C}$ compared to individuals captured at
390 resident colonies (Table 3). However, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and THg range did not vary between the
391 migratory and resident colonies (Table 3).

392 ***3.3. Relationship between isotopic niche and THg concentrations***

393 Both colony-corrected $\delta^{13}\text{C}$ and trophic position predicted THg concentration within individuals.
394 Specifically, individuals with a lower $\delta^{13}\text{C}$ value (phytoplankton-based foraging) had higher THg
395 values (Table 3, Figure 3). Additionally, THg significantly increased with trophic position,
396 where individuals with higher trophic positions had greater THg values (Table 3, Figure 3).

397 **4. Discussion**

398 Using data collected from ten eider colonies located throughout their circumpolar range,
399 including both Arctic and subarctic sites, 3-dimensional niche was quantified size using $\delta^{15}\text{N}$,
400 $\delta^{13}\text{C}$ and THg to determine colony niche size and ranges. Determination of 3-dimensional niche
401 size allowed for broad comparison of a snapshot of diet breadth at multiple eider colonies in
402 relation to environmental and behavioural differences, as well as inference of their potential for

403 flexibility in response to environmental change. The benefits of using multiple chemical tracers
404 are demonstrated when assessing the effects of spatial variation and environmental gradients on
405 the foraging ecology of highly mobile consumers.

406 ***4.1. Colony foraging flexibility and resiliency predictions***

407 Generally, colonies that utilize broader, more generalist diets are expected to have larger
408 foraging niches, thus are expected to be inherently less vulnerable to change since they have
409 greater flexibility in their prey source as they forage on a wide variety of organisms and habitats
410 (Jakubas et al. 2017; Both et al. 2010). Colonies with restricted, specialist diets are expected to
411 have smaller foraging niches, influenced by both prey availability and foraging distance, and are
412 generally viewed as more vulnerable to environmental change (Bolnick et al. 2003; Araújo et al.
413 2011; Pratte et al. 2019). While the interpretation of MDND is not necessarily straightforward,
414 due to complex relationships and multiple factors influencing each dimension, MDND may be
415 useful in predicting the resiliency of common eider colonies to ongoing climate change across
416 their range, although numerous other factors should also be considered including multiple
417 biogeochemical metrics, colony recruitment and individual fitness (Paredes et al. 2012; Smith
418 and Reeves 2012; Sydeman et al. 2012). Thus, this analysis provides a snapshot of niche
419 characteristics at a singular time frame that may assist with colony-wide resiliency predictions in
420 combination with future research on changing niche dynamics at these colonies.

421 When grouped for similarity, niche size generated the following general pattern in this
422 study: Iceland, East Bay Island and Faroe Islands > Christiansø and John's Island >
423 Kongsfjorden, Alaska and Russia > Tern Island and Grindøya (Figure 1). Using this 3-
424 dimensional view of niche size, it was predicted that colonies with wider (i.e., more generalist)
425 3-dimensional niches such as those in Iceland and Faroe Islands, or colonies comprised of

426 migrants from multiple locations such as East Bay will show greater resiliency to shifts in food
427 web dynamics compared to colonies with a smaller (i.e., more restricted, specialist) niche similar
428 to Tern Island and Grindøya. Smaller niches are predicted to be at a disadvantage in a changing
429 climate as these alterations may change or eliminate food sources, leaving a colony or species
430 more vulnerable if they do not have the flexibility to adapt and shift their diet with this changing
431 prey base (Both et al. 2010; Le Bohec et al. 2013; Ceia and Ramos 2015). However, climate
432 change may present an opportunity for Arctic colonies with smaller niches to expand their prey
433 sources with advancing phenology of spring phytoplankton blooms and more open water
434 sources. For those with broader niches at southern latitudes, that niche size may be critical along
435 with further changes in the distribution and availability of key prey (Staudinger et al. 2019).
436 Nevertheless, more research that integrates measures of breeding success and colony
437 demographics is necessary to test these resiliency hypotheses over long temporal scales to
438 identify seasonal and annual variation in inter- and intra- colony foraging ecology.

439 ***4.2. Variation in niche size, niche metrics and THg to colony sea-ice cover***

440 Colony niche size was not correlated with sea-ice cover, possibly attributable to several factors.
441 First, despite the presence of sea ice likely restricting foraging locations, eiders may still be able
442 to access a diversity of resources, including the potential for prey sources such as ice-associated
443 amphipods as niche size was similar to locations that have more accessible, ice-free areas
444 (Karnovsky et al. 2008). Second, northern colonies may support a variety of individuals that
445 utilize both generalist and specialist strategies, thus adding to the flexibility and diversity of the
446 colony in the face of environmental change (Woo et al. 2008; Ceia and Ramos 2015; Pratte et al.
447 2019). Notably, the relative proportion of generalist and specialist individuals in populations

448 dramatically affects dietary niche size with generalist-based populations having wider niches
449 (Newsome et al. 2007).

450 Eider colonies with greater sea-ice cover had higher $\delta^{13}\text{C}$ values, which is not consistent
451 with the expected gradient based on ocean temperature (Sackett et al. 1965; Goericke and Fry
452 1994; McMahon et al. 2013). However, this pattern can be most likely explained by eiders
453 foraging on resources derived from ice algae associated with higher ice cover versus more
454 phytoplankton-derived resources in areas with lower sea-ice presence (Hobson et al. 1995;
455 Tamelander et al. 2006; McMahon et al. 2006). As well, macroalgal carbon has a higher $\delta^{13}\text{C}$
456 value than phytoplankton, and therefore could be a contributing carbon source to these spatial
457 differences. Nonetheless, spatial differences in carbon source use amongst eider colonies existed,
458 where some colonies use more phytoplankton-derived carbon than others. Furthermore, results
459 showed that in general, eider colonies with greater sea ice cover also had higher median
460 individual THg and $\delta^{15}\text{N}$, suggesting that sea-ice presence resulted in eiders foraging at higher
461 trophic levels, thus contributed to higher overall THg exposure. Potential reasons for higher
462 trophic-level foraging include eiders feeding on ice-associated sources of prey prior to laying,
463 such as amphipods, due to restricted access to benthic prey with sea ice present (Karnovsky et al.
464 2008). Amphipods seasonally forage on ice algae and this would decouple them from the pelagic
465 food web and result in higher $\delta^{13}\text{C}$ values (Werner 1997; Brown et al. 2017). Furthermore,
466 waters with sea ice present are supersaturated with dissolved THg, thus further contributing to
467 the elevation of THg in food webs (DiMento et al. 2019). Individual variation in foraging
468 behaviour is known to have a role in Hg accumulation (Anderson et al. 2009; Braune et al. 2014;
469 Le Croizier et al. 2019) and this exists within the colonies studied as demonstrated by the colony
470 ranges.

471 **4.3. Role of migration in shaping MDND and THg exposure**

472 It was predicted that migratory populations (see Table 1, Figure 1) would have larger niches due
473 to exposure to a variety of environmental conditions and prey types at both migratory and
474 breeding grounds where resources are stored to mobilize during their incubation fast (Herrera
475 1978; Gómez et al. 2016). In the present study, there was no pattern between with migratory
476 behaviour and niche size. However, two of the largest niche sizes found at two resident colonies
477 (Iceland and Faroe Islands) may stem from colony-wide expansion in dietary choice due to
478 increased prey availability. This has been reported in Iceland where eiders within the colony
479 selected a wide array of both benthic and pelagic prey (Kristjánsson et al. 2013). Waters around
480 Iceland are a mix of Arctic (East-Greenland Current), as well as Atlantic origins (North Atlantic
481 Current), and this, together with greater lack of sea ice, would provide a diverse range of prey
482 options to pre-breeding eiders (Vincent 2010; Kristjánsson et al. 2013; Casanova- Masjoan et al.
483 2020). The East Bay Island colony, consisting of migrants from Greenland and Newfoundland,
484 had the second largest niche size potentially in part due to a mixing of individuals from both
485 overwintering sites (Steenweg et al. 2017). Additionally, individual variation in migration
486 distance and strategy within a colony, although not included in the present study, may lead to
487 broader colony niche ranges (Mallory et al. 2020).

488 Colonies supporting migratory eiders had higher THg concentrations and foraged at
489 higher trophic levels compared to colonies supporting residents, suggesting that colonies of
490 migratory individuals had access to higher trophic-level prey, or relied on these prey to store
491 resources necessary for incubation. Colonies with resident eiders had higher individual $\delta^{13}\text{C}$
492 levels indicating diets with greater foraging based on ice algae, potentially due to residing at their
493 Arctic breeding sites year-round while migratory colonies move to more suitable areas with

494 presumably lower sea ice. Combined with the results on colony sea ice cover, these dynamics
495 show that changes in environmental conditions and variability may have different effects on
496 migratory and resident seabird colonies dependent on future colony flexibility, thus should be
497 factored into future analyses especially regarding climate change effects within Arctic
498 ecosystems.

499 ***4.4. Relationship between trophic position, foraging location and THg concentrations***

500 With increasing industrial activity and contaminant deposition due to long-distance transport in
501 northern latitudes, as well as the release of stored Hg from melting cryosphere and increased
502 erosion of terrestrial sources, Arctic-inhabiting species are potentially becoming more at risk for
503 contaminants exposure and a suite of possible negative neurological, physiological and
504 reproductive impacts (Dietz et al. 2013; Scheuhammer et al. 2015; Soerensen et al. 2016, Cossa
505 et al. 2018). This is especially a potential population stability concern for harvested species, such
506 as common eider, which are an important, harvested species for many Indigenous communities
507 in the North (Nakashima and Murray 1988; Priest and Usher 2004). Concentrations of THg for
508 the eider colonies in this study are comparable to those observed in previous eider research
509 (Provencher et al. 2016; Albert et al. 2019; Ma et al. 2020; Dietz et al. 2021). The mean
510 concentrations of THg in the Alaska, Christiansø and East Bay colonies were above 0.95 µg/g
511 dw, suggesting that three of the 10 colonies studied, and 40% of sampled eiders, were above
512 general environmental background concentrations (Eagles-Smith et al. 2008; Ackerman et al.
513 2016). Nonetheless, concentrations were still sufficiently low to assign them a general “low risk”
514 status regarding concerns for health, physiology, behaviour and reproductive effects (Ackerman
515 et al. 2016; Dietz et al. 2019; 2021). The individual eider with the highest Hg concentration was
516 from the Iceland colony (2.55 µg/g dw compared to the colony mean of 0.95 µg/g dw). Iceland

517 had less sea ice than other regions, such as Alaska that had the highest sea ice cover and colony
518 THg average (1.23 $\mu\text{g/g dw}$).

519 With a rapidly declining sea-ice cover, a rise in phytoplankton production and resulting
520 eider consumption of prey derived from phytoplankton carbon sources could be related to higher,
521 individual THg concentrations (Stern et al. 2012). Combined with the results in section 4.2
522 showing higher median THg concentrations at colonies with greater sea-ice cover, these results
523 demonstrate that within colonies, individuals with greater phytoplankton-based consumption had
524 higher THg concentrations. The relationship between individual $\delta^{13}\text{C}$ and THg, combined with
525 effects of trophic position (determined using $\delta^{15}\text{N}$) on THg may potentially have future effects
526 on seabird health, behaviour and reproduction in those with at-risk Hg exposure. However, it is
527 likely that any possible effects would not be consistent across the entire range of a species,
528 especially given the regional difference in which climate change is altering the Arctic (Muir et al.
529 1999; Mallory and Braune 2012; Swart et al. 2015). Nevertheless, variation among colonies was
530 detected, suggesting regional differences in the relationship between $\delta^{13}\text{C}$, trophic position and
531 THg; for instance, the Christiansø and Kongsfjorden colonies showed opposite relationships
532 between THg and $\delta^{13}\text{C}$ (Figure 3). Thus, more in-depth analyses of the environmental factors at
533 each site would allow for site-specific investigation into the relationships between foraging
534 behaviour and THg uptake. Additionally, further knowledge of baseline variation (THg, $\delta^{15}\text{N}$,
535 $\delta^{13}\text{C}$) in colony-specific prey at a varying spatio-temporal inter-annual scale, parallel with eider
536 sampling, would aid future interpretation of eider niche size, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and sources of
537 individual and colony THg. Additionally, the contribution of terrestrial carbon sources and
538 agricultural runoff to marine areas around some of these colonies may also contribute to
539 variation in individual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and affect exposure to THg and its accumulation

Commented [A1]: Maybe I missed it, but do you have any isotope data on ice algae?

Commented [A2R1]: Thank you for your comment. We did not gather any ice algae isotope data for this project and instead related our data to known relationships between ice algae and phytoplankton carbon values.

540 (Dunton et al. 2006; Laursen et al. 2018; Renedo et al. 2020). Overall, the relationship between
541 environmental conditions and THg concentrations presents a complex system and paired with the
542 rapid changes in ecosystem dynamics currently being observed (i.e., sea ice abundance),
543 underscores the necessity of future, consistent annual monitoring, especially in key ecosystem
544 indicators like marine birds.

545 **5. Conclusion**

546 Inter-colony, 3-dimensional niche size, isotopic and THg ranges, and the relationships between
547 $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and THg within individuals was examined. Our results suggest that common eider
548 colonies across the Arctic and subarctic have a wide degree of diet variation, potentially
549 influenced by environmental changes including spatio-temporal differences in primary
550 productivity. It was found that consideration of colony-level variation in life histories (migratory
551 vs resident) was important for assessing the level of risk to which a colony may be exposed.
552 Further, inter-annual MDND analyses using simultaneous local $\delta^{13}\text{C}$ marine isoscapes to correct
553 for eider $\delta^{13}\text{C}$, in addition to corrections for baseline THg, would provide greater insight into the
554 temporal variation in niche size that exists at both an inter- and intra-colony scale. Taken
555 together, exploring MDND is an increasingly valuable tool to provide insight into how diet
556 breadth differs across a species' range, especially when combined with temporal and spatial
557 variation in environmental conditions and key components to variation in life history such as
558 migration.

559 **Acknowledgments**

560 We thank the field crews and regional volunteers at all locations who assisted in sample
561 collection and logistics. As well, thank you to the lab technicians at Research and Productivity
562 Council (RPC) in New Brunswick, Canada and Littoral Environment et Sociétés (LIENSs, La

563 Rochelle) for sample analysis. We are also grateful to the plateformes ‘Analyses Élémentaires’
564 and ‘Spectrométrie Isotopique’ (La Rochelle University - LIENSs) for their assistance with
565 laboratory work. We also thank Environment and Climate Change Canada (ECCC), the Natural
566 Sciences and Engineering Research Council of Canada, Canada Research Chairs Program, the
567 Nunavut Wildlife Management Board, Northern Scientific Training Program, Polar Continental
568 Shelf Project, Polar Knowledge Canada, Baffinland Iron Mine, the Canadian Network of Centres
569 of Excellence (ArcticNet), Mitacs Globalink Research, The Danish Environmental Protection
570 Agency, Danish Hunters' Association, Hunters' Nature Fund, the Government of Ontario and the
571 University of Windsor for logistical support, research and/or personal funding. This study is also
572 a contribution to the ARCTOX initiative (arctox.cnrs.fr) and the ARCTIC-STRESSORS project
573 (ANR-20-CE34-0006-01). Animal care approval for this project was granted through the
574 University of Windsor Committee for Animal Care (AUPP #11-06; Reproductive Strategies of
575 Arctic-Breeding Common Eiders), and ECCC Animal Care (EC-PN-15-026).
576

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1101

1102 **Tables and Figures**

1103 **Table 1.** Locations of common eider colonies included in this study, sample size (number of
 1104 individual birds from each colony included in the study), month samples were obtained,
 1105 coordinates (latitude and longitude), whether a colony is known to be predominately migratory
 1106 or resident, and the proportion of sea ice cover in a 100km area around the colony during the
 1107 appropriate timeframe reflecting isotope data.

Location	n	Sampling month	Latitude	Longitude	Migratory behaviour	Sea ice cover (%)
Kaktovik, Alaska	33	July	70.340	-147.776	Migratory	43.45
Breiðafjörður, Iceland	23	June	65.078	-22.736	Resident	3.10
Christiansø, Denmark	25	May	55.330	15.188	Migratory	0
Grindøya, Norway	17	June	69.633	18.844	Resident	0
John's Island, Canada	19	July	43.645	-66.041	Migratory	0
Kirkjubøhólmur, Faroe Islands	16	July	61.950	-6.799	Resident	0
Kongsfjorden, Norway	16	June	78.918	11.910	Migratory	0
East Bay Island, Canada	43	June	64.023	-81.790	Migratory	34.34
Onega Bay, Russia	24	June	65.048	35.774	Resident	0
Tern Island, Canada	24	June	69.547	-80.812	Migratory	36.47

1108

1109 Table 2. Isotopic signatures ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$ in ‰) of typical common eider bivalve prey as
 1110 determined by the most spatio-temporally appropriate literature values available at the time of
 1111 analysis. Prey stable isotope data was used to correct common eider isotope data to allow for
 1112 inter-colony comparison.

Location	Prey Species	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Reference
Beaufort Sea, Alaska	<i>Cyrtodaria kurriana</i>	-25.20	7.90	Dunton et al. 2012
Breiðafjörður, Iceland	<i>Mytilus edulis</i>	-19.60	7.40	Sarà et al. 2007
Christiansø, Denmark	<i>Limecola balthica</i>	-20.40	7.20	Ek et al. 2018
Grindøya, Norway	<i>Hiatella arctica</i>	-19.32	7.26	Fredriksen 2003
John's Island, Canada	<i>Mytilus edulis</i>	-19.99	7.17	English et al. 2015
Kirkjubøhólmur, Faroe Islands	<i>Mytilus edulis</i>	-19.20	8.41	Bustamante, unpub.
Kongsfjorden, Norway	<i>Hiatella arctica</i>	-20.30	6.90	Vieweg et al. 2012
East Bay Island, Canada	<i>Hiatella arctica</i>	-18.22	8.64	Sénéchal et al. 2011
Onega Bay, Russia	<i>Styela rustica</i>	-21.60	6.49	Yakovis et al. 2012
Tern Island, Canada	<i>Hiatella arctica</i>	-18.22	8.64	Sénéchal et al. 2011

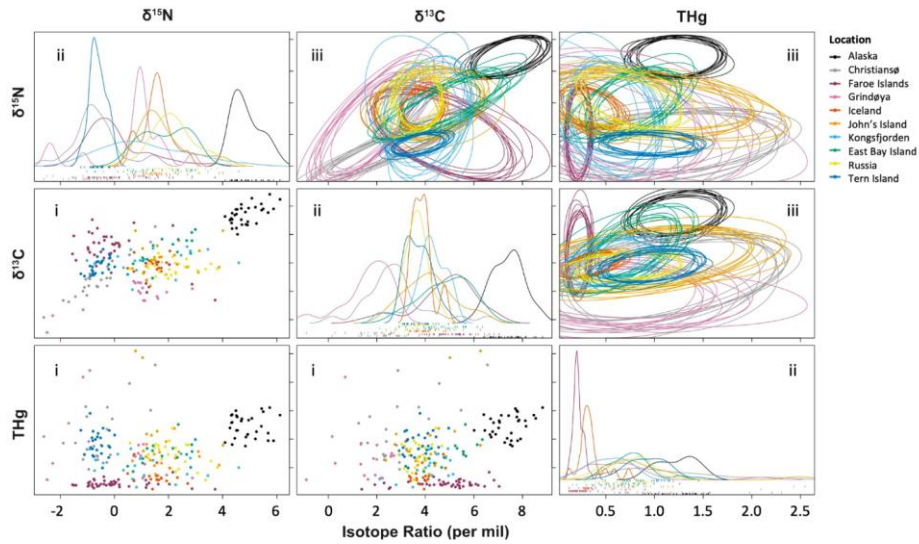
1113

1114 **Table 3.** Results of three sets of statistical analyses: a) seven 2-tailed t-tests relating migratory
 1115 status to colony niche size, isotope and THg ranges, as well as individual colony-corrected
 1116 isotope and THg values; b) seven GLM results relating colony sea ice cover to colony niche size,
 1117 isotope and THg ranges as well as median colony isotope and THg values; c) GLMM results
 1118 relating common eider trophic position, calculated using baseline and individual $\delta^{15}\text{N}$ and
 1119 colony-corrected $\delta^{13}\text{C}$ to individual THg values. All log-transformed values were determined
 1120 using the natural log and used to meet model assumptions.

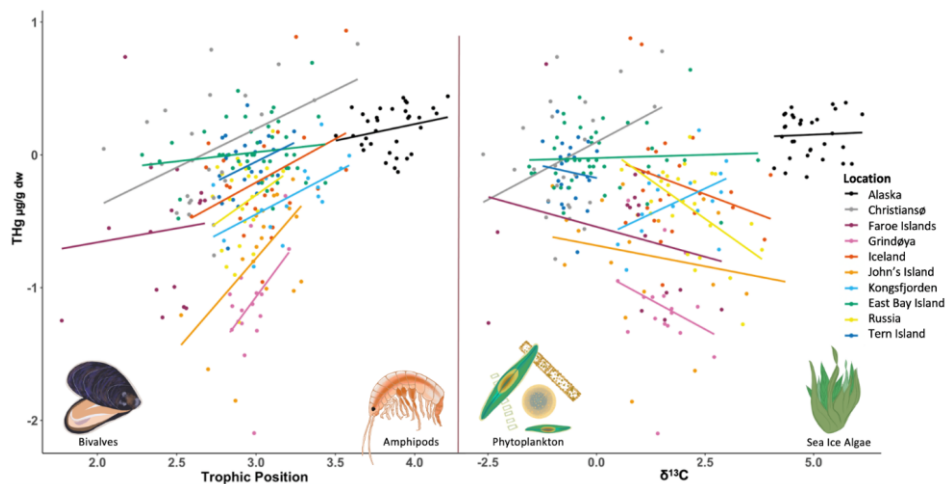
Variable	Estimate (β)	SE	df	t	p
a) 2-tailed t-test – Migratory Status					
log(Niche size)			4	-0.609	0.573
log($\delta^{13}\text{C}$ Range)			8	-0.339	0.743
$\delta^{15}\text{N}$ Range			7	0.996	0.353
log(THg Range)			5	-0.600	0.576
Individual $\delta^{13}\text{C}$			238	2.218	0.028
Individual $\delta^{15}\text{N}$			220	-6.858	<0.001
log(Individual THg)			124	-6.329	<0.001
b) GLM – Sea Ice Cover					
log(Niche size)	-0.0125	0.019	8	-0.639	0.541
log($\delta^{13}\text{C}$ Range)	-0.013	0.008	8	-1.635	0.141
$\delta^{15}\text{N}$ Range	-0.002	0.014	8	-0.106	0.919
log(THg Range)	-0.004	0.009	8	-0.459	0.658
log(Median $\delta^{13}\text{C}$)	0.028	0.010	8	2.936	0.032
Median $\delta^{15}\text{N}$	0.052	0.022	8	2.332	0.048
log(Median THg)	0.014	0.006	8	2.525	0.036
c) GLMM – Individual log(THg)					
Intercept	-1.923	0.304	142.233	-6.330	<0.0001
Trophic position	0.563	0.096	234.614	5.862	<0.001
$\delta^{13}\text{C}$	-0.063	0.022	232.943	-2.813	0.005



1121
 1122 **Figure 1.** Map of the circumpolar-Arctic, and locations of the 10 common eider colonies used in
 1123 this study (stars) designated by whether a colony is primarily resident (circles) or migratory
 1124 (stars). Shape colour represents four groupings of similar median 3-dimensional niche size (95%
 1125 Bayesian credible intervals). By ascending niche size, colours represent: 1 (smallest; red), 2
 1126 (white), 3 (grey), and 4 (largest; black). Dashed line indicates the Arctic Circle, and the solid line
 1127 indicates the Arctic boundary according to the Arctic Monitoring and Assessment Programme
 1128 (AMAP; map provided by globalcitymap.com).



1129
 1130 **Figure 2.** 2-dimensional projections of ten 3-dimensional niche regions produced using the R
 1131 package nicheROVER v1.0 (Swanson et al. 2015). Corrected stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in
 1132 ‰) and THg data (in $\mu\text{g/g dw}$) were used from individuals at 10 pan-Arctic or subarctic common
 1133 eider colonies. Sections show, i) The raw stable isotope and THg data in pairs, ii) density
 1134 estimates of $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and THg individually, and iii) pairings of $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and THg showing 2-
 1135 dimensional projections of 95% probabilistic niche regions based on 3-dimensional data.



1136
 1137 **Figure 3.** Relationship between THg (natural log-transformed) with trophic position (calculated
 1138 based on $\delta^{15}\text{N}$; see Methods) and colony-corrected $\delta^{13}\text{C}$ (in ‰) for individuals at 10 pan-Arctic
 1139 or subarctic common eider colonies, identified by colour.
 1140

1141 **Supplemental Materials**

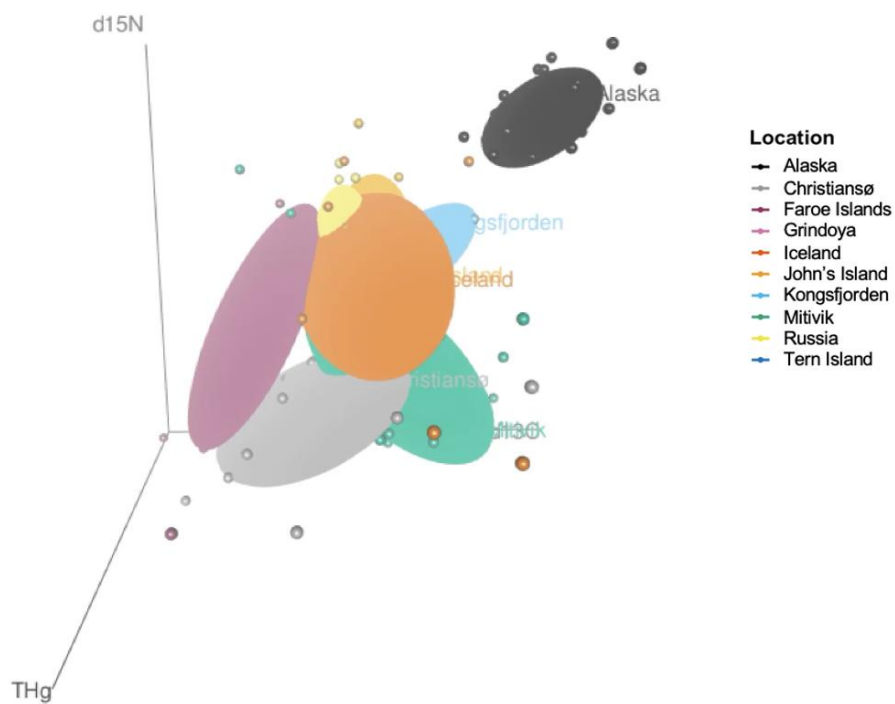
1142 Sample sizes (n), means \pm SD, Min-Max (in ‰) for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and total Hg (THg in $\mu\text{g/g dw}$)
 1143 (values in brackets corrected for colony baseline ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) and standardized for units ($\delta^{13}\text{C}$,
 1144 $\delta^{15}\text{N}$ and THg)), medians and range of 3-dimensional niche size (95% Bayesian credible
 1145 intervals), and $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and THg ranges (maximum-minimum values using corrected and
 1146 standardized values) of 10 pan-Arctic and subarctic common eider colonies.

Location	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	THg	Niche size	$\delta^{13}\text{C}$ range	$\delta^{15}\text{N}$ range	THg range
Alaska	33	-20.1 \pm 0.5 (1.8)	15.3 \pm 0.7 (1.8)	1.2 \pm 0.2 (0.9)	3.3 (2.3, 5.2)	0.866	1.461	1.689
Christiansø	25	-21.2 \pm 0.9 (-1.0)	10.0 \pm 1.3 (-0.9)	1.1 \pm 0.5 (0.6)	9.7 (6.6, 16.7)	1.379	2.923	4.590
Faroe Islands	16	-18.5 \pm 1.4 (-0.3)	10.1 \pm 1.0 (-1.5)	0.7 \pm 0.4 (-0.6)	18.8 (11.5, 36.8)	2.059	2.106	4.508
Grindøya	17	-17.8 \pm 0.6 (0.1)	11.1 \pm 0.4 (-0.3)	0.4 \pm 0.1 (-1.4)	1.4 (0.8, 2.6)	0.834	0.907	1.528
Iceland	23	-17.8 \pm 0.9 (0.3)	11.6 \pm 1.0 (-0.1)	0.9 \pm 0.5 (0.1)	21.7 (14.2, 37.7)	1.407	2.257	5.410
John's Island	19	-16.9 \pm 1.5 (-0.1)	12.0 \pm 0.8 (-0.1)	0.5 \pm 0.2 (-0.9)	9.1 (5.7, 16.5)	2.250	1.633	1.688
Kongsfjorden	16	-18.4 \pm 0.8 (0.3)	11.8 \pm 1.0 (0.3)	0.8 \pm 0.2 (-0.3)	4.6 (2.8, 9.1)	1.217	2.128	2.068
East Bay Island	43	-18.2 \pm 1.1 (-0.6)	13.5 \pm 1.3 (0.3)	1.0 \pm 0.3 (0.4)	18.5 (13.6, 27.9)	1.904	2.897	3.571
Russia	24	-19.4 \pm 0.8 (0.4)	10.2 \pm 0.4 (-0.4)	0.7 \pm 0.2 (-0.4)	3.3 (2.2, 5.8)	1.175	0.962	2.278
Tern Island	24	-18.8 \pm 0.3 (-1.0)	12.4 \pm 0.5 (-0.4)	0.9 \pm 0.2 (0.1)	1.4 (0.9, 2.4)	0.475	1.141	2.398

1147

1148

1149 3-dimensional representation of ten 3-dimensional niche regions produced using the R package
1150 rgl v.0.100.54 (Adler and Murdoch 2017). Corrected stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in ‰)
1151 and THg concentrations (in $\mu\text{g/g dw}$) were used from individuals at ten pan-Arctic or subarctic
1152 common eider colonies to obtain 3-dimensional niche regions using the R package nicheROVER
1153 v1.0 (Swanson et al. 2015).



1154
1155 (Still image of a video showing the 3-dimensional plot in rotating view – see video upload for
1156 actual file to be used for publication).

Graphical Abstract



Migratory Colonies



↑ $\delta^{15}\text{N}$

↑ THg

↓ $\delta^{13}\text{C}$

↑ Sea-Ice Cover



↑ $\delta^{15}\text{N}$

↑ THg

↑ $\delta^{13}\text{C}$

Highlights

1. Common eider colonies vary in their 3-dimensional ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$, THg) niche size
2. Colonies with higher sea-ice cover had higher $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and THg
3. Colonies considered migratory had higher average $\delta^{15}\text{N}$ and THg, but lower $\delta^{13}\text{C}$
4. Individuals with lower $\delta^{13}\text{C}$ and higher trophic positions had higher THg

1 **Environmental and life-history factors influence inter-colony multidimensional niche**
2 **metrics of a breeding Arctic marine bird**

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28 **Keywords**

29 Stable isotopes; carbon-13; nitrogen-15; THg; climate change; common eider

30 **Abstract**

31 Human industrialization has resulted in rapid climate change, leading to wide-scale
32 environmental shifts. These shifts can modify food web dynamics by altering the abundance and
33 distribution of primary producers (ice algae and phytoplankton), as well as animals at higher
34 trophic levels. Methylmercury (MeHg) is a neuro-endocrine disrupting compound which
35 biomagnifies in animals as a function of prey choice, and as such bioavailability is affected by
36 altered food web dynamics and adds an important risk-based dimension in studies of foraging
37 ecology. Multidimensional niche dynamics (MDND; $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, THg; total mercury) were
38 determined among breeding common eider (*Somateria mollissima*) ducks sampled from 10
39 breeding colonies distributed across the circumpolar Arctic and subarctic. Results showed high
40 variation in MDND among colonies as indicated by niche size and ranges in $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and THg
41 values in relation to spatial differences in primary production inferred from sea-ice presence and
42 colony migratory status. Colonies with higher sea-ice cover during the pre-incubation period had
43 higher median colony THg, $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$. Individuals at migratory colonies had relatively
44 higher THg and $\delta^{15}\text{N}$, and lower $\delta^{13}\text{C}$, suggesting a higher trophic position and a greater reliance
45 on phytoplankton-based prey. It was concluded that variation in MDND exists amongst eider
46 colonies which influenced individual blood THg concentrations. Further exploration of spatial
47 ecotoxicology and MDND at each individual site is important to examine the relationships
48 between anthropogenic activities, foraging behaviour, and the related risks of contaminant
49 exposure at even low, sub-lethal concentrations that may contribute to deleterious effects on
50 population stability over time. Overall, multidimensional niche analysis that incorporates
51 multiple isotopic and contaminant metrics could help identify those populations at risk to rapidly
52 altered food web dynamics.

53 **Highlights**

- 54 1. Common eider colonies vary in their 3-dimensional ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$, THg) niche size
- 55 2. Colonies with higher sea-ice cover had higher $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and THg
- 56 3. Colonies considered migratory had higher median $\delta^{15}\text{N}$ and THg, but lower $\delta^{13}\text{C}$
- 57 4. Individuals with lower $\delta^{13}\text{C}$ and higher trophic positions had higher THg

58

59 **Graphical Abstract**



Migratory Colonies **↑ Sea-Ice Cover**



↑ $\delta^{15}\text{N}$
↑ THg
↓ $\delta^{13}\text{C}$



↑ $\delta^{15}\text{N}$
↑ THg
↑ $\delta^{13}\text{C}$

60

61 **1. Introduction**

62 Global anthropogenic activity has resulted in environmental shifts within Arctic systems
63 including rising air and ocean temperatures (Zhang 2005; Screen and Simmonds 2010; Najafi et
64 al. 2015), changes in wind and ocean circulation (Timmermans et al. 2011), and a dramatic
65 modification of sea-ice cover in marine systems (Johannessen et al. 2004; Hoegh-Guldberg and
66 Bruno 2010; IPCC 2019). These multiple stressors generate cumulative effects which have direct
67 and indirect influences on biological systems, ultimately having the potential to affect food web
68 characteristics including prey availability and selection (Vasseur and McCann 2005; Frederiksen
69 et al. 2006; Parmesan 2006). Arctic marine food-webs have been particularly impacted, leading
70 to abiotic shifts resulting in alterations of prey abundance and availability which have modified
71 the foraging niche of higher trophic-level organisms (Moline et al. 2008; Pecuchet et al. 2020).

72 The foraging niche of an organism includes both dietary and environmental components,
73 and therefore has been used to discern both trophic roles by consumers and changes in their
74 resource use (Newsome et al. 2007). Studies examining foraging niche size (the spatial and
75 trophic-level range at which a group forages) have been used to investigate the effect of
76 phenological changes in primary production on predators (Rabosky 2009). In polar regions,
77 changes in the abundance, distribution, and phenology of primary producers such as
78 phytoplankton and ice-algae can have effects on higher trophic-level wildlife (Frederiksen et al.
79 2006; Kohlbach et al. 2016; Renaut et al. 2018; Lewis et al. 2020). Sympagic-pelagic-benthic
80 coupling drives energy flow between the surface and benthic habitats and provides a foundation
81 for Arctic ecosystem functioning involving benthic consumers, but is being decoupled due to
82 changing sea-ice dynamics (Søreide et al. 2012; Kohlbach et al. 2016; Yurkowski et al. 2020a).
83 These shifts can generate bottom-up effects on the foraging ecology of higher trophic species,

84 especially those that rely on consuming resources that inhabit the sea floor (Leu et al. 2011; Post
85 et al. 2013; Post 2017; Cusset et al. 2019).

86 A further consequence of changing marine ecosystems is shifts in wildlife exposure to
87 contaminants (Muir et al. 1999; Macdonald et al. 2005; Stern et al. 2012). It is well established
88 that Arctic marine food webs are influenced by long-range transport of contaminants (Macdonald
89 et al. 2000; Braune et al. 2005; Kirk et al. 2012). On top of this, melting of the cryosphere is
90 releasing stored contaminants from years of higher contaminant output into the current system
91 (Rydberg et al. 2010; Schuster et al. 2018; Hawkings et al. 2021). Methylmercury (MeHg) is a
92 biologically converted form of mercury (Hg) and is a contaminant of concern due to its high
93 bioavailability in organic tissues and toxic effects at even low, sub-lethal concentrations (Wiener
94 et al. 2003; Whitney and Cristol 2017; Evers 2018). Uptake of MeHg into wildlife can disrupt
95 endocrine functioning, behaviour, and reproductive success (e.g., Cardona-Marek et al. 2009;
96 Chen and Hale 2010; Whitney and Cristol 2017). Specifically, reproductive effects in birds
97 include reduced clutch size, altered parental breeding behaviour and reduced hatching and
98 fledgling success (Braune et al. 2012; Tartu et al. 2013; Goutte et al. 2014; Hartman et al. 2019).

99 Climate change can affect the distribution and accumulation of Hg in Arctic ecosystems
100 (Stern et al. 2012; McKinney et al. 2015; Foster et al. 2019). Further, changes in Arctic food web
101 dynamics and trophic relationships may shift the flow of Hg between organisms (Braune et al.
102 2014). To study this, stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) are tracers that can
103 provide time-integrated information on habitat use and diet (Bearhop et al. 2006; Cherel and
104 Hobson 2007; Inger and Bearhop 2008). In coastal polar environments, $\delta^{13}\text{C}$ provides dietary
105 information on sources of primary productivity and foraging habitat, for example, between ^{13}C -
106 depleted phytoplankton-derived carbon and ^{13}C -enriched sea-ice derived carbon (Hobson et al.

107 2002; Kohlbach et al. 2016; Yurkowski et al. 2020a; Lewis et al. 2020). In addition, benthic or
108 nearshore environments with macroalgae are typically enriched in ^{13}C compared to pelagic or
109 offshore sources (Hobson and Welch 1992; Hobson et al. 1995; France 1995). Values of $\delta^{15}\text{N}$
110 indicates relative trophic level, with higher trophic levels associated with increased $\delta^{15}\text{N}$ values
111 (Hobson and Welch 1992). Thus, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values can help determine environmental and
112 dietary sources of Hg due to varying uptake with carbon-source and trophic level (Atwell et al.
113 1998; Cardona-Marek et al. 2009; Pomerleau et al. 2016; Carravieri et al. 2017). However, while
114 $\delta^{15}\text{N}$ values relate to Hg concentrations, high variability in Hg still occurs among individuals
115 despite similar $\delta^{15}\text{N}$ values (Atwell et al. 1998; Bearhop et al. 2000; DiMento et al. 2019).

116 While isotope biplots consisting of just $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ capture an incomplete portrayal of
117 ecological niche due to the inclusion of only two isotopic variables, a multidimensional niche,
118 including three or more total variables, can provide more information to assess foraging ecology,
119 albeit with greater complexity in interpretation (Swanson et al. 2015; Hobson et al. 2015;
120 O'Donovan et al. 2018). Therefore, including Hg in niche analyses along with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
121 provides a broader, risk-based method to quantify an individual and population's foraging
122 ecology and multidimensional niche dynamics (MDND; Yurkowski et al. 2020b). This analytical
123 approach, combining stable isotopes and contaminants, has been applied to multiple taxa
124 including mammals, fish, and reptiles (Guzzo et al. 2016; Jackson et al. 2016; Purwandana et al.
125 2016; Yurkowski et al. 2020b). However, a MDND approach to determine niche size has not
126 been investigated in seabirds despite them being considered sentinels of ecosystem change (Le
127 Bohec et al. 2013). Arctic seabirds demonstrate varying foraging specializations on a diversity of
128 prey items reflecting climate-induced trophic shifts and can inform spatial variation and temporal

129 changes in sea-ice and ocean dynamics that propagate up the food web, making them an ideal
130 model to research MDND (Pratte et al. 2019; Albert et al. 2020; Renedo et al. 2020).

131 An inter-colony and inter-individual approach was used to examine spatial variation in
132 the 3-dimensional niche of common eiders (*Somateria mollissima*, hereafter eiders). Eiders are a
133 long-lived, colonial-nesting marine bird with high site fidelity and widely dispersed breeding
134 populations across the Arctic. Across their range, eiders are likely exposed to diverse
135 environmental conditions that influence colony demographics at varying intensities that may
136 influence foraging decisions and, although typically at low concentrations in eiders, Hg exposure
137 (Mallory et al. 2004; 2017; Jónsson et al. 2013; Goudie et al. 2020; Noel et al. 2021). Eider prey
138 primarily includes a diversity of benthic invertebrates (e.g., urchins, mussels, and gastropods) as
139 well as pelagic macroinvertebrates to a lesser extent (e.g., amphipods; Sénéchal et al. 2011;
140 Kristjánsson et al. 2013; Waltho and Coulson 2015). The abundance and distribution of these
141 prey groups vary spatio-temporally and correlate with both predator Hg concentrations and
142 phenological shifts in primary production (Mouritsen et al. 2005; Barber et al. 2015; Fort et al.
143 2016; Savoy et al. 2017). Thus, examining $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and Hg niche dynamics of a coastal,
144 primarily benthic-foraging species provides an avenue to investigate prey shifts and Hg exposure
145 (Sénéchal et al. 2011), as well as relative differences in ice algae and phytoplankton-based food
146 webs in relation to sea-ice cover (Søreide et al. 2012; Kohlbach et al. 2016).

147 A 3-dimensional approach combining $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and total Hg (THg) measurements
148 collected from individuals at 10 eider breeding colonies located across their circumpolar range
149 was used to evaluate variation in eider foraging ecology and Hg exposure. It was anticipated that
150 colonies would show differences in 3-dimensional niche size which were influenced by spatial
151 differences in primary productivity (i.e., sea-ice algae and phytoplankton) and migratory

152 behaviour. To examine these possible drivers of colony-level variation in niche size, colony sea-
153 ice cover was examined during a period reflecting periods of isotopic integration in blood.
154 Specifically, it was predicted that colonies with higher sea-ice cover would have smaller niche
155 sizes than those with no sea ice present due to more restricted foraging habitat and likely less
156 diverse prey availability (Yurkowski et al. 2016; Pratte et al. 2019). Niche size along with colony
157 migratory behaviour was also examined with a prediction that eiders from resident colonies
158 would have smaller niche sizes compared to migratory colonies, given that residents remain at
159 the same geographical location year-round and are likely exposed to a narrower range of
160 environmental conditions (Herrera 1978; Gómez et al. 2016).

161 Next, as individual values and colony ranges of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and THg provide important
162 and unique information about foraging ecology, these values were related to colony sea-ice cover
163 during the pre-breeding period when birds foraging at high rates to obtain body condition needed
164 to breed. It was predicted that colonies with higher sea-ice cover would have lower $\delta^{13}\text{C}$, $\delta^{15}\text{N}$
165 and THg ranges due to restricted foraging locations available because of higher sea-ice
166 concentrations. It was also predicted higher individual $\delta^{13}\text{C}$ related to ice algae presence, higher
167 THg due to greater environmental Hg via melting sea-ice, and higher $\delta^{15}\text{N}$ related to higher
168 trophic level foraging through reduced benthic access. Second, these metrics were related to
169 colony migratory status with the prediction that that migratory colonies would have wider $\delta^{13}\text{C}$,
170 $\delta^{15}\text{N}$ and THg ranges due to a presumed broader distribution and use of habitat. It was also
171 predicted that higher individual THg, $\delta^{15}\text{N}$ and lower $\delta^{13}\text{C}$ at migratory colonies due to foraging
172 in areas with greater year-round phytoplankton abundance.

173 Finally, the relationship between trophic position (the vertical placement of an individual
174 in the food-web based on prey and individual $\delta^{15}\text{N}$ values) and inter-individual $\delta^{13}\text{C}$ values on

175 THg concentrations was examined with a prediction that THg would increase with higher trophic
176 position due to the biomagnification of THg, and lower $\delta^{13}\text{C}$ values because of a greater
177 consumption of resources derived from phytoplankton (Atwell et al. 1998; McMahon et al. 2006;
178 Stern et al. 2012). Examination of 3-dimensional niche size among eider colonies allowed for
179 identification of key environmental and behavioural factors that may have influenced niche
180 dynamics. Furthermore, MDND can be used to infer colony-level variability in resource use and
181 overall niche diversity which allowed for broad predictions about flexibility and resiliency to
182 environmental change (Vander Zanden et al. 2010; Paredes et al. 2012; Smith and Reeves 2012;
183 Sydeman et al. 2012). As such, it was also considered how this measurement of niche size may
184 help predict the resiliency of eider colonies to environmental change.

185 **2. Methods**

186 ***2.1. Study sites and sample collection***

187 Whole blood samples were collected from pre-incubating or incubating eiders in 2018 at 10
188 breeding colonies (total number of individuals = 240) across the Arctic and subarctic (spanning a
189 longitude from -147.776 to 35.774 and latitude from 78.918 to 43.645; Figure 1, Table 1). Eiders
190 were captured using colony- and breeding stage-specific techniques. Pre-incubating eiders were
191 sampled at East Bay Island (within in the Qaqsauqtuuq (East Bay) Migratory Bird Sanctuary,
192 Nunavut, Canada), whereas incubating eiders were sampled at the other nine locations.

193 At East Bay Island, eiders were captured using large flight nets. Birds were collected
194 from the nets and a 1-mL tarsal blood sample was obtained from each female eider (Hennin et al.
195 2015). These samples were used for isotopic analyses and were collected using a 23G thin-wall,
196 1-inch needle attached to a sodium-heparinized 1 mL syringe (Lemons et al. 2012). After
197 transferring to a heparinized 1.5 mL Eppendorf tube, samples were kept cool ($\sim 10^{\circ}\text{C}$), and

198 within 8 h, were centrifuged at 10,000 rpm for 10 min to separate red blood cells (RBCs) and
199 plasma. Plasma was then transferred by pipetting into a separate cryovial and stored along with
200 RBC samples at -20°C until isotopic analysis. During the same capture period as the first sample,
201 a second blood sample of 1-mL was obtained from the jugular vein using 23G thin wall, 1-inch
202 needles attached to heparinized 3mL syringes to be used for Hg analysis. The whole blood
203 sample was placed in acid-rinsed cryovials and kept at ~10°C, and frozen within 6 hours of
204 collection until analysis.

205 At the other nine colonies, female eiders were captured on their nest during incubation
206 using either a bownet, noose pole or dogs (John's Island location only; Milton et al. 2016). The
207 specific incubation stage could not be determined at all sites or for all individuals and was
208 excluded from analysis. For most sites, a 200-1000 µL blood sample was collected from the
209 tarsal vein using a 23G thin-wall, 1-inch needle attached to a heparinized 1 mL syringe. At the
210 Alaskan site, up to 5mL of blood was collected from the jugular vein using a non-heparinized
211 syringe, while at the Icelandic site, blood was collected from the brachial vein. After collection,
212 samples were kept cool and transferred to heparinized 1.5mL cryovials. Generally, within 8-12 h
213 samples were centrifuged for 5-10 min to separate red blood cells (RBCs) and plasma. Plasma
214 was then placed into a separate cryovial and stored along with RBC samples at a minimum of -
215 20°C until analysis.

216 ***2.2. Stable isotope analysis***

217 Stable isotopes of elements turnover at different rates based on dietary composition, metabolic
218 rate and specific metabolic activity of the tissue, as well as individual body size and temperature
219 exposure (Hobson and Clark 1992; Carleton and Martinez del Rio 2005). While specific turnover
220 times have not been established for eiders, for avian blood components generally, plasma has a

221 faster turnover rate that reflects recent diet (days), while the turnover rate of RBCs is slower and
222 reflects diet over a longer period (weeks; Hobson and Clark 1992; Hahn et al. 2012; Barquete et
223 al. 2013). Further, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ usually have similar turnover times, hence are comparable
224 (Bearhop et al. 2002). Stable isotope ratios were measured in plasma of pre-incubating eiders at
225 East Bay Island, and in RBCs of incubating eiders at the other nine colonies. Therefore, despite
226 sampling colonies at different life history stages, by using tissues with relatively shorter (plasma)
227 and longer (RBC) turnover times for analysis, we were able to compare them within a similar
228 stage including the pre-incubation period while eiders are heavily foraging, either at resident
229 sites or in the last period of migration to build up stored resources for their incubation fast.

230 Samples were freeze-dried for approximately 72 h after collection. Samples were then
231 ground into a fine, homogenized powder using a metal spatula cleaned with acetone. Plasma
232 samples were then lipid extracted using a 2:1 chloroform:methanol solution (Søreide et al. 2006).
233 Specifically, 2:1 chloroform:methanol solution (1.9mL) was added to 100 μL of each plasma
234 sample, which were then placed in a water bath at 30°C for 24 h. Samples were then centrifuged
235 at 15,000 rpm for 10 min to separate the lipid solution from the plasma pellet. A p1000 pipette
236 was used to remove the lipid solution, leaving the plasma pellet behind. The pellet was washed
237 again with an additional 1.9 mL of the chloroform:methanol solution and centrifuged for a final
238 10 min at 15,000 rpm. The remaining lipid solution was removed, leaving only a plasma pellet.
239 Samples were left open in the fume hood for 24 h to allow for any remaining
240 chloroform:methanol solution to evaporate. Since RBCs have minimal lipids present, they did
241 not undergo lipid extraction (Hobson and Clark 1992).

242 Plasma and RBC samples were weighed into individual tin-capsules using a 4-digit
243 balance to obtain 0.3-0.5 mg of sample. Plasma samples were prepared at the University of

244 Windsor, and plasma stable isotopes were analysed at the Environment and Climate Change
245 Canada Stable Isotope Laboratory in Saskatoon, Saskatchewan, using continuous-flow isotope-
246 ratio mass spectrometry (CFIRMS; Harris et al. 1997). Samples were weighed into pre-
247 combusted tin capsules. Encapsulated plasma was combusted at 1030°C in a Carlo Erba NA1500
248 or Eurovector 3000 elemental analyser. The resulting N₂ and CO₂ were separated
249 chromatographically and introduced to an Elementar Isoprime or a Nu Instruments Horizon
250 isotope ratio mass spectrometer. Two reference materials were used to normalize the results to
251 VPDB and AIR: BWBIII keratin ($\delta^{13}\text{C} = -20.18$, $\delta^{15}\text{N} = +14.31$ ‰, respectively) and PRCgel
252 ($\delta^{13}\text{C} = -13.64$, $\delta^{15}\text{N} = +5.07$ ‰, respectively). Within run (n = 5) precisions as determined from
253 both reference and sample duplicate analyses were ± 0.1 ‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

254 The RBC samples were prepared for isotope analysis at La Rochelle University, France,
255 and were analysed at the LIENS Institute (La Rochelle, France) as detailed in Fort et al. (2014).
256 Plasma and RBC samples were combusted using a Eurovector 3000 (Milan, Italy) elemental
257 analyser which results in production of N₂ and CO₂ gases. These were separated by gas
258 chromatography and introduced into a NU Horizon (Nu Instruments, Wrexham, UK) triple-
259 collector isotope-ratio mass-spectrometer via an open split. Ratios of carbon (¹³C/¹²C) and
260 nitrogen (¹⁵N/¹⁴N) were expressed in typical delta notation (δ) as per mil (‰) deviation from the
261 primary standards (Vienna Pee Dee Belemnite (VDPB) and atmospheric nitrogen (AIR),
262 respectively). Replicate measurements (n = 20) per run of laboratory standards (USGS-61 and
263 USGS-62) indicated that the measurement accuracy was <0.2‰ for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values.

264 Baseline stable isotopes of Arctic marine food webs vary spatiotemporally, thus
265 measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of biota from different regions can only be compared if corrected
266 for such baseline variance (Bowen 2010; Hobson et al. 2012; de la Vega et al. 2019). Based on

267 previously published $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of known eider bivalve prey at the different breeding
268 sites, stable isotope data was corrected by subtracting baseline bivalve isotope values from the
269 eider tissue values to obtain “corrected” isotopic values (Table 2). However, THg values were
270 not corrected to baseline values. Additionally, we were unable to account for the potential impact
271 of incubation stage on $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ or Hg values. Both Hg and $\delta^{15}\text{N}$ values can be elevated in
272 blood due to mobilization of internal nutrient stores during the incubation fast (Hobson et al.
273 1993; Wayland et al. 2005). However, use of RBCs instead of plasma at all but one site (East
274 Bay Island) to determine incubating female $\delta^{15}\text{N}$ values minimized this effect (Cherel et al.
275 2005). Furthermore, sampling of eiders during incubation, when Hg is known to increase
276 (Wayland et al. 2005), lessens, but does not mitigate the potential bias of East Bay Island pre-
277 breeding eiders having elevated Hg relative to the other colonies, as the pre-breeding eiders have
278 not yet depurated Hg to their eggs during laying (Akearok et al. 2010). Hence, caution should be
279 taken when comparing Hg values between East Bay Island and the other nine colonies.

280 Diet-tissue isotopic discrimination factors allow modeling of isotopic trophic positions or
281 nutrient source tracing (e.g., Wolf et al. 2009; Federer et al. 2010; Bond and Diamond 2011).
282 Such factors have not been established for common eiders, so those reported by Federer et al.
283 (2010) for spectacled eider (*Somateria fischeri*) (plasma: +4.9‰; RBC: +4.0‰) were used.
284 Trophic position was calculated using baseline $\delta^{15}\text{N}$ bivalve values for the individual’s colony
285 ($\delta^{15}\text{N}_{\text{base}}$), discrimination factors from the respective tissue of spectacled eiders ($\delta^{15}\text{N}_{\text{TDF}}$; Federer
286 et al. 2010), trophic position (TP) of baseline prey values (TP_{base} ; value of 2 consistent with eider
287 prey), and the non-colony corrected $\delta^{15}\text{N}$ values for that individual eider ($\delta^{15}\text{N}_{\text{eider}}$; Hobson and
288 Welch 1992; Vander Zanden et al. 1997; Vander Zanden and Rasmussen 1999).

289
$$\text{TP} = ((\delta^{15}\text{N}_{\text{eider}} - \delta^{15}\text{N}_{\text{base}}) / \delta^{15}\text{N}_{\text{TDF}}) + \text{TP}_{\text{base}}$$

290 **2.3. THg analysis**

291 Whole blood collected at East Bay Island was sent to the Research and Productivity Council
292 (RPC) in New Brunswick, Canada for THg analysis. Each sample was prepared by microwave-
293 assisted digestion in nitric acid (SOP 4.M26). Mercury was then analysed by cold vapour atomic
294 absorption spectroscopy (AAS; SOP 4.M52 & SOP 4.M53) to obtain THg concentrations.
295 Quality assurance/control procedures included analysis of four reagent blanks as well as four
296 randomly selected duplicate samples. Previous quality assurance/control procedures using CRM
297 (certified reference materials) were conducted on common eider samples from East Bay in
298 previous sampling years (Provencher et al. 2016, 2017). Mercury concentrations were converted
299 from wet weight to dry weight for comparison with the other colonies following known
300 equations and moisture values for avian blood at 79% (Eagles-Smith et al. 2008).

301 For the remaining nine colonies, THg analyses were conducted at LIENSs Institute using
302 RBCs separated from plasma collected from incubating females. These eiders were captured
303 while incubating (Hanssen et al. 2002; Bottitta et al. 2003; Sénéchal et al. 2011), thus by
304 collecting and analysing RBCs alone, the timeframe which the RBCs represent (weeks) aligns
305 with the timeframe represented in the East Bay Island eiders (days) since whole blood has a
306 turnover rate approximately intermediate of plasma and RBC (Cherel et al. 2005). Therefore, this
307 provides justification for including the colony in our analysis despite potential differences in
308 physiology due to their reproductive stages. Freeze-dried blood was analysed using an Advanced
309 Hg Analyser spectrophotometer (Altec AMA 254). A quality control program included running
310 blanks prior to the analysis at the limit of detection of 0.05 ng of Hg. Certified reference
311 materials (DOLT-2 and TORT-2) were analysed every 15 samples (certified Hg concentrations:
312 $0.44 \pm 0.18 \mu\text{g/g dw}$ for DOLT-2 and $0.27 \pm 0.06 \mu\text{g/g dw}$ for TORT-2, measured

313 concentrations: $0.44 \pm 0.01 \mu\text{g/g dw}$ for DOLT-2 and $0.26 \pm 0.01 \mu\text{g/g dw}$ for TORT-2). Samples
314 were analyzed for THg since Hg exists as primarily MeHg in avian blood (near 1:1 ratio; Wiener
315 et al. 2003; Rimmer et al. 2005).

316 **2.4. Statistical analysis**

317 Colony 3-dimensional niche size (using THg, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and ranges along the THg, $\delta^{13}\text{C}$ and
318 $\delta^{15}\text{N}$ axes were determined for 10 eider colonies using the R package nicheROVER v1.0
319 (Swanson et al. 2015) in R version 3.6.2 (R Development Core Team). NicheROVER uses
320 Bayesian statistical methods to calculate a multidimensional niche region in multivariate space
321 that represents the spatial breadth and placement of a group's (i.e., colony's) niche in relation to
322 other groups, and infers the niche size of each group based on that group's individual values for
323 each dimension (Swanson et al. 2015). Since the variables are in different units ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$:
324 ‰ vs. THg: $\mu\text{g/g dw}$), all values were scaled and centred by subtracting the mean for each
325 variable and dividing it by the standard deviation, thereby standardizing all data. To determine if
326 there were any correlations among variables prior to analysis, independence was tested by
327 calculating Spearman's correlation coefficient between THg and colony-corrected $\delta^{15}\text{N}$ which
328 showed a significant but relatively weak correlation ($R=0.43$, $p<0.001$). Thus, THg and $\delta^{15}\text{N}$,
329 while related, do possess independent variation that allowed for inclusion of both metrics in our
330 analysis to account for spatial variation in THg concentrations. A 95% probability niche region
331 in multivariate space was calculated at 10,000 iterations using diffuse priors (Swanson et al.
332 2015; Yurkowski et al. 2020b). Additional script at 10,000 iterations was conducted to obtain
333 $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and THg ranges (difference between the highest and lowest values; Swanson et al.
334 2015; Yurkowski et al. 2020b). Three-dimensional models of the niche ranges were visualized

335 using the scatter3D function in the car package v.3.0-9 (Fox and Weisberg 2019) and the rgl
336 package v.0.100.54 (Adler and Murdoch 2017; see Supplemental Materials).

337 Primary migratory status of each colony, not including the potential for individual
338 variation, was determined by consulting previous studies (Schamel 1997; Bønløkke et al. 2006;
339 Hanssen et al. 2016; Steenweg et al. 2017; Mallory et al. 2020) and through spatial tracking data
340 collected by the SEATRACK program (<https://seapop.no/en/seatrack/>). Moreover, the proportion
341 of sea-ice cover surrounding each colony within a timeframe reflecting turnover rates of isotope
342 sampling was determined (plasma within a week of sampling, RBC within a month of sampling;
343 Hobson and Clark 1992; Barquete et al. 2013). Sea-ice cover was analyzed via a satellite image
344 of a 100 km area around each colony on a cloud-less day from NASA Worldview dataset
345 (EOSDIS, <https://worldview.earthdata.nasa.gov>). Land pixels were removed from the image
346 manually and the remaining pixels were categorized into two groups (open water or sea ice)
347 using a K-means clustering procedure via RGB values of the pixels
348 (<http://mkweb.bcgsc.ca/color-summarizer/>). The resulting proportion of pixels was used as a
349 proxy for the proportion of sea ice around the colony during the time of isotopic turnover for
350 each colony (Cusset et al. 2019).

351 A preliminary 2-tailed *t*-test was used to determine independence between colony sea-ice
352 cover and migratory behaviour, which were not significantly correlated ($t_5=2.11$, $p=0.09$).
353 Therefore, to determine sources of niche variation with sea ice cover, a general linear model
354 (GLM) was used to examine how log-transformed niche size varied by colony sea-ice cover.
355 Next, six GLMs were used to analyze the relationship between sea ice cover and colony $\delta^{15}\text{N}$,
356 log-transformed $\delta^{13}\text{C}$ and THg ranges, as well as median individual colony-corrected $\delta^{15}\text{N}$, and
357 log-transformed $\delta^{13}\text{C}$ and THg values for each of the 10 colonies. Median values were used to

358 avoid data skewed by high/low individual values within a mean and better represent general
359 colony values.

360 To examine variation in niche dynamics between migratory and resident colonies, a 2-
361 tailed *t*-test was conducted to analyze how log-transformed colony niche size varied with
362 migratory status (migratory or resident being the two groups). Following this, six 2-tailed *t*-tests
363 were used to analyze whether migratory status of a colony resulted in different colony $\delta^{15}\text{N}$, and
364 log-transformed $\delta^{13}\text{C}$ and THg ranges, as well as individual colony-corrected eider $\delta^{13}\text{C}$, $\delta^{15}\text{N}$
365 and log-transformed THg values.

366 Finally, a general linear mixed model (GLMM) was used to examine the relationship
367 between colony-corrected isotopes indicating carbon source ($\delta^{13}\text{C}$), trophic position of each
368 individual, and log-transformed THg. The model consisted of THg as the dependent variable,
369 with $\delta^{13}\text{C}$ and trophic position as independent variables, as well as colony as a random variable.
370 All models conducted throughout the study met statistical assumptions, and all log-
371 transformations were conducted using natural log.

372 **3. Results**

373 ***3.1. Niche size and underlying sources of variation***

374 Three-dimensional niche size was highly variable among colonies, ranging from 1.4 (Grindøya)
375 to 21.7 (Iceland), with an average niche size among all colonies of 9.2 ± 7.8 (Figure 2, see
376 Supplemental Materials). However, niche size was not correlated with colony sea ice cover ($t_8=-$
377 0.92 , $p=0.54$) or migratory status ($t_4=-0.61$, $p=0.57$). The Christiansø colony in Denmark had the
378 lowest colony-corrected $\delta^{13}\text{C}$ values, suggesting higher phytoplankton-derived carbon in their
379 diet, while the Alaskan colony had the highest colony-corrected $\delta^{13}\text{C}$ suggesting eiders were
380 feeding on prey reflecting more ice algae- or inshore-derived carbon (see Supplemental

381 Materials). The Alaskan colony also had the highest colony-corrected $\delta^{15}\text{N}$ values, with the
382 Faroe Islands having the lowest values, suggesting that Faroese eiders forage at lower trophic
383 levels, whereas the Alaskan eiders forage at higher trophic levels.

384 ***3.2. Relationship between colony migratory behaviour and sea-ice cover with isotopes and***
385 ***THg***

386 Inter-colony variation in sea-ice presence was positively correlated with median eider THg
387 concentrations, as well as $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (Table 3). However, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, as well as THg
388 ranges did not vary with colony sea-ice cover (Table 3). Migratory colonies had higher
389 individual $\delta^{15}\text{N}$ and THg, as well as lower individual $\delta^{13}\text{C}$ compared to individuals captured at
390 resident colonies (Table 3). However, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and THg range did not vary between the
391 migratory and resident colonies (Table 3).

392 ***3.3. Relationship between isotopic niche and THg concentrations***

393 Both colony-corrected $\delta^{13}\text{C}$ and trophic position predicted THg concentration within individuals.
394 Specifically, individuals with a lower $\delta^{13}\text{C}$ value (phytoplankton-based foraging) had higher THg
395 values (Table 3, Figure 3). Additionally, THg significantly increased with trophic position,
396 where individuals with higher trophic positions had greater THg values (Table 3, Figure 3).

397 **4. Discussion**

398 Using data collected from ten eider colonies located throughout their circumpolar range,
399 including both Arctic and subarctic sites, 3-dimensional niche was quantified size using $\delta^{15}\text{N}$,
400 $\delta^{13}\text{C}$ and THg to determine colony niche size and ranges. Determination of 3-dimensional niche
401 size allowed for broad comparison of a snapshot of diet breadth at multiple eider colonies in
402 relation to environmental and behavioural differences, as well as inference of their potential for

403 flexibility in response to environmental change. The benefits of using multiple chemical tracers
404 are demonstrated when assessing the effects of spatial variation and environmental gradients on
405 the foraging ecology of highly mobile consumers.

406 ***4.1. Colony foraging flexibility and resiliency predictions***

407 Generally, colonies that utilize broader, more generalist diets are expected to have larger
408 foraging niches, thus are expected to be inherently less vulnerable to change since they have
409 greater flexibility in their prey source as they forage on a wide variety of organisms and habitats
410 (Jakubas et al. 2017; Both et al. 2010). Colonies with restricted, specialist diets are expected to
411 have smaller foraging niches, influenced by both prey availability and foraging distance, and are
412 generally viewed as more vulnerable to environmental change (Bolnick et al. 2003; Araújo et al.
413 2011; Pratte et al. 2019). While the interpretation of MDND is not necessarily straightforward,
414 due to complex relationships and multiple factors influencing each dimension, MDND may be
415 useful in predicting the resiliency of common eider colonies to ongoing climate change across
416 their range, although numerous other factors should also be considered including multiple
417 biogeochemical metrics, colony recruitment and individual fitness (Paredes et al. 2012; Smith
418 and Reeves 2012; Sydeman et al. 2012). Thus, this analysis provides a snapshot of niche
419 characteristics at a singular time frame that may assist with colony-wide resiliency predictions in
420 combination with future research on changing niche dynamics at these colonies.

421 When grouped for similarity, niche size generated the following general pattern in this
422 study: Iceland, East Bay Island and Faroe Islands > Christiansø and John's Island >
423 Kongsfjorden, Alaska and Russia > Tern Island and Grindøya (Figure 1). Using this 3-
424 dimensional view of niche size, it was predicted that colonies with wider (i.e., more generalist)
425 3-dimensional niches such as those in Iceland and Faroe Islands, or colonies comprised of

426 migrants from multiple locations such as East Bay will show greater resiliency to shifts in food
427 web dynamics compared to colonies with a smaller (i.e., more restricted, specialist) niche similar
428 to Tern Island and Grindøya. Smaller niches are predicted to be at a disadvantage in a changing
429 climate as these alterations may change or eliminate food sources, leaving a colony or species
430 more vulnerable if they do not have the flexibility to adapt and shift their diet with this changing
431 prey base (Both et al. 2010; Le Bohec et al. 2013; Ceia and Ramos 2015). However, climate
432 change may present an opportunity for Arctic colonies with smaller niches to expand their prey
433 sources with advancing phenology of spring phytoplankton blooms and more open water
434 sources. For those with broader niches at southern latitudes, that niche size may be critical along
435 with further changes in the distribution and availability of key prey (Staudinger et al. 2019).
436 Nevertheless, more research that integrates measures of breeding success and colony
437 demographics is necessary to test these resiliency hypotheses over long temporal scales to
438 identify seasonal and annual variation in inter- and intra- colony foraging ecology.

439 *4.2. Variation in niche size, niche metrics and THg to colony sea-ice cover*

440 Colony niche size was not correlated with sea-ice cover, possibly attributable to several factors.
441 First, despite the presence of sea ice likely restricting foraging locations, eiders may still be able
442 to access a diversity of resources, including the potential for prey sources such as ice-associated
443 amphipods as niche size was similar to locations that have more accessible, ice-free areas
444 (Karnovsky et al. 2008). Second, northern colonies may support a variety of individuals that
445 utilize both generalist and specialist strategies, thus adding to the flexibility and diversity of the
446 colony in the face of environmental change (Woo et al. 2008; Ceia and Ramos 2015; Pratte et al.
447 2019). Notably, the relative proportion of generalist and specialist individuals in populations

448 dramatically affects dietary niche size with generalist-based populations having wider niches
449 (Newsome et al. 2007).

450 Eider colonies with greater sea-ice cover had higher $\delta^{13}\text{C}$ values, which is not consistent
451 with the expected gradient based on ocean temperature (Sackett et al. 1965; Goericke and Fry
452 1994; McMahon et al. 2013). However, this pattern can be most likely explained by eiders
453 foraging on resources derived from ice algae associated with higher ice cover versus more
454 phytoplankton-derived resources in areas with lower sea-ice presence (Hobson et al. 1995;
455 Tamelander et al. 2006; McMahon et al. 2006). As well, macroalgal carbon has a higher $\delta^{13}\text{C}$
456 value than phytoplankton, and therefore could be a contributing carbon source to these spatial
457 differences. Nonetheless, spatial differences in carbon source use amongst eider colonies existed,
458 where some colonies use more phytoplankton-derived carbon than others. Furthermore, results
459 showed that in general, eider colonies with greater sea ice cover also had higher median
460 individual THg and $\delta^{15}\text{N}$, suggesting that sea-ice presence resulted in eiders foraging at higher
461 trophic levels, thus contributed to higher overall THg exposure. Potential reasons for higher
462 trophic-level foraging include eiders feeding on ice-associated sources of prey prior to laying,
463 such as amphipods, due to restricted access to benthic prey with sea ice present (Karnovsky et al.
464 2008). Amphipods seasonally forage on ice algae and this would decouple them from the pelagic
465 food web and result in higher $\delta^{13}\text{C}$ values (Werner 1997; Brown et al. 2017). Furthermore,
466 waters with sea ice present are supersaturated with dissolved THg, thus further contributing to
467 the elevation of THg in food webs (DiMento et al. 2019). Individual variation in foraging
468 behaviour is known to have a role in Hg accumulation (Anderson et al. 2009; Braune et al. 2014;
469 Le Croizier et al. 2019) and this exists within the colonies studied as demonstrated by the colony
470 ranges.

471 **4.3. Role of migration in shaping MDND and THg exposure**

472 It was predicted that migratory populations (see Table 1, Figure 1) would have larger niches due
473 to exposure to a variety of environmental conditions and prey types at both migratory and
474 breeding grounds where resources are stored to mobilize during their incubation fast (Herrera
475 1978; Gómez et al. 2016). In the present study, there was no pattern between with migratory
476 behaviour and niche size. However, two of the largest niche sizes found at two resident colonies
477 (Iceland and Faroe Islands) may stem from colony-wide expansion in dietary choice due to
478 increased prey availability. This has been reported in Iceland where eiders within the colony
479 selected a wide array of both benthic and pelagic prey (Kristjánsson et al. 2013). Waters around
480 Iceland are a mix of Arctic (East-Greenland Current), as well as Atlantic origins (North Atlantic
481 Current), and this, together with greater lack of sea ice, would provide a diverse range of prey
482 options to pre-breeding eiders (Vincent 2010; Kristjánsson et al. 2013; Casanova- Masjoan et al.
483 2020). The East Bay Island colony, consisting of migrants from Greenland and Newfoundland,
484 had the second largest niche size potentially in part due to a mixing of individuals from both
485 overwintering sites (Steenweg et al. 2017). Additionally, individual variation in migration
486 distance and strategy within a colony, although not included in the present study, may lead to
487 broader colony niche ranges (Mallory et al. 2020).

488 Colonies supporting migratory eiders had higher THg concentrations and foraged at
489 higher trophic levels compared to colonies supporting residents, suggesting that colonies of
490 migratory individuals had access to higher trophic-level prey, or relied on these prey to store
491 resources necessary for incubation. Colonies with resident eiders had higher individual $\delta^{13}\text{C}$
492 levels indicating diets with greater foraging based on ice algae, potentially due to residing at their
493 Arctic breeding sites year-round while migratory colonies move to more suitable areas with

494 presumably lower sea ice. Combined with the results on colony sea ice cover, these dynamics
495 show that changes in environmental conditions and variability may have different effects on
496 migratory and resident seabird colonies dependent on future colony flexibility, thus should be
497 factored into future analyses especially regarding climate change effects within Arctic
498 ecosystems.

499 ***4.4. Relationship between trophic position, foraging location and THg concentrations***

500 With increasing industrial activity and contaminant deposition due to long-distance transport in
501 northern latitudes, as well as the release of stored Hg from melting cryosphere and increased
502 erosion of terrestrial sources, Arctic-inhabiting species are potentially becoming more at risk for
503 contaminants exposure and a suite of possible negative neurological, physiological and
504 reproductive impacts (Dietz et al. 2013; Scheuhammer et al. 2015; Soerensen et al. 2016, Cossa
505 et al. 2018). This is especially a potential population stability concern for harvested species, such
506 as common eider, which are an important, harvested species for many Indigenous communities
507 in the North (Nakashima and Murray 1988; Priest and Usher 2004). Concentrations of THg for
508 the eider colonies in this study are comparable to those observed in previous eider research
509 (Provencher et al. 2016; Albert et al. 2019; Ma et al. 2020; Dietz et al. 2021). The mean
510 concentrations of THg in the Alaska, Christiansø and East Bay colonies were above 0.95 µg/g
511 dw, suggesting that three of the 10 colonies studied, and 40% of sampled eiders, were above
512 general environmental background concentrations (Eagles-Smith et al. 2008; Ackerman et al.
513 2016). Nonetheless, concentrations were still sufficiently low to assign them a general “low risk”
514 status regarding concerns for health, physiology, behaviour and reproductive effects (Ackerman
515 et al. 2016; Dietz et al. 2019; 2021). The individual eider with the highest Hg concentration was
516 from the Iceland colony (2.55 µg/g dw compared to the colony mean of 0.95 µg/g dw). Iceland

517 had less sea ice than other regions, such as Alaska that had the highest sea ice cover and colony
518 THg average (1.23 $\mu\text{g/g dw}$).

519 With a rapidly declining sea-ice cover, a rise in phytoplankton production and resulting
520 eider consumption of prey derived from phytoplankton carbon sources could be related to higher,
521 individual THg concentrations (Stern et al. 2012). Combined with the results in section 4.2
522 showing higher median THg concentrations at colonies with greater sea-ice cover, these results
523 demonstrate that within colonies, individuals with greater phytoplankton-based consumption had
524 higher THg concentrations. The relationship between individual $\delta^{13}\text{C}$ and THg, combined with
525 effects of trophic position (determined using $\delta^{15}\text{N}$) on THg may potentially have future effects
526 on seabird health, behaviour and reproduction in those with at-risk Hg exposure. However, it is
527 likely that any possible effects would not be consistent across the entire range of a species,
528 especially given the regional difference in which climate change is altering the Arctic (Muir et al.
529 1999; Mallory and Braune 2012; Swart et al. 2015). Nevertheless, variation among colonies was
530 detected, suggesting regional differences in the relationship between $\delta^{13}\text{C}$, trophic position and
531 THg; for instance, the Christiansø and Kongsfjorden colonies showed opposite relationships
532 between THg and $\delta^{13}\text{C}$ (Figure 3). Thus, more in-depth analyses of the environmental factors at
533 each site would allow for site-specific investigation into the relationships between foraging
534 behaviour and THg uptake. Additionally, further knowledge of baseline variation (THg, $\delta^{15}\text{N}$,
535 $\delta^{13}\text{C}$) in colony-specific prey at a varying spatio-temporal inter-annual scale, parallel with eider
536 sampling, would aid future interpretation of eider niche size, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and sources of
537 individual and colony THg. Additionally, the contribution of terrestrial carbon sources and
538 agricultural runoff to marine areas around some of these colonies may also contribute to
539 variation in individual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and affect exposure to THg and its accumulation

540 (Dunton et al. 2006; Laursen et al. 2018; Renedo et al. 2020). Overall, the relationship between
541 environmental conditions and THg concentrations presents a complex system and paired with the
542 rapid changes in ecosystem dynamics currently being observed (i.e., sea ice abundance),
543 underscores the necessity of future, consistent annual monitoring, especially in key ecosystem
544 indicators like marine birds.

545 **5. Conclusion**

546 Inter-colony, 3-dimensional niche size, isotopic and THg ranges, and the relationships between
547 $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and THg within individuals was examined. Our results suggest that common eider
548 colonies across the Arctic and subarctic have a wide degree of diet variation, potentially
549 influenced by environmental changes including spatio-temporal differences in primary
550 productivity. It was found that consideration of colony-level variation in life histories (migratory
551 vs resident) was important for assessing the level of risk to which a colony may be exposed.
552 Further, inter-annual MDND analyses using simultaneous local $\delta^{13}\text{C}$ marine isoscapes to correct
553 for eider $\delta^{13}\text{C}$, in addition to corrections for baseline THg, would provide greater insight into the
554 temporal variation in niche size that exists at both an inter- and intra-colony scale. Taken
555 together, exploring MDND is an increasingly valuable tool to provide insight into how diet
556 breadth differs across a species' range, especially when combined with temporal and spatial
557 variation in environmental conditions and key components to variation in life history such as
558 migration.

559 **Acknowledgments**

560 We thank the field crews and regional volunteers at all locations who assisted in sample
561 collection and logistics. As well, thank you to the lab technicians at Research and Productivity
562 Council (RPC) in New Brunswick, Canada and Littoral Environment et Sociétés (LIENSs, La

563 Rochelle) for sample analysis. We are also grateful to the plateformes ‘Analyses Elémentaires’
564 and ‘Spectrométrie Isotopique’ (La Rochelle University - LIENSs) for their assistance with
565 laboratory work. We also thank Environment and Climate Change Canada (ECCC), the Natural
566 Sciences and Engineering Research Council of Canada, Canada Research Chairs Program, the
567 Nunavut Wildlife Management Board, Northern Scientific Training Program, Polar Continental
568 Shelf Project, Polar Knowledge Canada, Baffinland Iron Mine, the Canadian Network of Centres
569 of Excellence (ArcticNet), Mitacs Globalink Research, The Danish Environmental Protection
570 Agency, Danish Hunters' Association, Hunters' Nature Fund, the Government of Ontario and the
571 University of Windsor for logistical support, research and/or personal funding. This study is also
572 a contribution to the ARCTOX initiative (arctox.cnrs.fr) and the ARCTIC-STRESSORS project
573 (ANR-20-CE34-0006-01). Animal care approval for this project was granted through the
574 University of Windsor Committee for Animal Care (AUPP #11-06; Reproductive Strategies of
575 Arctic-Breeding Common Eiders), and ECCC Animal Care (EC-PN-15-026).
576

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1101

1102 **Tables and Figures**

1103 **Table 1.** Locations of common eider colonies included in this study, sample size (number of
 1104 individual birds from each colony included in the study), month samples were obtained,
 1105 coordinates (latitude and longitude), whether a colony is known to be predominately migratory
 1106 or resident, and the proportion of sea ice cover in a 100km area around the colony during the
 1107 appropriate timeframe reflecting isotope data.

Location	n	Sampling month	Latitude	Longitude	Migratory behaviour	Sea ice cover (%)
Kaktovik, Alaska	33	July	70.340	-147.776	Migratory	43.45
Breiðafjörður, Iceland	23	June	65.078	-22.736	Resident	3.10
Christiansø, Denmark	25	May	55.330	15.188	Migratory	0
Grindøya, Norway	17	June	69.633	18.844	Resident	0
John's Island, Canada	19	July	43.645	-66.041	Migratory	0
Kirkjubøhólmur, Faroe Islands	16	July	61.950	-6.799	Resident	0
Kongsfjorden, Norway	16	June	78.918	11.910	Migratory	0
East Bay Island, Canada	43	June	64.023	-81.790	Migratory	34.34
Onega Bay, Russia	24	June	65.048	35.774	Resident	0
Tern Island, Canada	24	June	69.547	-80.812	Migratory	36.47

1108

1109 Table 2. Isotopic signatures ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$ in ‰) of typical common eider bivalve prey as
 1110 determined by the most spatio-temporally appropriate literature values available at the time of
 1111 analysis. Prey stable isotope data was used to correct common eider isotope data to allow for
 1112 inter-colony comparison.

Location	Prey Species	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Reference
Beaufort Sea, Alaska	<i>Cyrtodaria kurriana</i>	-25.20	7.90	Dunton et al. 2012
Breiðafjörður, Iceland	<i>Mytilus edulis</i>	-19.60	7.40	Sarà et al. 2007
Christiansø, Denmark	<i>Limecola balthica</i>	-20.40	7.20	Ek et al. 2018
Grindøya, Norway	<i>Hiatella arctica</i>	-19.32	7.26	Fredriksen 2003
John's Island, Canada	<i>Mytilus edulis</i>	-19.99	7.17	English et al. 2015
Kirkjubøhólmur, Faroe Islands	<i>Mytilus edulis</i>	-19.20	8.41	Bustamante, unpub.
Kongsfjorden, Norway	<i>Hiatella arctica</i>	-20.30	6.90	Vieweg et al. 2012
East Bay Island, Canada	<i>Hiatella arctica</i>	-18.22	8.64	Sénéchal et al. 2011
Onega Bay, Russia	<i>Styela rustica</i>	-21.60	6.49	Yakovis et al. 2012
Tern Island, Canada	<i>Hiatella arctica</i>	-18.22	8.64	Sénéchal et al. 2011

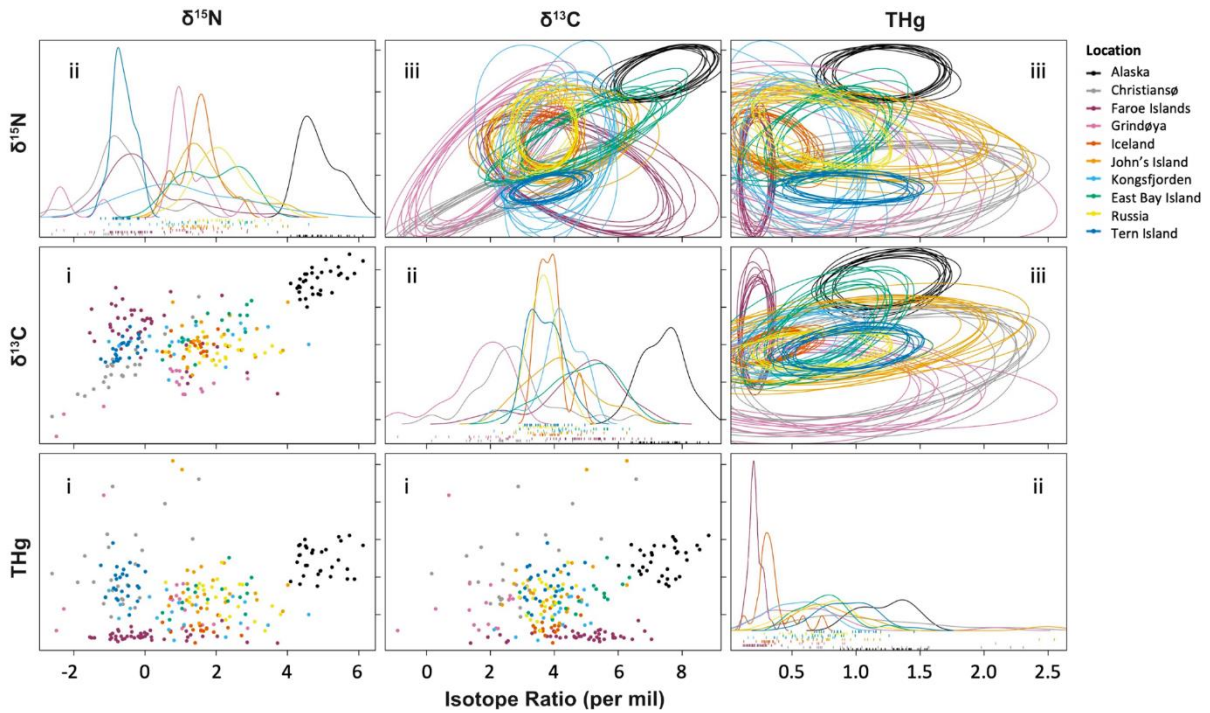
1113

1114 **Table 3.** Results of three sets of statistical analyses: a) seven 2-tailed t-tests relating migratory
 1115 status to colony niche size, isotope and THg ranges, as well as individual colony-corrected
 1116 isotope and THg values; b) seven GLM results relating colony sea ice cover to colony niche size,
 1117 isotope and THg ranges as well as median colony isotope and THg values; c) GLMM results
 1118 relating common eider trophic position, calculated using baseline and individual $\delta^{15}\text{N}$ and
 1119 colony-corrected $\delta^{13}\text{C}$ to individual THg values. All log-transformed values were determined
 1120 using the natural log and used to meet model assumptions.

Variable	Estimate (β)	SE	df	t	p
a) <u>2-tailed t-test – Migratory Status</u>					
log(Niche size)			4	-0.609	0.573
log($\delta^{13}\text{C}$ Range)			8	-0.339	0.743
$\delta^{15}\text{N}$ Range			7	0.996	0.353
log(THg Range)			5	-0.600	0.576
Individual $\delta^{13}\text{C}$			238	2.218	0.028
Individual $\delta^{15}\text{N}$			220	-6.858	<0.001
log(Individual THg)			124	-6.329	<0.001
b) <u>GLM – Sea Ice Cover</u>					
log(Niche size)	-0.0125	0.019	8	-0.639	0.541
log($\delta^{13}\text{C}$ Range)	-0.013	0.008	8	-1.635	0.141
$\delta^{15}\text{N}$ Range	-0.002	0.014	8	-0.106	0.919
log(THg Range)	-0.004	0.009	8	-0.459	0.658
log(Median $\delta^{13}\text{C}$)	0.028	0.010	8	2.936	0.032
Median $\delta^{15}\text{N}$	0.052	0.022	8	2.332	0.048
log(Median THg)	0.014	0.006	8	2.525	0.036
c) <u>GLMM – Individual log(THg)</u>					
Intercept	-1.923	0.304	142.233	-6.330	<0.0001
Trophic position	0.563	0.096	234.614	5.862	<0.001
$\delta^{13}\text{C}$	-0.063	0.022	232.943	-2.813	0.005

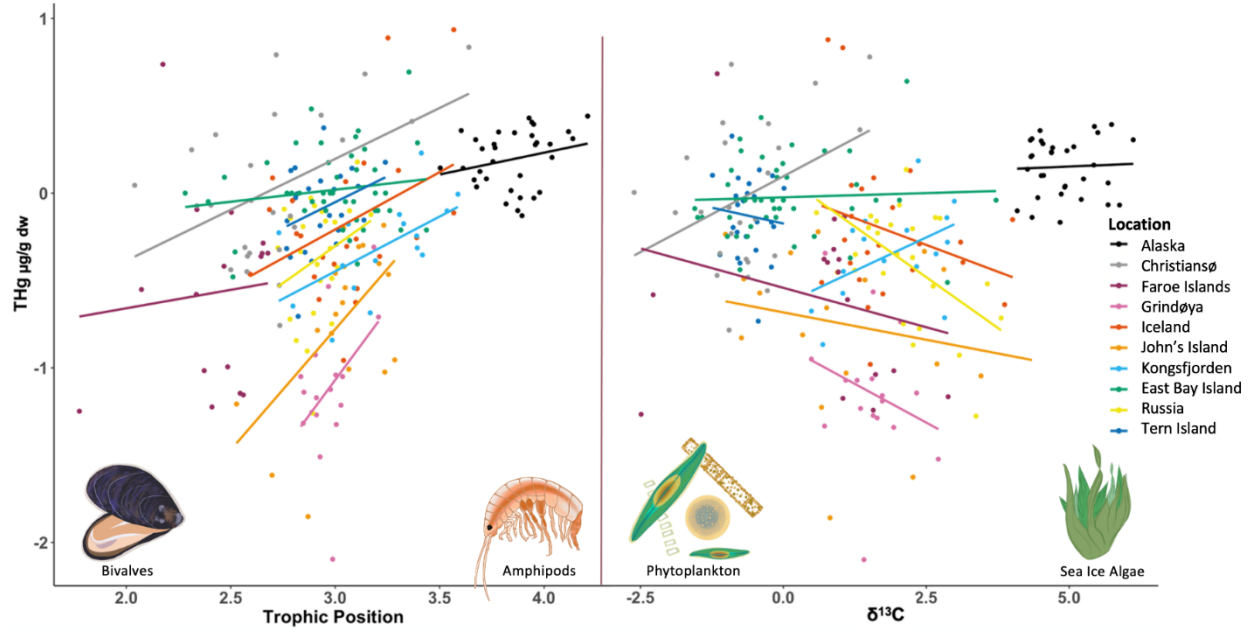


1121
 1122 **Figure 1.** Map of the circumpolar-Arctic, and locations of the 10 common eider colonies used in
 1123 this study (stars) designated by whether a colony is primarily resident (circles) or migratory
 1124 (stars). Shape colour represents four groupings of similar median 3-dimensional niche size (95%
 1125 Bayesian credible intervals). By ascending niche size, colours represent: 1 (smallest; red), 2
 1126 (white), 3 (grey), and 4 (largest; black). Dashed line indicates the Arctic Circle, and the solid line
 1127 indicates the Arctic boundary according to the Arctic Monitoring and Assessment Programme
 1128 (AMAP; map provided by globalcitymap.com).



1129

1130 **Figure 2.** 2-dimensional projections of ten 3-dimensional niche regions produced using the R
 1131 package nicheROVER v1.0 (Swanson et al. 2015). Corrected stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in
 1132 ‰) and THg data (in $\mu\text{g/g dw}$) were used from individuals at 10 pan-Arctic or subarctic common
 1133 eider colonies. Sections show, i) The raw stable isotope and THg data in pairs, ii) density
 1134 estimates of $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and THg individually, and iii) pairings of $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and THg showing 2-
 1135 dimensional projections of 95% probabilistic niche regions based on 3-dimensional data.



1136

1137 **Figure 3.** Relationship between THg (natural log-transformed) with trophic position (calculated

1138 based on $\delta^{15}\text{N}$; see Methods) and colony-corrected $\delta^{13}\text{C}$ (in ‰) for individuals at 10 pan-Arctic

1139 or subarctic common eider colonies, identified by colour.

1140

1141 **Supplemental Materials**

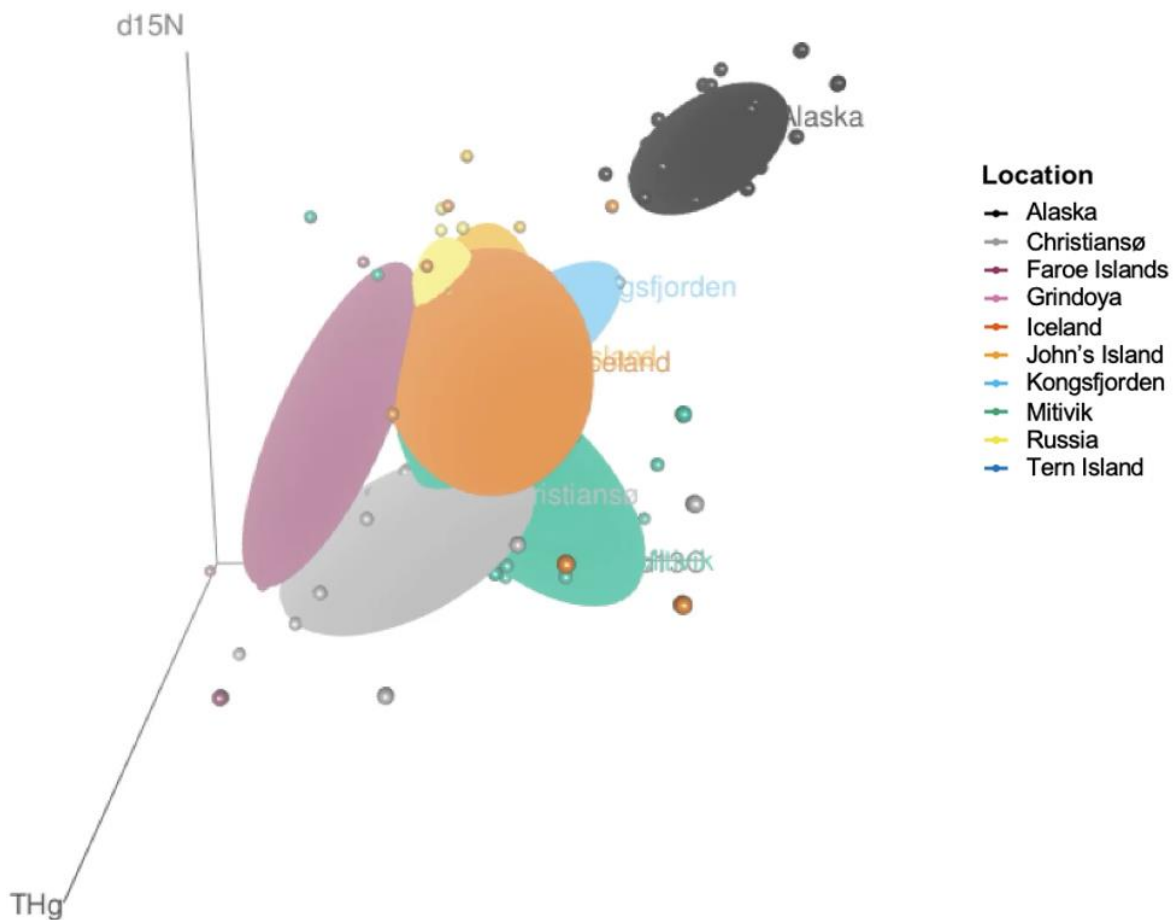
1142 Sample sizes (n), means \pm SD, Min-Max (in ‰) for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and total Hg (THg in $\mu\text{g/g dw}$)
 1143 (values in brackets corrected for colony baseline ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) and standardized for units ($\delta^{13}\text{C}$,
 1144 $\delta^{15}\text{N}$ and THg)), medians and range of 3-dimensional niche size (95% Bayesian credible
 1145 intervals), and $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and THg ranges (maximum-minimum values using corrected and
 1146 standardized values) of 10 pan-Arctic and subarctic common eider colonies.

Location	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	THg	Niche size	$\delta^{13}\text{C}$ range	$\delta^{15}\text{N}$ range	THg range
Alaska	33	-20.1 \pm 0.5 (1.8)	15.3 \pm 0.7 (1.8)	1.2 \pm 0.2 (0.9)	3.3 (2.3, 5.2)	0.866	1.461	1.689
Christiansø	25	-21.2 \pm 0.9 (-1.0)	10.0 \pm 1.3 (-0.9)	1.1 \pm 0.5 (0.6)	9.7 (6.6, 16.7)	1.379	2.923	4.590
Faroe Islands	16	-18.5 \pm 1.4 (-0.3)	10.1 \pm 1.0 (-1.5)	0.7 \pm 0.4 (-0.6)	18.8 (11.5, 36.8)	2.059	2.106	4.508
Grindøya	17	-17.8 \pm 0.6 (0.1)	11.1 \pm 0.4 (-0.3)	0.4 \pm 0.1 (-1.4)	1.4 (0.8, 2.6)	0.834	0.907	1.528
Iceland	23	-17.8 \pm 0.9 (0.3)	11.6 \pm 1.0 (-0.1)	0.9 \pm 0.5 (0.1)	21.7 (14.2, 37.7)	1.407	2.257	5.410
John's Island	19	-16.9 \pm 1.5 (-0.1)	12.0 \pm 0.8 (-0.1)	0.5 \pm 0.2 (-0.9)	9.1 (5.7, 16.5)	2.250	1.633	1.688
Kongsfjorden	16	-18.4 \pm 0.8 (0.3)	11.8 \pm 1.0 (0.3)	0.8 \pm 0.2 (-0.3)	4.6 (2.8, 9.1)	1.217	2.128	2.068
East Bay Island	43	-18.2 \pm 1.1 (-0.6)	13.5 \pm 1.3 (0.3)	1.0 \pm 0.3 (0.4)	18.5 (13.6, 27.9)	1.904	2.897	3.571
Russia	24	-19.4 \pm 0.8 (0.4)	10.2 \pm 0.4 (-0.4)	0.7 \pm 0.2 (-0.4)	3.3 (2.2, 5.8)	1.175	0.962	2.278
Tern Island	24	-18.8 \pm 0.3 (-1.0)	12.4 \pm 0.5 (-0.4)	0.9 \pm 0.2 (0.1)	1.4 (0.9, 2.4)	0.475	1.141	2.398

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1149 3-dimensional representation of ten 3-dimensional niche regions produced using the R package
1150 rgl v.0.100.54 (Adler and Murdoch 2017). Corrected stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in ‰)
1151 and THg concentrations (in $\mu\text{g/g dw}$) were used from individuals at ten pan-Arctic or subarctic
1152 common eider colonies to obtain 3-dimensional niche regions using the R package nicheROVER
1153 v1.0 (Swanson et al. 2015).



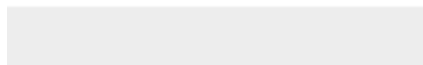
1154
1155 (Still image of a video showing the 3-dimensional plot in rotating view – see video upload for
1156 actual file to be used for publication).



[Click here to access/download](#)

Video

[NichemodellingMS_SupplementalMaterials.mov](#)



Environmental and life-history factors influencing inter-colony and multidimensional niche metrics of breeding common eider

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: