



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

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HIGHLIGHTS

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

GRAPHICAL ABSTRACT



Migratory Colonies ↑ Sea-Ice Cover



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



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

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ABSTRACT

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 (*Somateria mollissima*) 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

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Nitrogen-15
THg
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and $\delta^{15}\text{N}$, and lower $\delta^{13}\text{C}$, suggesting a higher trophic position and a greater reliance on phytoplankton-based prey. It was concluded that variation in MDND exists among 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.

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1. Introduction

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

The foraging niche of an organism includes both dietary and environmental components, and therefore has been used to discern both trophic roles by consumers and changes in their resource use (Newsome et al., 2007). Studies examining foraging niche size (the spatial and trophic-level range at which a group forages) have been used to investigate the effect of phenological changes in primary production on predators (Rabosky, 2009). In polar regions, changes in the abundance, distribution, and phenology of primary producers such as phytoplankton and ice-algae can have effects on higher trophic-level wildlife (Frederiksen et al., 2006; Kohlbach et al., 2016; Renaut et al., 2018; Lewis et al., 2020). Sympagic-pelagic-benthic coupling drives energy flow between the surface and benthic habitats and provides a foundation for Arctic ecosystem functioning involving benthic consumers, but is being decoupled due to changing sea-ice dynamics (Søreide et al., 2013; Kohlbach et al., 2016; Yurkowski et al., 2020a). These shifts can generate bottom-up effects on the foraging ecology of higher trophic species, especially those that rely on consuming resources that inhabit the sea floor (Leu et al., 2011; Post et al., 2013; Post, 2017; Cusset et al., 2019).

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

Climate change can affect the distribution and accumulation of Hg in Arctic ecosystems (Stern et al., 2012; McKinney et al., 2015; Foster et al., 2019). Further, changes in Arctic food web dynamics and trophic

relationships may shift the flow of Hg between organisms (Braune et al., 2014). To study this, stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) are tracers that can provide time-integrated information on habitat use and diet (Bearhop et al., 2006; Cherel and Hobson, 2007; Inger and Bearhop, 2008). In coastal polar environments, $\delta^{13}\text{C}$ provides dietary information on sources of primary productivity and foraging habitat, for example, between ^{13}C -depleted phytoplankton-derived carbon and ^{13}C -enriched sea-ice derived carbon (Hobson et al., 2002; Kohlbach et al., 2016; Yurkowski et al., 2020a; Lewis et al., 2020). In addition, benthic or nearshore environments with macroalgae are typically enriched in ^{13}C compared to pelagic or offshore sources (Hobson and Welch, 1992; Hobson et al., 1995; France, 1995). Values of $\delta^{15}\text{N}$ indicates relative trophic level, with higher trophic levels associated with increased $\delta^{15}\text{N}$ values (Hobson and Welch, 1992). Thus, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values can help determine environmental and dietary sources of Hg due to varying uptake with carbon-source and trophic level (Atwell et al., 1998; Cardona-Marek et al., 2009; Pomerleau et al., 2016; Carravieri et al., 2017). However, while $\delta^{15}\text{N}$ values relate to Hg concentrations, high variability in Hg still occurs among individuals despite similar $\delta^{15}\text{N}$ values (Atwell et al., 1998; Bearhop et al., 2000; DiMento et al., 2019).

While isotope biplots consisting of just $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ capture an incomplete portrayal of ecological niche due to the inclusion of only two isotopic variables, a multidimensional niche, including three or more total variables, can provide more information to assess foraging ecology, albeit with greater complexity in interpretation (Swanson et al., 2015; Hobson et al., 2015; O'Donovan et al., 2018). Therefore, including Hg in niche analyses along with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ provides a broader, risk-based method to quantify an individual and population's foraging ecology and multidimensional niche dynamics (MDND; Yurkowski et al., 2020b). This analytical approach, combining stable isotopes and contaminants, has been applied to multiple taxa including mammals, fish, and reptiles (Guzzo et al., 2016; Jackson et al., 2016; Purwandana et al., 2016; Yurkowski et al., 2020b). However, a MDND approach to determine niche size has not been investigated in seabirds despite them being considered sentinels of ecosystem change (Le Bohec et al., 2013). Arctic seabirds demonstrate varying foraging specializations on a diversity of prey items reflecting climate-induced trophic shifts and can inform spatial variation and temporal changes in sea-ice and ocean dynamics that propagate up the food web, making them an ideal model to research MDND (Pratte et al., 2019; Albert et al., 2021; Renedo et al., 2020).

An inter-colony and inter-individual approach was used to examine spatial variation in the 3-dimensional niche of common eiders (*Somateria mollissima*, hereafter eiders). Eiders are a long-lived, colonial-nesting marine bird with high site fidelity and widely dispersed breeding populations across the Arctic. Across their range, eiders are likely exposed to diverse environmental conditions that influence colony demographics at varying intensities that may influence foraging decisions and, although typically at low concentrations in eiders, Hg exposure (Mallory et al., 2004, 2017; Jónsson et al., 2013; Goudie et al., 2020; Noel et al., 2021). Eider prey primarily includes a diversity of benthic invertebrates (e.g., urchins, mussels, and gastropods) as well as pelagic macroinvertebrates to a lesser extent (e.g., amphipods; Sénéchal et al., 2011; Kristjánsson et al., 2013; Waltho and Coulson,

2015). The abundance and distribution of these prey groups vary spatio-temporally and correlate with both predator Hg concentrations and phenological shifts in primary production (Mouritsen et al., 2005; Barber et al., 2015; Fort et al., 2016; Savoy et al., 2017). Thus, examining $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and Hg niche dynamics of a costal, primarily benthic-foraging species provides an avenue to investigate prey shifts and Hg exposure (Sénéchal et al., 2011), as well as relative differences in ice algae and phytoplankton-based food webs in relation to sea-ice cover (Søreide et al., 2013; Kohlbach et al., 2016).

A 3-dimensional approach combining $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and total Hg (THg) measurements collected from individuals at 10 eider breeding colonies located across their circumpolar range was used to evaluate variation in eider foraging ecology and Hg exposure. It was anticipated that colonies would show differences in 3-dimensional niche size which were influenced by spatial differences in primary productivity (i.e., sea-ice algae and phytoplankton) and migratory behaviour. To examine these possible drivers of colony-level variation in niche size, colony sea-ice cover was examined during a period reflecting periods of isotopic integration in blood. Specifically, it was predicted that colonies with higher sea-ice cover would have smaller niche sizes than those with no sea ice present due to more restricted foraging habitat and likely less diverse prey availability (Yurkowski et al., 2016; Pratte et al., 2019). Niche size along with colony migratory behaviour was also examined with a prediction that eiders from resident colonies would have smaller niche sizes compared to migratory colonies, given that residents remain at the same geographical location year-round and are likely exposed to a narrower range of environmental conditions (Herrera, 1978; Gómez et al., 2016).

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

Finally, the relationship between trophic position (the vertical placement of an individual in the food-web based on prey and individual $\delta^{15}\text{N}$ values) and inter-individual $\delta^{13}\text{C}$ values on THg concentrations was examined with a prediction that THg would increase with higher trophic position due to the biomagnification of THg, and lower $\delta^{13}\text{C}$ values because of a greater consumption of resources derived from phytoplankton (Atwell et al., 1998; McMahon et al., 2006; Stern et al., 2012). Examination of 3-dimensional niche size among eider colonies allowed for identification of key environmental and behavioural factors that may have influenced niche dynamics. Furthermore, MDND can be used to infer colony-level variability in resource use and overall niche diversity which allowed for broad predictions about flexibility and resiliency to environmental change (Vander Zanden et al., 2010; Paredes et al., 2012; Smith and Reeves, 2012; Sydeman et al., 2012). As such, it was also considered how this measurement of niche size may help predict the resiliency of eider colonies to environmental change.

2. Methods

2.1. Study sites and sample collection

Whole blood samples were collected from pre-incubating or incubating eiders in 2018 at 10 breeding colonies (total number of

individuals = 240) across the Arctic and subarctic (spanning a longitude from -147.776 to 35.774 and latitude from 78.918 to 43.645 ; Fig. 1, Table 1). Eiders were captured using colony- and breeding stage-specific techniques. Pre-incubating eiders were sampled at East Bay Island (within in the Qaqsauqtuuq (East Bay) Migratory Bird Sanctuary, Nunavut, Canada), whereas incubating eiders were sampled at the other nine locations.

At East Bay Island, eiders were captured using large flight nets. Birds were collected from the nets and a 1-mL tarsal blood sample was obtained from each female eider (Hennin et al., 2015). These samples were used for isotopic analyses and were collected using a 23G thin-wall, 1-in. needle attached to a sodium-heparinized 1 mL syringe (Lemons et al., 2012). After transferring to a heparinized 1.5 mL Eppendorf tube, samples were kept cool ($\sim 10^\circ\text{C}$), and within 8 h, were centrifuged at 10,000 rpm for 10 min to separate red blood cells (RBCs) and plasma. Plasma was then transferred by pipetting into a separate cryovial and stored along with RBC samples at -20°C until isotopic analysis. During the same capture period as the first sample, a second blood sample of 1-mL was obtained from the jugular vein using 23G thin wall, 1-in. needles attached to heparinized 3 mL syringes to be used for Hg analysis. The whole blood sample was placed in acid-rinsed cryovials and kept at $\sim 10^\circ\text{C}$, and frozen within 6 h of collection until analysis.

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

2.2. Stable isotope analysis

Stable isotopes of elements turnover at different rates based on dietary composition, metabolic rate and specific metabolic activity of the tissue, as well as individual body size and temperature exposure (Hobson and Clark, 1992; Carleton and Martinez del Rio, 2005). While specific turnover times have not been established for eiders, for avian blood components generally, plasma has a faster turnover rate that reflects recent diet (days), while the turnover rate of RBCs is slower and reflects diet over a longer period (weeks; Hobson and Clark, 1992; Hahn et al., 2012; Barquete et al., 2013). Further, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ usually have similar turnover times, hence are comparable (Bearhop et al., 2002). Stable isotope ratios were measured in plasma of pre-incubating eiders at East Bay Island, and in RBCs of incubating eiders at the other nine colonies. Therefore, despite sampling colonies at different life history stages, by using tissues with relatively shorter (plasma) and longer (RBC) turnover times for analysis, we were able to compare them within a similar stage including the pre-incubation period while eiders are heavily foraging, either at resident sites or in the last period of migration to build up stored resources for their incubation fast.

Samples were freeze-dried for approximately 72 h after collection. Samples were then ground into a fine, homogenized powder using a metal spatula cleaned with acetone. Plasma samples were then lipid extracted using a 2:1 chloroform:methanol solution (Søreide et al., 2006). Specifically, 2:1 chloroform:methanol solution (1.9 mL) was added to 100 μL of each plasma sample, which were then placed in a water bath at 30°C for 24 h. Samples were then centrifuged at 15,000 rpm for 10 min to separate the lipid solution from the plasma pellet. A



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

p1000 pipette was used to remove the lipid solution, leaving the plasma pellet behind. The pellet was washed again with an additional 1.9 mL of the chloroform:methanol solution and centrifuged for a final 10 min at 15,000 rpm. The remaining lipid solution was removed, leaving only a plasma pellet. Samples were left open in the fume hood for 24 h to allow for any remaining chloroform:methanol solution to evaporate. Since RBCs have minimal lipids present, they did not undergo lipid extraction ([Hobson and Clark, 1992](#)).

Plasma and RBC samples were weighed into individual tin-capsules using a 4-digit balance to obtain 0.3–0.5 mg of sample. Plasma samples were prepared at the University of Windsor, and plasma stable isotopes were analysed at the Environment and Climate Change Canada Stable Isotope Laboratory in Saskatoon, Saskatchewan, using continuous-flow

isotope-ratio mass spectrometry (CFIRMS; [Harris et al., 1997](#)). Samples were weighed into pre-combusted tin capsules. Encapsulated plasma was combusted at 1030 °C in a Carlo Erba NA1500 or Eurovector 3000 elemental analyser. The resulting N₂ and CO₂ were separated chromatographically and introduced to an Elemental Isoprime or a Nu Instruments Horizon isotope ratio mass spectrometer. Two reference materials were used to normalize the results to VPDB and AIR: BWPB keratin ($\delta^{13}\text{C} = -20.18$, $\delta^{15}\text{N} = +14.31\%$, respectively) and PRCgel ($\delta^{13}\text{C} = -13.64$, $\delta^{15}\text{N} = +5.07\%$, respectively). Within run ($n = 5$) precisions as determined from both reference and sample duplicate analyses were $\pm 0.1\%$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

The RBC samples were prepared for isotope analysis at La Rochelle University, France, and were analysed at the LIENS Institute (La

Table 1

Locations of common eider colonies included in this study, sample size (number of individual birds from each colony included in the study), month samples were obtained, coordinates (latitude and longitude), whether a colony is known to be predominately migratory or resident, and the proportion of sea ice cover in a 100 km area around the colony during the 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
Breidafjörður, 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
Kirkjubæhólmur, 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

Rochelle, France) as detailed in Fort et al. (2014). Plasma and RBC samples were combusted using a Eurovector 3000 (Milan, Italy) elemental analyser which results in production of N₂ and CO₂ gases. These were separated by gas chromatography and introduced into a NU Horizon (Nu Instruments, Wrexham, UK) triple-collector isotope-ratio mass-spectrometer via an open split. Ratios of carbon (¹³C/¹²C) and nitrogen (¹⁵N/¹⁴N) were expressed in typical delta notation (δ) as per mil (‰) deviation from the primary standards (Vienna Pee Dee Belemnite (VDPB) and atmospheric nitrogen (AIR), respectively). Replicate measurements (n = 20) per run of laboratory standards (USGS-61 and USGS-62) indicated that the measurement accuracy was <0.2‰ for both δ¹⁵N and δ¹³C values.

Baseline stable isotopes of Arctic marine food webs vary spatiotemporally, thus measured δ¹³C and δ¹⁵N values of biota from different regions can only be compared if corrected for such baseline variance (Bowen, 2010; Hobson et al., 2012; de la Vega et al., 2019). Based on previously published δ¹³C and δ¹⁵N values of known eider bivalve prey at the different breeding sites, stable isotope data was corrected by subtracting baseline bivalve isotope values from the eider tissue values to obtain “corrected” isotopic values (Table 2). However, THg values were not corrected to baseline values. Additionally, we were unable to account for the potential impact of incubation stage on δ¹⁵N, δ¹³C or Hg values. Both Hg and δ¹⁵N values can be elevated in blood due to mobilization of internal nutrient stores during the incubation fast (Hobson et al., 1993; Wayland et al., 2005). However, use of RBCs instead of plasma at all but one site (East Bay Island) to determine incubating female δ¹⁵N values minimized this effect (Cherel et al., 2005). Furthermore, sampling of eiders during incubation, when Hg is known to increase (Wayland et al., 2005), lessens, but does not mitigate the potential bias of East Bay Island pre-breeding eiders having elevated Hg relative to the other colonies, as the pre-breeding eiders have not yet depurated Hg to their eggs during laying (Akearok et al., 2010). Hence, caution should be taken when comparing Hg values between East Bay Island and the other nine colonies.

Diet-tissue isotopic discrimination factors allow modeling of isotopic trophic positions or nutrient source tracing (e.g., Wolf et al., 2009; Federer et al., 2010; Bond and Diamond, 2011). Such factors have not been established for common eiders, so those reported by Federer et al. (2010) for spectacled eider (*Somateria fischeri*) (plasma: +4.9‰; RBC: +4.0‰) were used. Trophic position was calculated using baseline δ¹⁵N bivalve values for the individual's colony (δ¹⁵N_{base}), discrimination factors from the respective tissue of spectacled eiders (δ¹⁵N_{TDF}; Federer et al., 2010), trophic position (TP) of baseline prey values (TP_{base}; value of 2 consistent with eider prey), and the non-colony corrected δ¹⁵N values for that individual eider (δ¹⁵N_{eider}; Hobson and Welch, 1992; Vander Zanden et al., 1997; Vander Zanden and Rasmussen, 1999).

$$TP = \left(\left(\delta^{15}N_{eider} - \delta^{15}N_{base} \right) / \delta^{15}N_{TDF} \right) + TP_{base}$$

Table 2

Isotopic signatures (δ¹³C, δ¹⁵N in ‰) of typical common eider bivalve prey as determined by the most spatio-temporally appropriate literature values available at the time of analysis. Prey stable isotope data was used to correct common eider isotope data to allow for inter-colony comparison.

Location	Prey species	δ ¹³ C (‰)	δ ¹⁵ 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

2.3. THg analysis

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

For the remaining nine colonies, THg analyses were conducted at LIENSs Institute using RBCs separated from plasma collected from incubating females. These eiders were captured while incubating (Hanssen et al., 2002; Bottitta et al., 2003; Sénéchal et al., 2011), thus by collecting and analysing RBCs alone, the timeframe which the RBCs represent (weeks) aligns with the timeframe represented in the East Bay Island eiders (days) since whole blood has a turnover rate approximately intermediate of plasma and RBC (Cherel et al., 2005). Therefore, this provides justification for including the colony in our analysis despite potential differences in physiology due to their reproductive stages. Freeze-dried blood was analysed using an Advanced Hg Analyser spectrophotometer (Altec AMA 254). A quality control program included running blanks prior to the analysis at the limit of detection of 0.05 ng of Hg. Certified reference materials (DOLT-2 and TORT-2) were analysed every 15 samples (certified Hg concentrations: 0.44 ± 0.18 µg/g dw for DOLT-2 and 0.27 ± 0.06 µg/g dw for TORT-2, measured concentrations: 0.44 ± 0.01 µg/g dw for DOLT-2 and 0.26 ± 0.01 µg/g dw for TORT-2). Samples were analysed for THg since Hg exists as primarily MeHg in avian blood (near 1:1 ratio; Wiener et al., 2003; Rimmer et al., 2005).

2.4. Statistical analysis

Colony 3-dimensional niche size (using THg, δ¹³C and δ¹⁵N) and ranges along the THg, δ¹³C and δ¹⁵N axes were determined for 10 eider colonies using the R package nicheROVER v1.0 (Swanson et al., 2015) in R version 3.6.2 (R Development Core Team). NicheROVER uses Bayesian statistical methods to calculate a multidimensional niche region in multivariate space that represents the spatial breadth and placement of a group's (i.e., colony's) niche in relation to other groups, and infers the niche size of each group based on that group's individual values for each dimension (Swanson et al., 2015). Since the variables are in different units (δ¹³C and δ¹⁵N: ‰ vs. THg: µg/g dw), all values were scaled and centred by subtracting the mean for each variable and dividing it by the standard deviation, thereby standardizing all data. To determine if there were any correlations among variables

prior to analysis, independence was tested by calculating Spearman's correlation coefficient between THg and colony-corrected $\delta^{15}\text{N}$ which showed a significant but relatively weak correlation ($R = 0.43$, $p < 0.001$). Thus, THg and $\delta^{15}\text{N}$, while related, do possess independent variation that allowed for inclusion of both metrics in our analysis to account for spatial variation in THg concentrations. A 95% probability niche region in multivariate space was calculated at 10,000 iterations using diffuse priors (Swanson et al., 2015; Yurkowski et al., 2020b). Additional script at 10,000 iterations was conducted to obtain $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and THg ranges (difference between the highest and lowest values; Swanson et al., 2015; Yurkowski et al., 2020b). Three-dimensional models of the niche ranges were visualized using the scatter3D function in the car package v.3.0–9 (Fox and Weisberg, 2019) and the rgl package v.0.100.54 (Adler and Murdoch, 2017; see Supplemental Materials).

Primary migratory status of each colony, not including the potential for individual variation, was determined by consulting previous studies (Schamel, 1977; Bønløkke et al., 2006; Hanssen et al., 2016; Steenweg et al., 2017; Mallory et al., 2020) and through spatial tracking data collected by the SEATRACK program (<https://seapop.no/en/seatrack/>). Moreover, the proportion of sea-ice cover surrounding each colony within a timeframe reflecting turnover rates of isotope sampling was determined (plasma within a week of sampling, RBC within a month of sampling; Hobson and Clark, 1992; Barquete et al., 2013). Sea-ice cover was analysed via a satellite image of a 100 km area around each colony on a cloud-less day from NASA Worldview dataset (EOSDIS, <https://worldview.earthdata.nasa.gov>). Land pixels were removed from the image manually and the remaining pixels were categorized into two groups (open water or sea ice) using a K-means clustering procedure via RGB values of the pixels (<http://mkweb.bcgsc.ca/color-summarizer/>). The resulting proportion of pixels was used as a proxy for the proportion of sea ice around the colony during the time of isotopic turnover for each colony (Cusset et al., 2019).

A preliminary 2-tailed t -test was used to determine independence between colony sea-ice cover and migratory behaviour, which were not significantly correlated ($t_5 = 2.11$, $p = 0.09$). Therefore, to determine sources of niche variation with sea ice cover, a general linear

model (GLM) was used to examine how log-transformed niche size varied by colony sea-ice cover. Next, six GLMs were used to analyze the relationship between sea ice cover and colony $\delta^{15}\text{N}$, log-transformed $\delta^{13}\text{C}$ and THg ranges, as well as median individual colony-corrected $\delta^{15}\text{N}$, and log-transformed $\delta^{13}\text{C}$ and THg values for each of the 10 colonies. Median values were used to avoid data skewed by high/low individual values within a mean and better represent general colony values.

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

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

3. Results

3.1. Niche size and underlying sources of variation

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

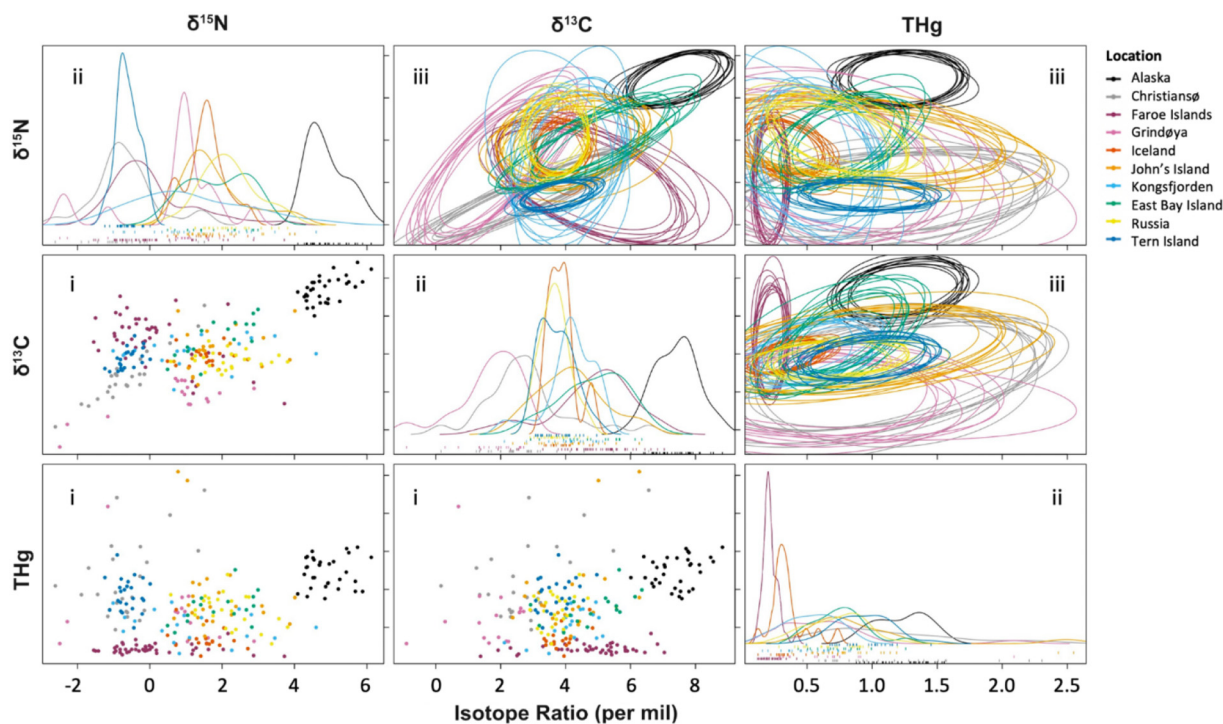


Fig. 2. 2-dimensional projections of ten 3-dimensional niche regions produced using the R package nicheROVER v1.0 (Swanson et al., 2015). Corrected stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in ‰) and THg data (in $\mu\text{g/g dw}$) were used from individuals at 10 pan-Arctic or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

suggesting eiders were feeding on prey reflecting more ice algae- or inshore-derived carbon (see Supplemental Materials). The Alaskan colony also had the highest colony-corrected $\delta^{15}\text{N}$ values, with the Faroe Islands having the lowest values, suggesting that Faroese eiders forage at lower trophic levels, whereas the Alaskan eiders forage at higher trophic levels.

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

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

3.3. Relationship between isotopic niche and THg concentrations

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

4. Discussion

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

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

4.1. Colony foraging flexibility and resiliency predictions

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

When grouped for similarity, niche size generated the following general pattern in this study: Iceland, East Bay Island and Faroe Islands > Christiansø and John's Island > Kongsfjorden, Alaska and Russia > Tern Island and Grindøya (Fig. 1). Using this 3-dimensional view of niche size, it was predicted that colonies with wider (i.e., more generalist) 3-dimensional niches such as those in Iceland and Faroe Islands, or colonies comprised of migrants from multiple locations such as East Bay will show greater resiliency to shifts in food web dynamics compared to colonies with a smaller (i.e., more restricted, specialist) niche similar to Tern Island and Grindøya. Smaller niches are predicted to be at a disadvantage in a changing climate as these alterations may change or eliminate food sources, leaving a colony or species more vulnerable if they do not have the flexibility to adapt and shift their diet with this changing prey base (Both et al., 2010; Le Bohec et al., 2013; Ceia and Ramos, 2015). However, climate change may present an opportunity for Arctic colonies with smaller niches to expand their prey sources with advancing phenology of spring phytoplankton blooms and more open water sources. For those with broader niches at southern latitudes, that niche size may be critical along with further changes in the distribution and availability of key prey (Staudinger et al., 2019). Nevertheless, more research that integrates measures of breeding success and colony demographics is necessary to test these resiliency hypotheses over long temporal scales to identify seasonal and annual variation in inter- and intra- colony foraging ecology.

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

Colony niche size was not correlated with sea-ice cover, possibly attributable to several factors. First, despite the presence of sea ice likely restricting foraging locations, eiders may still be able to access a diversity of resources, including the potential for prey sources such as ice-associated amphipods as niche size was similar to locations that have more accessible, ice-free areas (Karnovsky et al., 2008). Second, northern colonies may support a variety of individuals that utilize both generalist and specialist strategies, thus adding to the flexibility and diversity of the colony in the face of environmental change (Woo et al., 2008; Ceia and Ramos, 2015; Pratte et al., 2019). Notably, the relative proportion of generalist and specialist individuals in populations dramatically affects dietary niche size with generalist-based populations having wider niches (Newsome et al., 2007).

Table 3

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

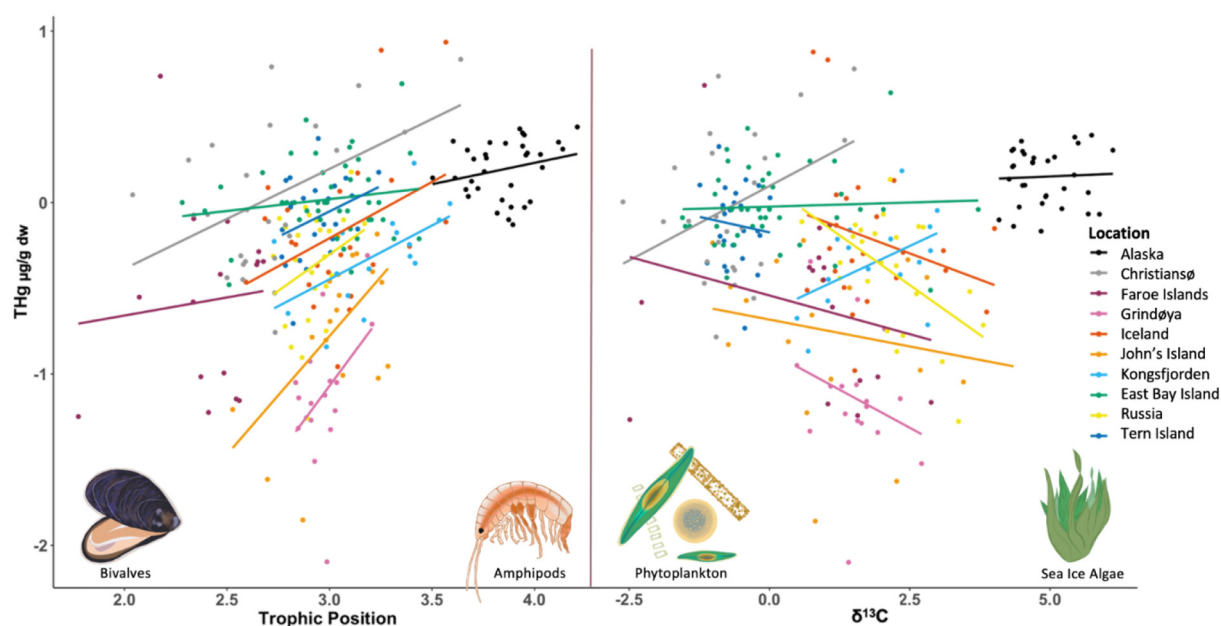


Fig. 3. Relationship between THg (natural log-transformed) with trophic position (calculated based on $\delta^{15}\text{N}$; see Methods) and colony-corrected $\delta^{13}\text{C}$ (in ‰) for individuals at 10 pan-Arctic or subarctic common eider colonies, identified by colour.

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

4.3. Role of migration in shaping MDND and THg exposure

It was predicted that migratory populations (see Table 1, Fig. 1) would have larger niches due to exposure to a variety of environmental conditions and prey types at both migratory and breeding grounds where resources are stored to mobilize during their incubation fast (Herrera, 1978; Gómez et al., 2016). In the present study, there was no pattern between with migratory behaviour and niche size. However, two of the largest niche sizes found at two resident colonies (Iceland and Faroe Islands) may stem from colony-wide expansion in dietary choice due to increased prey availability. This has been reported in

Iceland where eiders within the colony selected a wide array of both benthic and pelagic prey (Kristjánsson et al., 2013). Waters around Iceland are a mix of Arctic (East-Greenland Current), as well as Atlantic origins (North Atlantic Current), and this, together with greater lack of sea ice, would provide a diverse range of prey options to pre-breeding eiders (Vincent, 2010; Kristjánsson et al., 2013; Casanova-Masjoan et al., 2020). The East Bay Island colony, consisting of migrants from Greenland and Newfoundland, had the second largest niche size potentially in part due to a mixing of individuals from both overwintering sites (Steenweg et al., 2017). Additionally, individual variation in migration distance and strategy within a colony, although not included in the present study, may lead to broader colony niche ranges (Mallory et al., 2020).

Colonies supporting migratory eiders had higher THg concentrations and foraged at higher trophic levels compared to colonies supporting residents, suggesting that colonies of migratory individuals had access to higher trophic-level prey, or relied on these prey to store resources necessary for incubation. Colonies with resident eiders had higher individual $\delta^{13}\text{C}$ levels indicating diets with greater foraging based on ice algae, potentially due to residing at their Arctic breeding sites year-round while migratory colonies move to more suitable areas with presumably lower sea ice. Combined with the results on colony sea ice cover, these dynamics show that changes in environmental conditions and variability may have different effects on migratory and resident seabird colonies dependent on future colony flexibility, thus should be factored into future analyses especially regarding climate change effects within Arctic ecosystems.

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

With increasing industrial activity and contaminant deposition due to long-distance transport in northern latitudes, as well as the release of stored Hg from melting cryosphere and increased erosion of terrestrial sources, Arctic-inhabiting species are potentially becoming more at risk for contaminants exposure and a suite of possible negative neurological, physiological and reproductive impacts (Dietz et al., 2013; Scheuhammer et al., 2015; Soerensen et al., 2016; Cossa et al., 2018). This is especially a potential population stability concern for harvested

species, such as common eider, which are an important, harvested species for many Indigenous communities in the North (Nakashima and Murray, 1988; Priest and Usher, 2004). Concentrations of THg for the eider colonies in this study are comparable to those observed in previous eider research (Provencher et al., 2016; Albert et al., 2019; Ma et al., 2020; Dietz et al., 2021). The mean concentrations of THg in the Alaska, Christiansø and East Bay colonies were above 0.95 µg/g dw, suggesting that three of the 10 colonies studied, and 40% of sampled eiders, were above general environmental background concentrations (Eagles-Smith et al., 2008; Ackerman et al., 2016). Nonetheless, concentrations were still sufficiently low to assign them a general “low risk” status regarding concerns for health, physiology, behaviour and reproductive effects (Ackerman et al., 2016; Dietz et al., 2019, 2021). The individual eider with the highest Hg concentration was from the Iceland colony (2.55 µg/g dw compared to the colony mean of 0.95 µg/g dw). Iceland had less sea ice than other regions, such as Alaska that had the highest sea ice cover and colony THg average (1.23 µg/g dw).

With a rapidly declining sea-ice cover, a rise in phytoplankton production and resulting eider consumption of prey derived from phytoplankton carbon sources could be related to higher, individual THg concentrations (Stern et al., 2012). Combined with the results in Section 4.2 showing higher median THg concentrations at colonies with greater sea-ice cover, these results demonstrate that within colonies, individuals with greater phytoplankton-based consumption had higher THg concentrations. The relationship between individual $\delta^{13}\text{C}$ and THg, combined with effects of trophic position (determined using $\delta^{15}\text{N}$) on THg may potentially have future effects on seabird health, behaviour and reproduction in those with at-risk Hg exposure. However, it is likely that any possible effects would not be consistent across the entire range of a species, especially given the regional difference in which climate change is altering the Arctic (Muir et al., 1999; Mallory and Braune, 2012; Swart et al., 2015). Nevertheless, variation among colonies was detected, suggesting regional differences in the relationship between $\delta^{13}\text{C}$, trophic position and THg; for instance, the Christiansø and Kongsfjorden colonies showed opposite relationships between THg and $\delta^{13}\text{C}$ (Fig. 3). Thus, more in-depth analyses of the environmental factors at each site would allow for site-specific investigation into the relationships between foraging behaviour and THg uptake. Additionally, further knowledge of baseline variation (THg, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$) in colony-specific prey at a varying spatio-temporal inter-annual scale, parallel with eider sampling, would aid future interpretation of eider niche size, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and sources of individual and colony THg. Additionally, the contribution of terrestrial carbon sources and agricultural runoff to marine areas around some of these colonies may also contribute to variation in individual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and affect exposure to THg and its accumulation (Dunton et al., 2006; Laursen et al., 2018; Renedo et al., 2020). Overall, the relationship between environmental conditions and THg concentrations presents a complex system and paired with the rapid changes in ecosystem dynamics currently being observed (i.e., sea ice abundance), underscores the necessity of future, consistent annual monitoring, especially in key ecosystem indicators like marine birds.

5. Conclusion

Inter-colony, 3-dimensional niche size, isotopic and THg ranges, and the relationships between $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and THg within individuals was examined. Our results suggest that common eider colonies across the Arctic and subarctic have a wide degree of diet variation, potentially influenced by environmental changes including spatio-temporal differences in primary productivity. It was found that consideration of colony-level variation in life histories (migratory vs resident) was important for assessing the level of risk to which a colony may be exposed. Further, inter-annual MDND analyses using simultaneous local $\delta^{13}\text{C}$ marine isoscapes to correct for eider $\delta^{13}\text{C}$, in addition to corrections for baseline THg, would provide greater insight into the temporal variation

in niche size that exists at both an inter- and intra-colony scale. Taken together, exploring MDND is an increasingly valuable tool to provide insight into how diet breadth differs across a species' range, especially when combined with temporal and spatial variation in environmental conditions and key components to variation in life history such as migration.

CRediT authorship contribution statement

Reyd A. Smith: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **David J. Yurkowski:** Methodology, Formal analysis, Writing – review & editing. **Kyle J.L. Parkinson:** Conceptualization, Investigation, Writing – review & editing. **Jérôme Fort:** Investigation, Resources, Writing – review & editing. **Holly L. Hennin:** Formal analysis, Writing – review & editing. **H. Grant Gilchrist:** Funding acquisition, Writing – review & editing. **Keith A. Hobson:** Investigation, Writing – review & editing. **Mark L. Mallory:** Resources, Writing – review & editing. **Jóhannis Danielsen:** Resources, Writing – review & editing. **Svend E. Garbus:** Resources, Writing – review & editing. **Sveinn A. Hanssen:** Resources, Writing – review & editing. **Jón Einar Jónsson:** Resources, Writing – review & editing. **Christopher J. Latty:** Resources, Writing – review & editing. **Ellen Magnúsdóttir:** Resources. **Børge Moe:** Resources, Writing – review & editing. **Glen J. Parsons:** Resources, Writing – review & editing. **Christian Sonne:** Resources, Writing – review & editing. **Grigori Tertitski:** Resources, Writing – review & editing. **Oliver P. Love:** Supervision, Formal analysis, Funding acquisition, Writing – review & editing.

Declaration of competing interest

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.148935>.

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