



Contribution to the Theme Section 'Species range shifts, biological invasions and ocean warming'

Comparison of feeding niches between Arctic and northward-moving sub-Arctic marine mammals in Greenland

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ABSTRACT: The climate change-induced northward movement of sub-Arctic marine mammals increases their range overlap and interactions with native Arctic species. We compared feeding patterns of 11 marine mammal species (4 Arctic and 7 sub-Arctic) in Greenland using stable isotope ratios and fatty acid signatures, and also assessed the effects of lipid extraction on stable isotope ratios. Lipid extraction showed limited increases in $\delta^{13}\text{C}$, intermediate effects on $\delta^{15}\text{N}$, and significant depletion of $\delta^{34}\text{S}$ in muscle of some marine mammals. Arctic and sub-Arctic species differed in stable isotope ratios, indicating some use of separate food resources, while likely also reflecting baseline isotopic variation. Proportions of some of the most abundant fatty acids (20:1n9, 22:1n11, 20:5n3, 22:6n3) varied between Arctic and sub-Arctic species, indicating that sub-Arctic species rely mostly on a pelagic food web, while Arctic species exploit an ice-associated and benthic food web, although the sub-Arctic harp and hooded seals and Arctic narwhal showed opposite patterns. Sub-Arctic species had the largest niche breadths, implying diet flexibility and potential to adapt to further changes. Overall patterns in dietary tracers demonstrate separation of feeding niches between most Arctic and sub-Arctic marine mammals, but potential niche overlap and shared food resources for some species. Sub-Arctic seal species overlap the feeding niches of native Arctic species the most of all range-shifters, and of Arctic species, narwhal appear to be the most vulnerable to niche overlap and potential food competition with northward-shifting species.

KEY WORDS: Foraging · Niche breadth · Whale · Seal · Lipid extraction · ^{13}C · ^{15}N · ^{34}S · Stable isotopes · Fatty acids

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1. INTRODUCTION

Climate change is causing shifts in the geographic distribution of species globally, as rising temperatures are driving species up in elevation, down in water depth, and toward the poles (Sorte et al. 2010,

Chen et al. 2011, Pecl et al. 2017). In marine ecosystems, range shifts are an order of magnitude faster than terrestrial shifts and almost all shifts are poleward (Sorte et al. 2010). Among marine mammals, many sub-Arctic and temperate species are demonstrating such changes in distributions into polar areas

as oceans warm, sea ice decreases, and prey species redistribute, and these shifts are predicted to continue (Heide-Jørgensen et al. 2007, Higdon & Ferguson 2009, Lambert et al. 2011, Kerosky et al. 2012, Albrecht et al. 2021).

Models of future climate change scenarios project that species invasions will be greatest toward the poles (Cheung et al. 2009), and climate-induced range shifts are prevalent in the Arctic, where climate change has caused more dramatic environmental changes than elsewhere (Post et al. 2009). Arctic temperatures have increased nearly 4 times faster than the global mean (Rantanen et al. 2022), leading to substantial changes in sea ice cover, with many areas transitioning from multi-year sea ice to seasonal, first-year sea ice (Maslanik et al. 2011, Comiso 2012); these changes directly impact ice-obligate and ice-associated Arctic marine mammals (Laidre et al. 2008, Moore & Huntington 2008, Chambault et al. 2020). Simultaneously, over the past several decades, historically sub-Arctic marine mammals have expanded their geographic ranges into the Arctic and migratory species have extended the portion of the year that they spend within Arctic waters, including baleen whales in the Pacific Arctic (Clarke et al. 2013, Moore 2016), killer whales in the eastern Canadian Arctic (Higdon & Ferguson 2009), and various cetaceans around Svalbard (Kovacs et al. 2011). In Greenland, both climate warming and range-shifting species are evident. Seasonal sea ice formation in northwest Greenland is now delayed several weeks compared to the last 40 yr, and climate models project that on both the east and west coasts, by 2060, air temperatures will increase and sea ice will decrease outside of ranges observed in the last 100 yr (Laidre et al. 2012, Straneo et al. 2022). Limited evidence from recent subsistence harvests suggests a rapid increase in the number of sub-Arctic marine mammals present in waters around Greenland, including humpback whales *Megaptera novaeangliae*, long-finned pilot whales *Globicephala melas*, and white-beaked dolphins *Lagenorhynchus albirostris* (NAM MCO 2019). Yet native Arctic species in Greenland and other Arctic regions are less capable of shifting distributions in response to changing conditions because of contracting Arctic area and specialized habitat requirements, e.g. the strong association of narwhal *Monodon monoceros* with deep waters and pack ice (Chambault et al. 2020).

As the northward movement of historically sub-Arctic marine mammal species increases both the geographic and temporal overlap with native Arctic species, species interactions may change. Species

reorganizing geographically can cause new or increasing overlap between species with similar ecological roles, leading to potential competition for limited resources (Pecl et al. 2017). For native species, new or increasingly abundant competitors may reduce food availability (Hamel et al. 2013), relegate native species to lower quality habitat (Milazzo et al. 2013), and reduce survival and development (Alexander et al. 2015). New competition with non-native species for prey resources may add yet more pressure to native Arctic species that are already vulnerable to ecosystem changes (Laidre et al. 2008).

While the overlap between native and range-expanding marine mammal species in the Arctic suggests that new competitive interactions are possible, the extent to which this is occurring is largely unknown. Throughout the Arctic, there is evidence of a 'borealization' of fish communities, with sub-Arctic fishes being observed at increasingly higher latitudes (Fossheim et al. 2015, Pedro et al. 2020). This trend suggests that sub-Arctic marine mammals may be following traditional prey north, as opposed to switching to consuming Arctic prey. There is also evidence of some native Arctic marine mammals shifting to sub-Arctic prey, particularly in the Canadian Arctic, where northward-shifting capelin *Mallotus villosus* are replacing polar cod *Boreogadus saida* in the diets of both beluga *Delphinapterus leucas* and ringed seal *Pusa hispida* (Marcoux et al. 2012, Chambellant et al. 2013, Choy et al. 2020). In Greenland, increased catches of boreal fishes suggest a transitioning marine ecosystem (Straneo et al. 2022), but it is not evident how much, if at all, these changes are influencing Greenland marine mammal diets. In the Norwegian Arctic and Pacific, there is evidence of niche segregation between some native and new marine mammal species, suggesting that, at least in these areas, feeding niche overlap between species may be limited (Moore et al. 2019, MacKenzie et al. 2022).

While competition is challenging to observe directly, niche overlap is a necessary condition for competition that comes from sharing limited resources, such as food (Alley 1982). Chemical tracers, particularly stable isotopes and, more recently, fatty acid signatures, are often used as proxies to model species' feeding niches and can be useful in assessing the degree of niche overlap between species of unknown diets (Newsome et al. 2012, Swanson et al. 2015, Bowes et al. 2017, Pedro et al. 2020, MacKenzie et al. 2022). In marine mammals, stable isotope ratios of carbon ($\delta^{13}\text{C}$) indicate the base carbon source of an animal's prey, nitrogen ($\delta^{15}\text{N}$) identifies trophic position, and sulfur ($\delta^{34}\text{S}$) can separate benthic and pe-

logic resources and migration pathways (Newsome et al. 2012, Szpak & Buckley 2020). Together, all 3 elements provide a footprint of the overall dietary niche. However, one challenge in using stable isotopes to study marine mammals is that their tissues are high in lipids, which have lower $\delta^{13}\text{C}$ ratios that can bias overall carbon isotope ratios. Lipid extraction processes that correct for this issue with $\delta^{13}\text{C}$ can affect the $\delta^{15}\text{N}$ values (Yurkowski et al. 2015, Larocque et al. 2021). In other taxa, there is conflicting evidence on whether lipid extraction affects $\delta^{34}\text{S}$, and this question has not been studied in marine mammal muscle tissue (Elliott et al. 2014, Larocque et al. 2021, Riverón et al. 2022). Analysis of fatty acids from marine mammal blubber samples can similarly reflect dietary patterns as, in particular, long-chain polyunsaturated fatty acids (PUFAs) are only acquired through diet; thus, fatty acid analysis can also reflect the degree of feeding niche overlap among species, often with greater detail than stable isotopes alone (Budge et al. 2006, Pedro et al. 2020).

In this study, we compared the feeding patterns of 11 species of marine mammals in Greenland, using both stable isotope ratios and fatty acid signatures to elucidate their overlap and potential food competition. We included 4 native Arctic species: bearded seal *Erignathus barbatus*, ringed seal, Atlantic walrus *Odobenus rosmarus rosmarus*, and narwhal, and 7 sub-Arctic species in Greenland: harp seal *Pagophilus groenlandicus*, hooded seal *Cystophora cristata*, harbor porpoise *Phocoena phocoena*, white-beaked dolphin, long-finned pilot whale, minke whale *Balaenoptera acutorostrata*, and humpback whale. We first assessed the effects of lipid extraction on isotopic ratios of carbon, nitrogen, and sulfur in the muscle tissue of each species. Next, we compared stable isotope ratios and fatty acid signatures among species. Finally, we compared niche breadth of all 11 species and quantified niche overlap between Arctic and sub-Arctic species to determine the degree of potential feeding niche overlap between native and northward-range-shifting marine mammals.

2. MATERIALS AND METHODS

2.1. Sample collection

We opportunistically obtained blubber and muscle tissue samples from all species (except blubber and liver for harbor porpoise) after local subsistence harvest by communities in Greenland. Sample selection was entirely determined by which animals were

encountered and collected by hunters and which tissues were subsequently made available to researchers, so sample size, location, and year vary by species. All collections occurred from 2010 to 2018, except for one minke whale sampled in 2000 and 2 minke whales and one humpback whale with unknown year (Table S1 in the Supplement at www.int-res.com/articles/suppl/m14440_supp.pdf, Fig. 1), which were retained due to small sample size for these species.

2.2. Stable isotope analysis

The majority of stable isotope samples were analyzed in the Ecological Tracers Lab at McGill University. These samples constituted muscle tissue from 9 species (bearded seal $n = 8$, ringed seal $n = 13$, walrus $n = 2$, narwhal $n = 2$, humpback whale $n = 14$, minke whale $n = 8$, long-finned pilot whale $n = 20$, white-beaked dolphin $n = 99$, harp seal $n = 5$) and liver tissue from harbor porpoise ($n = 10$) (harbor porpoise liver used only in the lipid-extracted versus non-lipid-extracted analysis; see Section 2.4). Samples of bearded seal, ringed seal, and walrus were stored as a full blubber–muscle profile and muscle was subsampled for analysis, while all other species were subsampled on collection and muscle was stored independently. Samples were analyzed twice: once each for lipid-extracted and non-lipid-extracted analysis. A 0.4 g sample of each tissue was weighed, cut into small pieces, and oven-dried overnight at 80°C (Barrow et al. 2008). Samples were ground using a glass mortar and pestle, and half of the dried sample was reserved for non-lipid-extracted analysis. To extract lipids from the remaining half of each sample, 2 ml of 2:1 chloroform:methanol was added and samples were incubated for 24 h at 30°C, subsequently rinsed twice with 2:1 chloroform:methanol and then allowed to dry completely (Stern et al. 2021). For a small number of samples (3 minke whale, 3 white-beaked dolphin, 2 long-finned pilot whale) for which we had less than 0.4 g of tissue, lipids were not extracted and the whole sample was dried and ground for non-lipid-extracted analysis only.

A 1.2 mg mass of each powdered sample was weighed into a tin capsule and analyzed on a Thermo Scientific EA Isolink Flash Elemental Analyzer with ramped gas chromatography oven paired with a Delta V Plus Isotope Ratio Mass Spectrometer (IRMS) configured to simultaneously measure carbon, nitrogen, and sulfur (CNS) isotopes. To compensate for low amounts of sulfur in our samples relative to car-

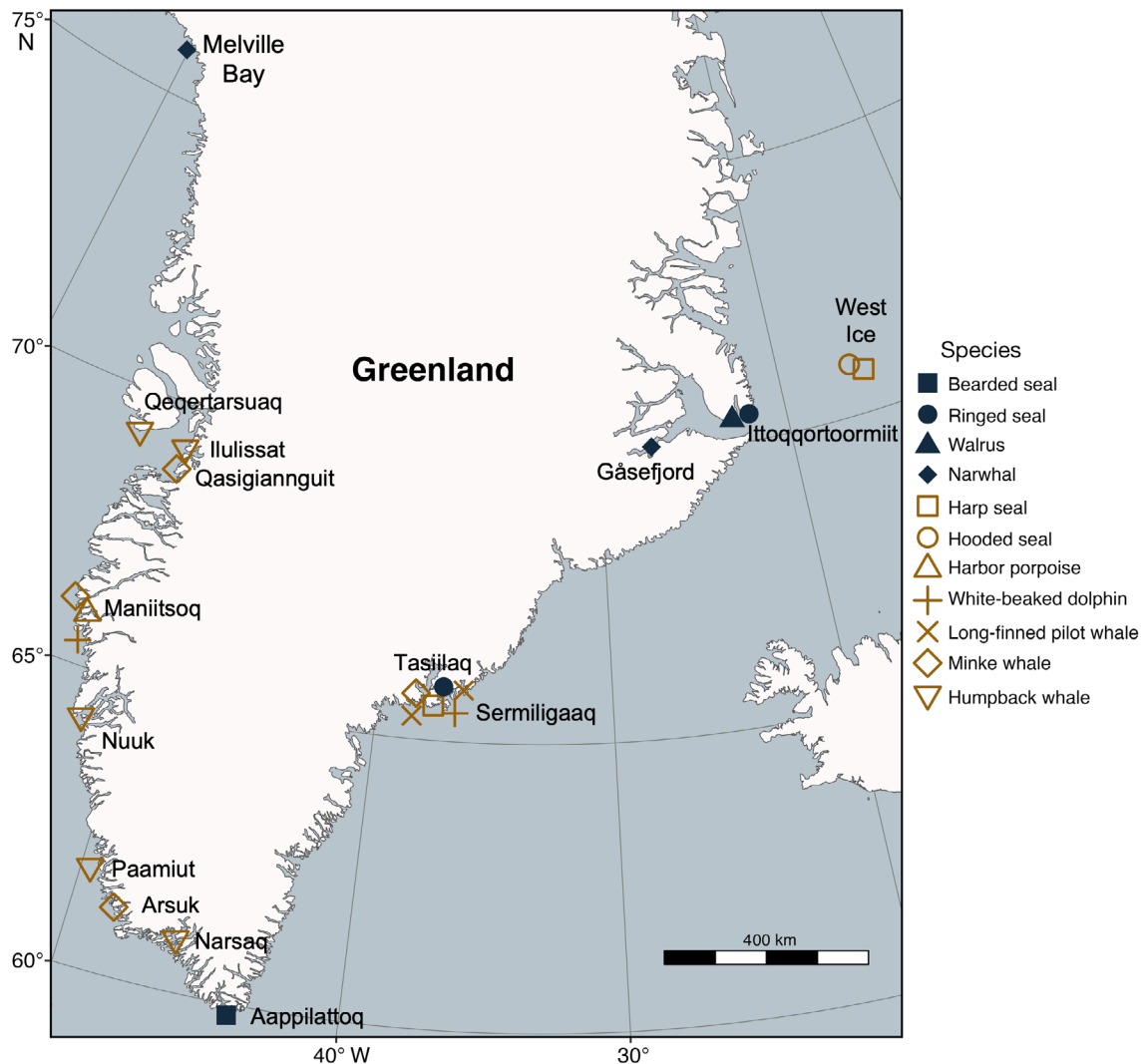


Fig. 1. Sampling locations for 11 species collected around Greenland primarily from 2010 to 2018. Four species are Arctic: bearded seal *Erignathus barbatus*, ringed seal *Pusa hispida*, Atlantic walrus *Odobenus rosmarus rosmarus*, and narwhal *Monodon monoceros*; 7 are range-shifting sub-Arctic species: harp seal *Pagophilus groenlandicus*, hooded seal *Cystophora cristata*, harbor porpoise *Phocoena phocoena*, white-beaked dolphin *Lagenorhynchus albirostris*, long-finned pilot whale *Globicephala melas*, minke whale *Balaenoptera acutorostrata*, and humpback whale *Megaptera novaengliae*. Multiple species were collected near the same site in 4 locations (Maniitsoq, Tasilaq, Ittoqqortoormiit, West Ice) and points were shifted very slightly for readability. One minke whale from an unknown location is not shown

bon and nitrogen, helium flow through the elemental analyzer was reduced part-way through the run to concentrate sulfur and amplify the sulfur peak in the IRMS (Sayle et al. 2019). Duplicates were run for one in 10 samples.

Values were calibrated against international reference materials from the United States Geological Survey (USGS) and International Atomic Energy Agency (IAEA) (USGS40, USGS41a, IAEA-N-2, IAEA-S-1, IAEA-S-2, IAEA-S-3) to obtain $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$. The isotope ratio was calculated for each element as:

$$\delta X = \frac{R_{\text{sample}} - R_{\text{reference}}}{R_{\text{reference}}} \times 1000$$

Inter-day analytical precision was assessed using replicates of reference materials; specifically, USGS 40 and USGS41a for carbon and nitrogen, and IAEA-S-1 for sulfur. Standard deviations (SD) of both USGS standards were 0.09–0.11‰ for carbon (n = 108) and 0.08–0.09‰ for nitrogen (n = 108), while SD was 0.14‰ for sulfur (n = 55). We determined accuracy using standards USGS88, USGS89, and Elemental Microanalysis gelatin B2215 for carbon and nitrogen (n = 69), and gelatin B2215 only for sulfur (n = 24),

by calculating the mean difference from certified values for each element: $0.06 \pm 0.17\%$ for carbon, $0.17 \pm 0.08\%$ for nitrogen, and $0.16 \pm 0.28\%$ for sulfur. Intra-day precision based on duplicates run for 10% of samples ($n = 40$) showed a mean absolute difference of $0.10 \pm 0.16\%$ for carbon, $0.05 \pm 0.04\%$ for nitrogen, and $0.11 \pm 0.20\%$ for sulfur.

Additional samples of muscle tissue from harp ($n = 4$) and hooded seal ($n = 4$) from the West Ice, narwhal from Gåsefjord ($n = 17$), and ringed seal from Ittoqqortoormiit in 2018 ($n = 17$) were analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ at the Center for Permafrost at the University of Copenhagen, Denmark. Only non-lipid-extracted analysis was performed. Samples were analyzed with an elemental analyzer (CE 1110, Thermo Electron) paired with an IRMS (Finnigan MAT Delta PLUS, Thermo Scientific), using international reference materials (IAEA sucrose and ammonium sulfate) to calibrate internal reference gases, with an analytical precision of $<0.1\%$ SD. While no samples were run at both labs to allow direct comparison, ringed seal samples collected near Ittoqqortoormiit in different years (2012 for McGill, 2018 for Copenhagen) showed small mean differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($\leq 1.1\%$). These differences were well within expected intraspecies variation and not large enough to obscure inter-species differences, so data from both labs was retained.

2.3. Fatty acid signature analysis

We extracted fatty acids from the blubber of all species and included a standard reference material, NIST1945 Pilot Whale Blubber, with each batch of samples, as per established procedures (McKinney et al. 2013). In summary, we treated 0.3–0.5 g of blubber with 10.5 ml of 2:1 chloroform:methanol containing 0.01% butylated hydroxytoluene. After adding 2.6 ml of 0.9% sodium chloride, we extracted the chloroform–lipid layer and filtered extracts through anhydrous sodium sulfate before fully evaporating chloroform to determine lipid content. Extracted fatty acids were *trans*-esterified to fatty acid methyl esters (FAMES) using the Hilditch reagent. Extracted FAMES were diluted with hexane to 50 mg FAME per ml and then analyzed on an Agilent 8860 gas chromatograph (Agilent Technologies) with a flame ionization detector (Pedro et al. 2019, Facciola et al. 2022). A total of 69 monitored fatty acids were quantified as mass percent of total FAME. The accuracy was indicated by the percent error for NIST1945 values relative to the published values (Kucklick et al. 2010) and showed a

mean (\pm SD) of $16 \pm 23\%$. The intra-day precision, indicated by the relative percent difference between duplicate samples ($n = 6$), was $8 \pm 13\%$.

2.4. Data analysis

For all species analyzed for both lipid-extracted and non-lipid-extracted stable isotopes, and for which we had a sample size greater than 3, we compared raw $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, or $\delta^{34}\text{S}$ from lipid-extracted versus non-lipid-extracted tissues. To do so, we used paired *t*-tests with a Bonferroni correction ($\alpha / 21 = 0.0024$) to test for differences in mean $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, or $\delta^{34}\text{S}$ values between the 2 treatments.

To compare feeding patterns, we tested for differences in mean CNS isotope values among species using one-way ANOVAs. Harbor porpoise were excluded from all isotopic comparisons between species, as liver isotopic values are not always comparable to muscle in marine mammals, and muscle and liver have different turnover rates (Sinisalo et al. 2008, Loseto et al. 2008). Although there is a known latitudinal trend in the $\delta^{15}\text{N}$ isotopic baseline around Greenland (Hansen et al. 2012), correcting for this baseline did not reduce variation in the data, and appeared to over-correct for species collected in more southern latitudes. Additionally, because many of the sub-Arctic species are migratory (Heide-Jørgensen et al. 2023), collection location does not necessarily represent the main feeding location during other times of the year, so we did not baseline-adjust the $\delta^{15}\text{N}$ values. Trends in $\delta^{13}\text{C}$ baseline values are not consistent around Greenland (Hansen et al. 2012), and there is a lack of information on the sulfur isotopic baseline, so we did not attempt baseline adjustment for $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$. ANOVAs were run on the raw $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and $\delta^{34}\text{S}$ values, as the data were normally distributed and showed homogeneity of variances, confirmed through visual inspection of residual and *Q-Q* plots. We ran post hoc Tukey's HSD tests to determine which species differed significantly in their mean stable isotope ratios for each element.

We also tested for interspecific variation in feeding patterns based on fatty acid signatures. As fatty acid data are proportional, fatty acids from all 11 species were first transformed using a log-ratio transformation: $x_{\text{trans}} = \ln[x_i / g(x)]$, with $g(x)$ being the geometric mean of all fatty acid proportions in the sample (Aitchison 1983, Budge et al. 2008, Bourque et al. 2018). We next selected a limited set of fatty acids to use in further analyses to satisfy a minimum 5:1 sample:variable ratio for both principal component

analysis (PCA) and MANOVA (Budge et al. 2006). To do so, we calculated the mean of each fatty acid value for each species, and individual fatty acids were only used if they had a mean proportion of $\geq 0.1\%$ for all species to avoid measurement variability for low-concentration fatty acids. The set was then further limited to those fatty acids largely originating from diet rather than from de novo synthesis (Iverson et al. 2004). For the PCA, the number of fatty acids was further reduced to a final set of 14 by selecting those fatty acids from this reduced set of dietary fatty acids that had the highest mean proportions across species: 16:3n6, 18:2n6, 18:3n3, 18:4n3, 20:1n11, 20:1n9, 20:1n7, 20:2n6, 20:4n6, 20:4n3, 20:5n3, 22:1n11, 22:2n9, and 22:6n3. PCA then was performed on the transformed data using the package 'FactoMineR' in R (Lê et al. 2008). For MANOVA, because the number of response variables is limited to fewer than the number of the smallest group (Budge et al. 2006), we first grouped harp and hooded seals as 'sub-Arctic seals', given their overlapping fatty acid signatures (McKinney et al. 2013), and then used the 7 fatty acids from our limited set that had the highest mean proportions. MANOVA was performed to test whether the fatty acid profiles of each group were different, and because fatty acids did not show homogeneity of variance, post hoc Welch's ANOVAs were performed on each fatty acid to determine which specific fatty acids showed interspecific differences. For those fatty acids that showed differences, a post hoc Games-Howell test was used to test for pairwise differences in species' mean fatty acid concentrations. We did not consider sex, age, or year in these isotope and fatty acid analyses, as sex and age data were not available for all individuals and each species was not collected in all years (Table S1). Walrus were excluded from statistical tests of fatty acids with a sample size of 2. Fatty acids were interpreted based on known associations with lower trophic-level organisms, including 22:1n9 and 22:1n11 as *Calanus* copepod markers, 20:5n3 as a sea-ice algae diatom marker, and 22:6n3 as a dinoflagellate marker (Dalsgaard et al. 2003; our Table S2).

Feeding niche breadth and overlap using stable isotopes and fatty acids were primarily calculated using Bayesian estimates of probabilistic niche regions via the package 'nicheROVER' in R, using default non-informative priors and 10 000 repetitions (Swanson et al. 2015). In 2 dimensions, to measure niche breadth we instead used the package 'SIBER' in R to calculate standard ellipse area corrected for small sample sizes (SEA_C) (Jackson et al. 2011). The harbor porpoise was excluded again here for the analysis of stable isotope ratios, as only liver tissue was available. We first mod-

eled niche regions with only carbon and nitrogen to provide measures of isotopic niche breadth (SEA_C) comparable to previous studies that used these 2 isotopes. Calculations of niche breadth and overlap were then repeated using carbon, nitrogen, and sulfur in 3 dimensions, for all samples for which we measured all 3 elements, to assess the effect of adding sulfur on the separation of species' niches. Niche region size (N_R) was here used as a measurement of niche breadth while the probability of an individual from one species (species A) falling into the 95% probable niche region of another species (species B) was used to represent niche overlap of species B onto species A throughout. We then also calculated niche breadth (SEA_C) and overlap using PC1 and PC2 from the PCA of the fatty acid profiles to assess whether different tracers provided additional insight into overlap in species' feeding niches. All analyses were performed in R version 4.2.2 (R Core Team 2022). All data used in this study is accessible on the repository Zenodo (<https://doi.org/10.5281/zenodo.8125162>).

3. RESULTS

3.1. Impact of lipid extraction on stable isotope ratios

The effects of chemical lipid extraction varied by both species and element (Fig. 2, Table S3). In long-finned pilot whale and white-beaked dolphin, lipid extraction increased mean $\delta^{13}C$ values (Bonferroni-adjusted $p < 0.0001$) by 0.98 and 0.52‰, respectively. Lipid extraction did not significantly affect $\delta^{13}C$ values for all other (8 out of 10) species (Bonferroni-adjusted $p > 0.05$), but it did reduce the variance in $\delta^{13}C$ for most species. Lipid extraction increased mean $\delta^{15}N$ values of long-finned pilot whale, white-beaked dolphin, and bearded, ringed, and harp seals (Bonferroni-adjusted $p < 0.05$), while $\delta^{15}N$ values were not different after lipid extraction for the other 5 species (Bonferroni-adjusted $p > 0.05$). Increased $\delta^{15}N$ values after lipid extraction ranged from +0.41‰ for ringed seal to +0.60‰ for white-beaked dolphin. Values of $\delta^{34}S$ were lower after lipid extraction for bearded, ringed, and harp seals, and for harbor porpoise (Bonferroni-adjusted $p < 0.001$) but did not significantly differ between lipid-extracted and non-lipid-extracted tissues for the other 6 species (Bonferroni-adjusted $p > 0.05$). Decreased $\delta^{34}S$ values after lipid extraction ranged from -0.99‰ for harp seal to -0.72‰ for harbor porpoise. Lipid extraction did not affect any isotope in either of the

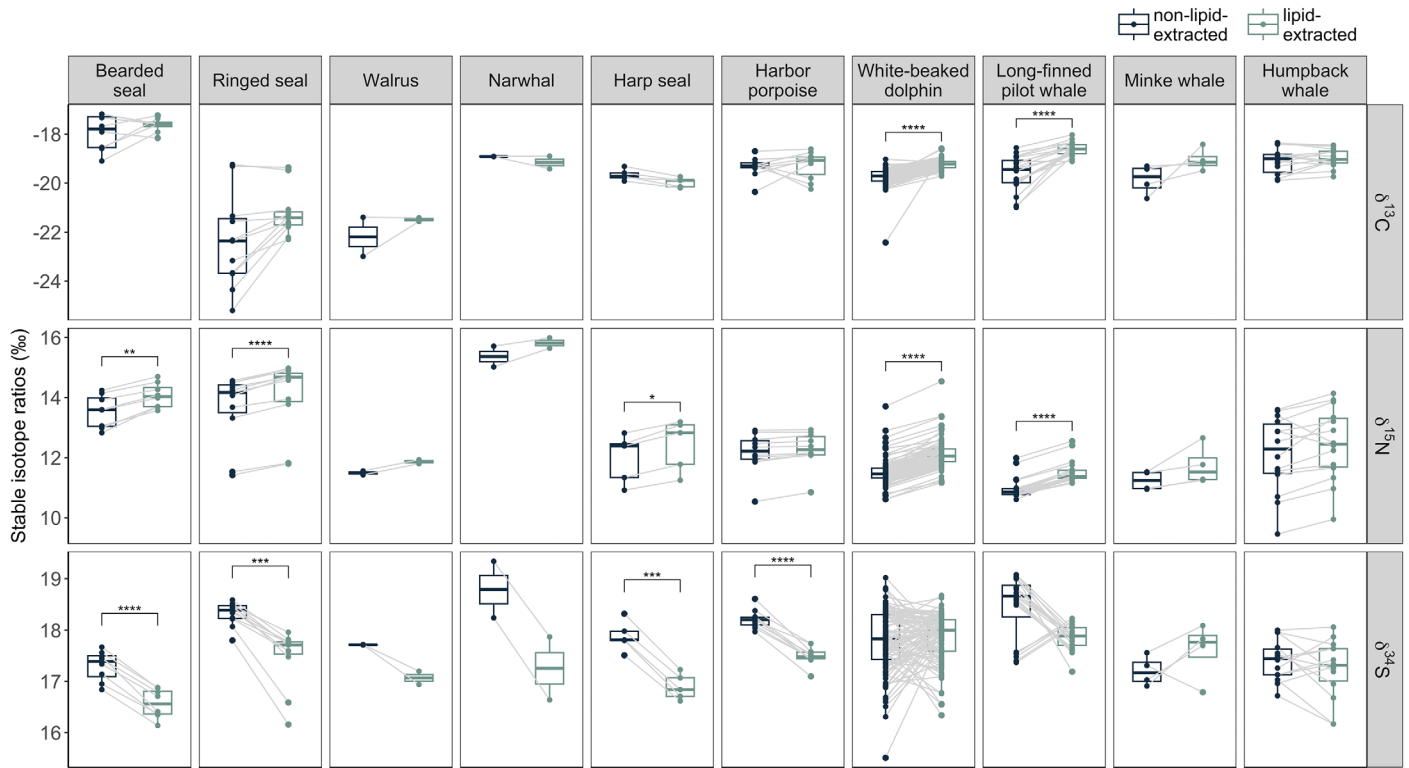


Fig. 2. Effect of chemical lipid extraction on stable isotope ratios of carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), and sulfur ($\delta^{34}\text{S}$) in marine mammal muscle tissues (except liver tissue for harbor porpoise) sampled in Greenland between 2010 and 2018 (except one minke whale from 2000 and 2 humpback whales from unknown years). Paired non-lipid-extracted and lipid-extracted samples from the same individuals are shown connected by gray lines. Paired t -tests were run for each element and species (excluding walrus and narwhal, for which $n = 2$), and Bonferroni-corrected equivalent of p -values are shown: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$. For each species and treatment, boxes represent quartile 1, median, and quartile 3, while whiskers show minimum and maximum excluding outliers. All data points are shown

baleen whale species. The variance in $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values was similar for each species between lipid-extracted and non-lipid-extracted tissues.

We used the results of our lipid-extracted and non-lipid-extracted stable isotope value comparisons to select whether to use lipid-extracted or non-lipid-extracted values for all subsequent analyses (Table S4). Because lipid extraction reduced the variance of $\delta^{13}\text{C}$ in most species and showed some significant effects on $\delta^{13}\text{C}$ values, whenever possible we used lipid-extracted carbon values for further comparison of stable isotopes between species. However, for a small number of minke whale samples ($n = 3$) that were analyzed for only non-lipid-extracted values because of small amounts of tissue, we used non-lipid-extracted $\delta^{13}\text{C}$ for subsequent analyses, as we found no difference between lipid- and non-lipid-extracted carbon signatures for this species. Additionally, all samples analyzed at the University of Copenhagen (some ringed seal, harp seal, hooded seal, and narwhal) were not lipid-extracted, but we

chose to include these $\delta^{13}\text{C}$ values in multi-species comparisons for the following reasons: (1) we found no significant differences in mean $\delta^{13}\text{C}$ for any seal samples analyzed for both treatments at McGill, and (2) for narwhal, although we were only able to analyze 2 samples for both treatments, the mean difference between lipid-extracted and non-lipid-extracted carbon signatures was small (-0.25‰). For $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$, lipid extraction significantly altered values for these isotopes for some species, and therefore we used non-lipid-extracted $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ for all subsequent inter-species comparisons.

3.2. Comparison of feeding patterns between species

For all 3 elements, interspecific differences were found (Fig. 3). One-way ANOVAs revealed differences in means of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ among species, with $F_{8,199} = 123.3$, $p < 0.0001$ for $\delta^{13}\text{C}$, $F_{8,199} =$

85.0, $p < 0.0001$ for $\delta^{15}\text{N}$, and $F_{6,157} = 10.3$, $p = 0.0001$ for $\delta^{34}\text{S}$. The species that showed different values varied by element, although the 2 baleen whale species did not differ from one another in the means of any of the 3 elements, and the 2 sub-Arctic pinnipeds, harp and hooded seals, did not differ in the means of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (hooded seals were not analyzed for $\delta^{34}\text{S}$).

For $\delta^{13}\text{C}$, the 4 Arctic species tended to have either high or low values, whereas more intermediate values were found for the sub-Arctic species. Bearded seal had the highest mean $\delta^{13}\text{C}$ of all species ($-17.63 \pm 0.29\text{‰}$, $p_{\text{adj}} < 0.0001$ for all pairwise comparisons). Ringed seal and walrus had the lowest $\delta^{13}\text{C}$ values, $-21.27 \pm 0.63\text{‰}$ and $-21.48 \pm 0.11\text{‰}$, respectively, and the ringed seal mean was significantly lower than all other species ($p_{\text{adj}} < 0.0001$), while walrus was excluded from statistical tests because of low sample size. The mean $\delta^{13}\text{C}$ for narwhal, the final Arctic spe-

cies, at $-20.48 \pm 0.63\text{‰}$, was significantly lower than all sub-Arctic species, except for harp and hooded seals, which had means of -20.07 ± 0.28 and $-20.07 \pm 1.04\text{‰}$, respectively. Among the 6 sub-Arctic species, these harp and hooded seals generally had lower $\delta^{13}\text{C}$ values than the sub-Arctic cetaceans, which had means ranging from -19.28 ± 0.77 to $-18.62 \pm 0.28\text{‰}$. Except for hooded seal and minke whale, all sub-Arctic cetaceans had significantly higher values than the sub-Arctic seals ($p_{\text{adj}} < 0.0052$).

Three Arctic species had among the highest mean $\delta^{15}\text{N}$ values, with $14.41 \pm 0.55\text{‰}$ for narwhal, $13.84 \pm 0.82\text{‰}$ for ringed seal, and $13.55 \pm 0.54\text{‰}$ for bearded seal, but walrus had one of the lowest $\delta^{15}\text{N}$ at $11.49 \pm 0.09\text{‰}$. The sub-Arctic seals also had relatively high $\delta^{15}\text{N}$ values, $12.62 \pm 1.02\text{‰}$ for harp seal and $13.79 \pm 0.72\text{‰}$ for hooded seal, relative to the 4 sub-Arctic cetacean species, which had lower $\delta^{15}\text{N}$ signatures than both the sub-Arctic seals and all Arctic species

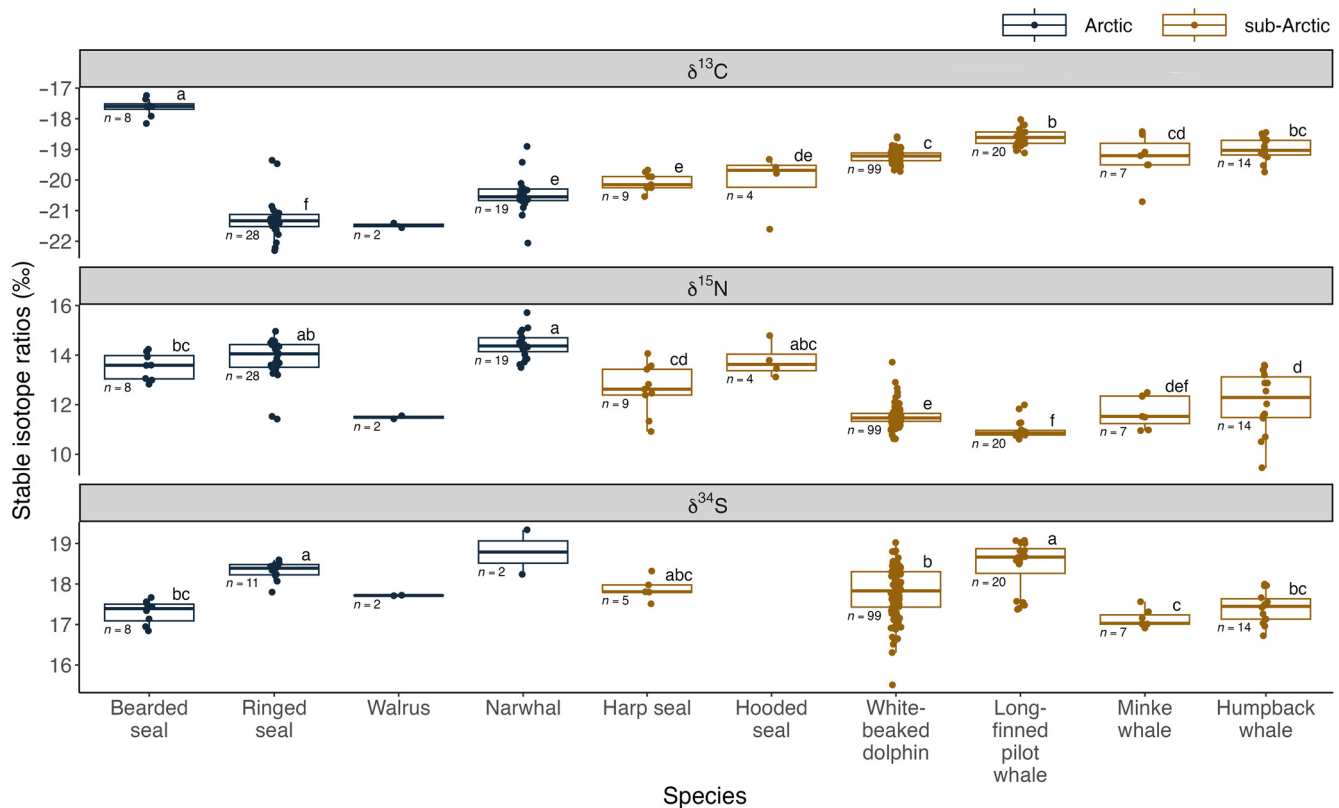


Fig. 3. Stable isotope ratios of carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), and sulfur ($\delta^{34}\text{S}$) in muscle samples of Arctic and sub-Arctic marine mammal species sampled around Greenland primarily from 2010 to 2018 (except one minke whale from 2000 and 2 humpback whales from unknown years). The $\delta^{13}\text{C}$ values are from lipid-extracted samples, while $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values are from non-lipid-extracted samples. The exception to this is that $\delta^{13}\text{C}$ for some minke whale ($n = 3$), ringed seal ($n = 17$), harp seal ($n = 4$), hooded seal ($n = 4$), and narwhal ($n = 17$) were only analyzed for non-lipid-extracted signatures, so non-lipid-extracted carbon ratios are shown. The same letters above boxplots represent groups with means that were not significantly different from each other, according to an ANOVA with post hoc Tukey HSD tests. Walrus was excluded from all statistical tests with a sample size of 2, while narwhal and hooded seal were also excluded from the test of sulfur isotopic ratios, with sample sizes of 2 and 0, respectively. Boxplot parameters as in Fig 2

except for walrus ($p < 0.0001$), apart from harp seal and the 2 baleen whales.

There was overall less variation in $\delta^{34}\text{S}$ between species relative to $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Fig. 3). The total $\delta^{34}\text{S}$ range (3.83‰) was smaller than for $\delta^{13}\text{C}$ (5.07‰) or $\delta^{15}\text{N}$ (6.26‰). No clear trends were visible either between sub-Arctic and Arctic species or between taxa. For means of all species and all elements, see Table S5.

Blubber profiles of the top 7 fatty acids of dietary origin differed by species (MANOVA, $p < 0.0001$) (Fig. 4, Table S6). When we tested each fatty acid individually, proportions of all were also affected by species (post hoc Welch's ANOVA, $p < 0.0001$). Fatty acids 22:1n11, 20:5n3, and 22:6n3 differed the most between Arctic and sub-Arctic species, with Arctic species generally having lower proportions of 22:1n11 and higher proportions of 20:5n3 and 22:6n3. The exception to this trend was for narwhal, for which the proportions of both fatty acids were more similar to sub-Arctic species. Additionally, harp and hooded seals had similarly high proportions of 20:5n3 and 22:6n3 as bearded seal, ringed seal, and walrus. Baleen whales had intermediate proportions of these 2 fatty acids, while all odontocetes ('toothed whales')

had the lowest proportions. The fatty acids 20:1n11 and 20:1n9 showed patterns similar to 22:1n11, but differences between Arctic and sub-Arctic species were less pronounced. Proportions of 18:4n3 varied by species, but without any clear trend on species grouping, while 18:2n6 was generally similar among all species. The mean proportions of all 7 fatty acids did not differ between the 2 baleen whale species ($p > 0.05$).

3.3. Feeding niche breadth and overlap

Visualizing niches of all marine mammal species using both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and a PCA of the fatty acid profiles revealed varying niche size, niche separation, and potential overlap between species (Figs. 5, 6, & S1). Patterns in niche breadth among species varied based on the metric used (Table 1). Isotopic niche breadth, measured as SEA_C using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, was highest in 3 sub-Arctic species, harp and hooded seals (grouped for this analysis), minke whale, and humpback whale (Fig. 5, Table 1). Ringed seal and narwhal had more intermediate niche sizes, while white-beaked dolphin, long-finned pilot whale, and bearded

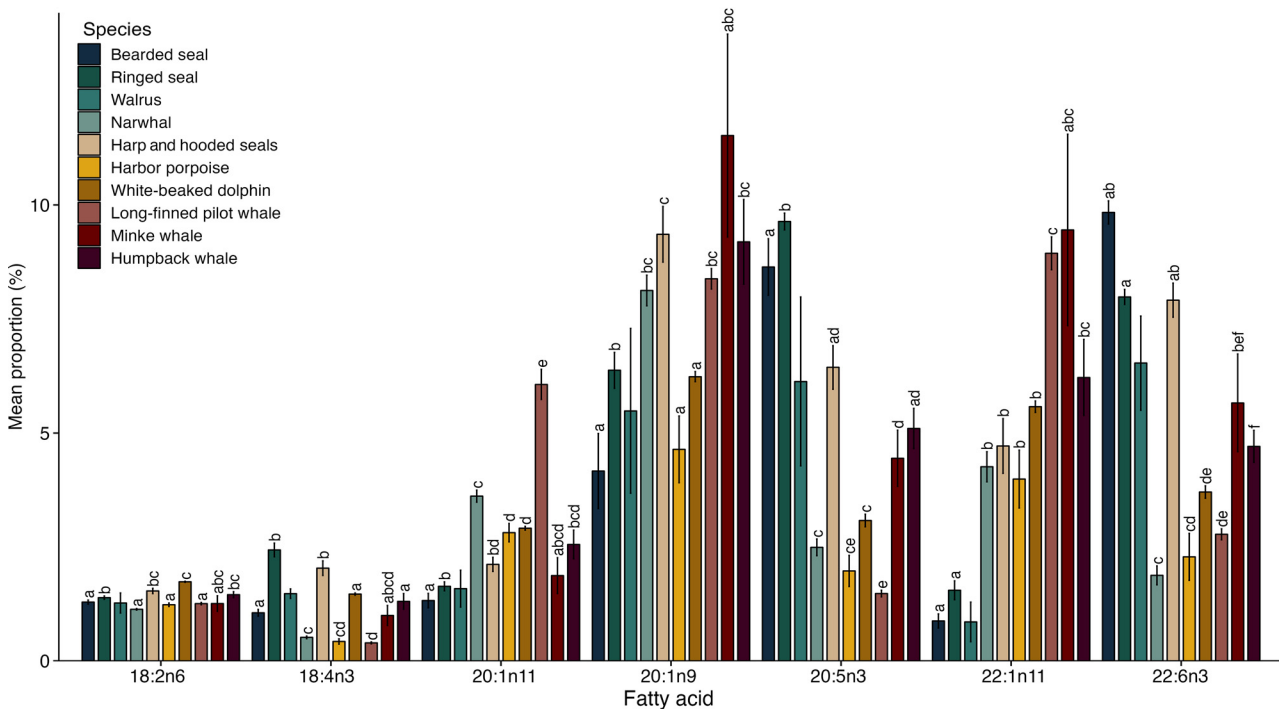


Fig. 4. Proportions of the major fatty acids of dietary origin in the blubber of Arctic and sub-Arctic marine mammal species sampled around Greenland primarily from 2010 to 2018 (except one minke whale from 2000 and 2 humpback whales from unknown years). A one-way MANOVA of these 7 fatty acids determined that fatty acid profile varies by species. Post hoc Welch's ANOVAs on each fatty acid determined that all individual fatty acids also varied by species, and pairwise comparisons are shown with letters above each bar. Within each individual fatty acid, the same letters indicate species that did not have significantly different mean proportions of that fatty acid. Error bars represent standard error

seal had the smallest SEA_C . However, when $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ were all used to calculate N_R , 42 individuals not analyzed for sulfur were excluded, and patterns differed (Fig. S1). Using N_R , humpback whale still had the largest niche, but harp and hooded seals and minke whale were smaller and more similar to all other species measured (Table S7). Because many individuals were removed, measures of niche breadth including sulfur are not directly comparable to measures including all individuals with $\delta^{13}C$ and $\delta^{15}N$ and fatty acids. For fatty acids, SEA_C based on PC1 and PC2 of a PCA of all individuals showed that minke whale (along with harbor porpoise) had the largest fatty acid niche, while humpback whale and harp and hooded seals were more comparable to the other species. Long-finned pilot whale and ringed seal had the smallest fatty acid niches, while all other species had similar or slightly larger SEA_C from fatty acids.

Fatty acid profiles, based on the top 14 dietary fatty acids in all species, separated species more by taxa

than Arctic vs. sub-Arctic grouping (Fig. 6). Pinnipeds loaded the most positively on PC1, followed by baleen whales, while odontocetes loaded more negatively. PC2 separated the odontocetes between larger (narwhal and long-finned pilot whale) and smaller (white-beaked dolphin and harbor porpoise) species. PC2 also separated the Arctic pinnipeds from the baleen whales and harp and hooded seals, which were more closely clustered.

For isotopic niches defined by $\delta^{13}C$ and $\delta^{15}N$, the most overlap was evident among all sub-Arctic species (Figs. 5 & 7). Arctic species tended to have isotopic signatures at the more extreme values, while all sub-Arctic species clustered with more intermediate values. Harp and hooded seals had the isotopic niche closest in isotopic space to, but still distinct from, narwhal and ringed seal, while bearded seal was not close to any other species. Including sulfur (Fig. S1) did not clarify separation of any species not already separated by $\delta^{13}C$ and $\delta^{15}N$. Calculated prob-

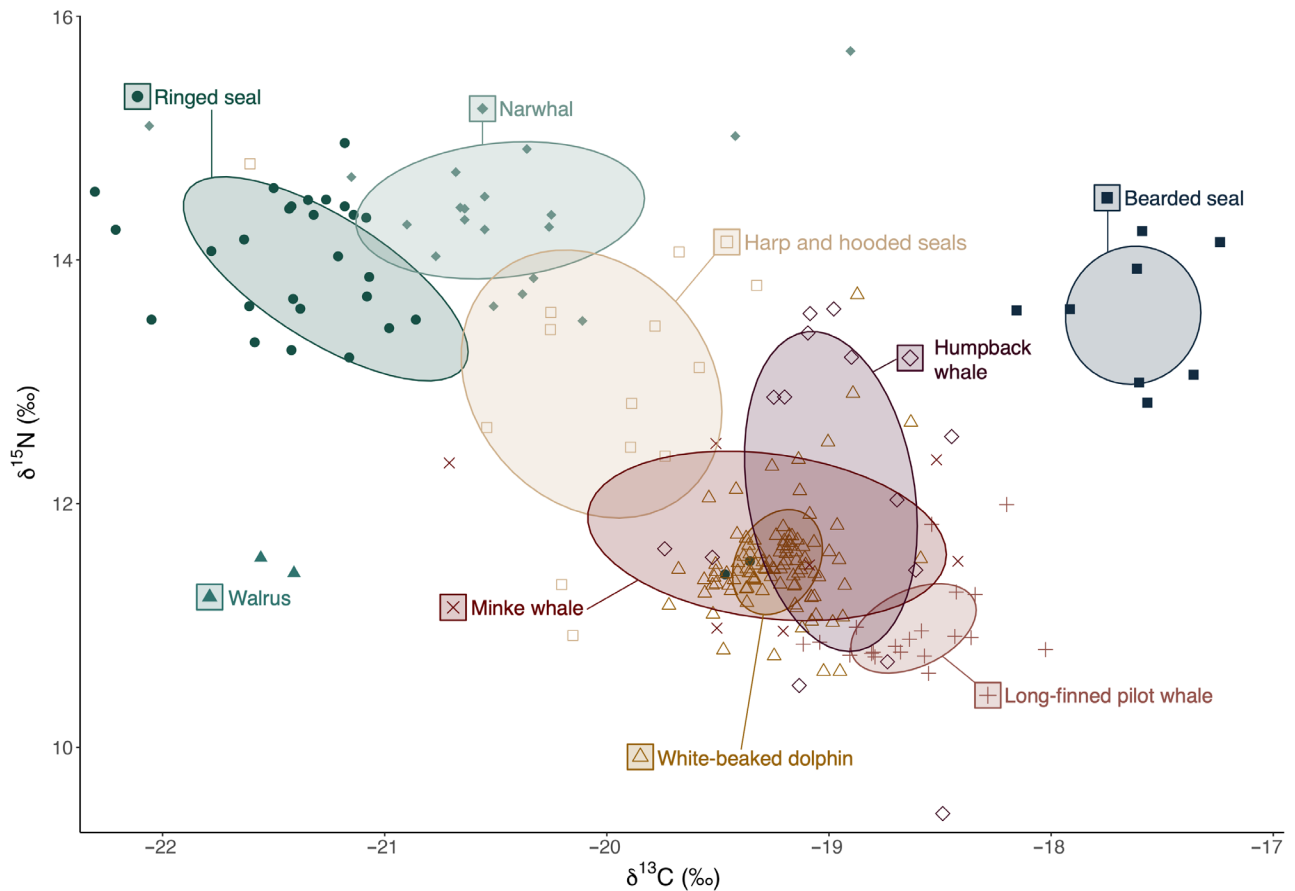


Fig. 5. Stable isotope ratio biplots of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in muscle samples of Arctic (filled shapes) and sub-Arctic (open shapes) marine mammal species sampled around Greenland primarily from 2010 to 2018 (except one minke whale from 2000 and 2 humpback whales of unknown year). Ellipses represent confidence intervals of 0.4 for each species.

Harp and hooded seals are grouped based on similar ecology and small sample sizes

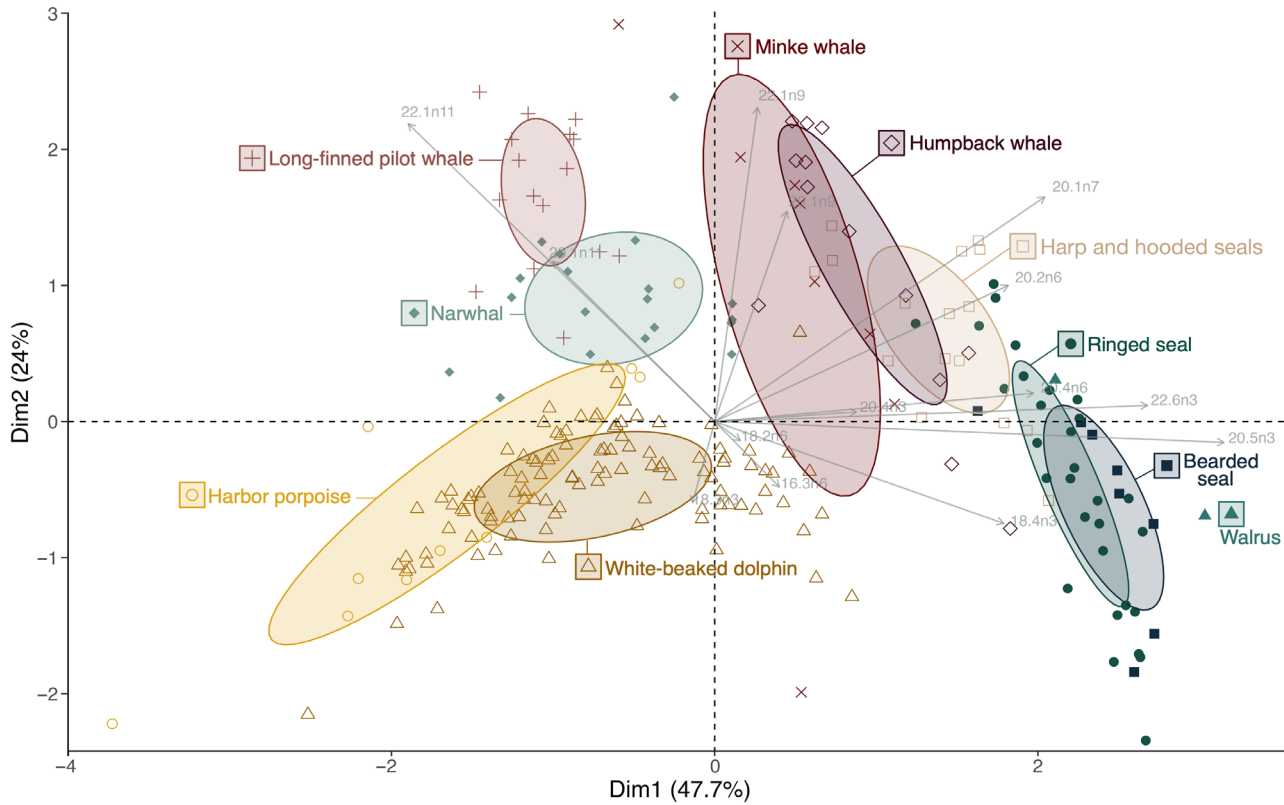


Fig. 6. Principal component analysis of fatty acid signatures from blubber samples of Arctic (filled shapes) and sub-Arctic (open shapes) marine mammal species sampled around Greenland primarily from 2010 to 2018 (except one minke whale from 2000 and 2 humpback whales of unknown year). The 14 fatty acids with the highest proportions in all species, and that are largely of dietary origin, were included. Percentages on axes labels indicate the percent of variance in fatty acid signatures explained by each PC. Ellipses represent confidence intervals of 0.4 for each species. Harp and hooded seals are grouped based on similar ecology, fatty acid patterns (McKinney et al. 2013), and small sample sizes

Table 1. Niche breadth of Arctic and sub-Arctic marine mammal species sampled around Greenland primarily from 2010 to 2018 (except one minke whale from 2000 and 2 humpback whales of unknown year), quantified through 3 metrics: (1) standard ellipse areas corrected for small sample sizes (SEA_C) calculated from stable isotope ratios of $\delta^{13}C$ and $\delta^{15}N$ and (2) SEA_C calculated from a principal component analysis of fatty acid signatures. SEA_C were calculated using the packages SIBER (Jackson et al. 2011) in R. SEA_C from fatty acids were calculated using axes PC1 and PC2 of a principal component analysis of the 14 most abundant fatty acids among all species that also derive primarily from diet

Species	SEA_C stable isotopes ($\delta^{13}C$, $\delta^{15}N$)	SEA_C fatty acids (PC1, PC2)
Bearded seal	0.57	0.69
Ringed seal	1.17	0.52
Narwhal	1.14	0.84
Harp and hooded seals	2.03	0.70
Harbor porpoise		1.60
White-beaked dolphin	0.26	0.86
Long-finned pilot whale	0.30	0.44
Minke whale	1.85	2.30
Humpback whale	1.60	0.91

abilities of niche overlap using $\delta^{13}C$ and $\delta^{15}N$ to define a 95% niche region also demonstrate the highest probabilities of overlap among sub-Arctic species, except for a high probability of harp and hooded seals overlapping both narwhal and ringed seal (Fig. 7a). Narwhal and ringed seal also had moderate probabilities of overlapping each other (43.3–58.2%), with quite low probabilities (<15%) of overlap from any other species, with bearded seal showing low overlap with all species. The niches of the 2 baleen whale species had overall the highest probabilities of overlapping others, with moderate to high probabilities (32.1–97.8%) of overlapping all other sub-Arctic species. Using fatty-acid-based niches, probability of overlap was high between species of similar taxa, except for high probabilities of overlap between harp and hooded seals and baleen whales (Fig. 7b). Of the Arctic species, narwhal had the highest probabilities of overlap by sub-Arctic species, showing moderate probability of overlap (14.9–57.3%) by the fatty acid niches of harbor porpoise, white-beaked dolphin, long-finned pilot whale, and minke whale.

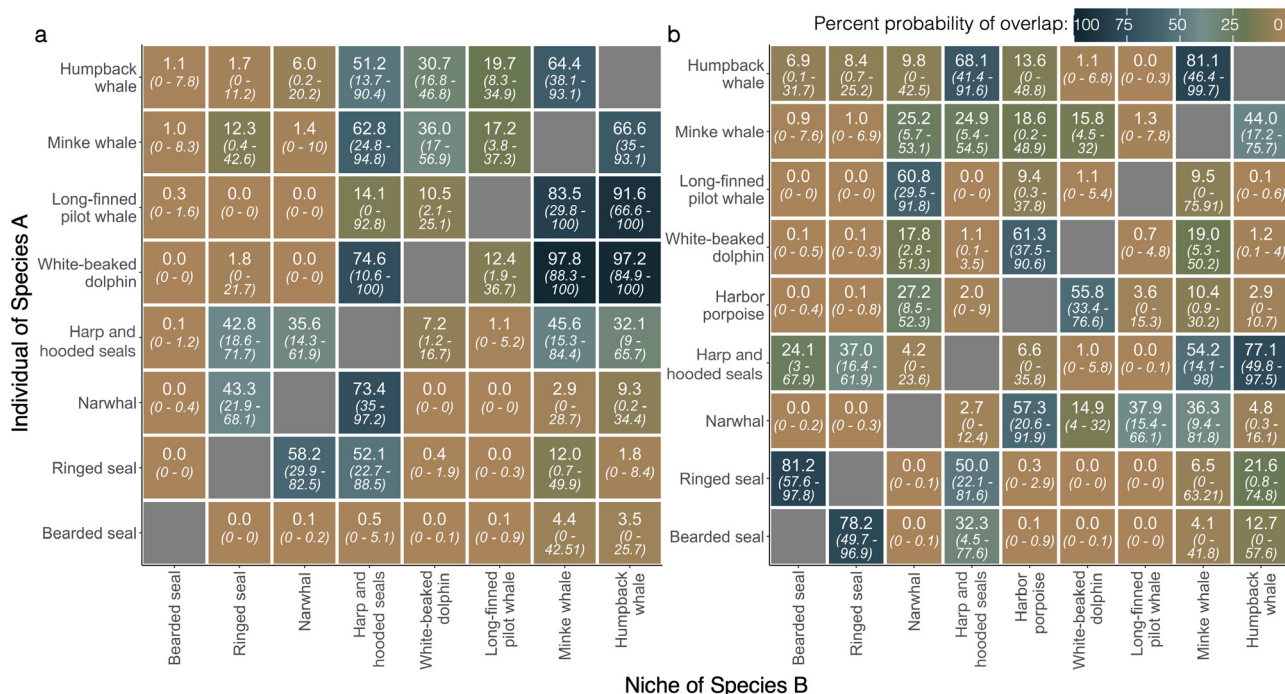


Fig. 7. Probability of tracer-based niche overlap of Arctic and sub-Arctic marine mammals collected around Greenland primarily from 2010 to 2018 (except one minke whale and 2 humpback whales), based on (a) stable isotope ratios of carbon and nitrogen and (b) axes PC1 and PC2 from a principal component analysis of fatty acid profiles. Numbers represent probability (as a percent) of an individual of species A (*y*-axis) falling into the 95% niche region of species B (*x*-axis), as described in the 'nicheROVER' package in R (Swanson et al. 2015). This indicates that the niche of species B overlaps species A. The 95% credibility intervals are shown below percent values

4. DISCUSSION

After assessing the effects of lipid extraction on stable isotope ratios in marine mammal tissues, we used both stable isotope ratios and fatty acid signatures to compare the feeding niches of 4 Arctic and 7 northward-shifting sub-Arctic marine mammal species in Greenland. We found that the effects of lipid extraction varied according to species and element (among carbon, nitrogen, and sulfur), although increases in carbon signatures after lipid extraction were small and rarely significant. There were more often significant effects of lipid extraction for $\delta^{15}\text{N}$, and we also demonstrate for the first time that $\delta^{34}\text{S}$ values for marine mammal muscle were significantly depleted for some species after lipid extraction. Subsequent interspecific comparisons showed differences in stable isotope values, as well as in the proportions of some of the most abundance fatty acids, between Arctic and sub-Arctic marine mammal species. In quantifying niche breadth, sub-Arctic species consistently had the largest niches, particularly the baleen whales, harbor porpoise, and harp and hooded seals. Patterns in niche overlap differed between isotopes and fatty acids but generally showed high degrees of

separation among species. However, there were some instances of overlap between Arctic and sub-Arctic species that emphasize areas of further potential for feeding competition as sub-Arctic species continue to shift north with the warming climate.

4.1. Effects of lipid extraction on stable isotope ratios

Lipid extraction affected $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, consistent with previous studies on marine mammal muscle (Horstmann-Dehn et al. 2012, Yurkowski et al. 2015). Nonetheless, like these other studies, the size of the effect on $\delta^{13}\text{C}$ was small (maximum of 1.16‰), and the effect was only significant for white-beaked dolphin and long-finned pilot whale. These 2 species showed higher $\delta^{13}\text{C}$ after lipid extraction but also had the largest sample sizes (99 and 20, respectively), so the higher power of the *t*-tests for these species may explain this result. We found no significant effect of lipid extraction on $\delta^{13}\text{C}$ for any seal species, which contrasts significant enrichment for harp seal and the somewhat unusual depletion for bearded seal previously reported (Yurkowski et al. 2015). The limited

effect size of lipid extraction on $\delta^{13}\text{C}$ values was likely caused by low lipid content in our samples. Although for most species, the C:N ratios of non-lipid-extracted tissues (Table S3) were above thresholds used for lipid extraction (3.4 or 3.5; e.g. Larocque et al. 2021, Yurkowski et al. 2015), the magnitude of changes in $\delta^{13}\text{C}$ relative to changes in C:N after lipid extraction were consistent with previous studies (Table S3, Yurkowski et al. 2015, Larocque et al. 2021).

For $\delta^{15}\text{N}$, we found an effect of lipid extraction for bearded seal, ringed seal, and harp seal, while Yurkowski et al. (2015) found effects for ringed and bearded but not harp seals. These studies together suggest that species may not be the only factor influencing lipid extraction effects on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for marine mammals and should not necessarily be the basis for decision-making around lipid extraction. Both studies overall found more significant effects on $\delta^{15}\text{N}$ than $\delta^{13}\text{C}$, likely caused by co-extraction of lipid-associated proteins (Sotiropoulos et al. 2004, Bodin et al. 2007), suggesting that the bias on $\delta^{15}\text{N}$ caused by lipid extraction may outweigh any benefits of lipid extraction for $\delta^{13}\text{C}$, depending on the research question. Nonetheless, the variance in $\delta^{13}\text{C}$ decreased after lipid extraction for most species, which could be caused by variation in lipid content among individuals (Post et al. 2007). Decreased variance was particularly noticeable for samples stored as a full muscle–blubber profile (ringed seal, bearded seal, walrus) versus muscle stored separately from blubber (all other species). Although only a qualitative observation, it may suggest that studies not planning to lipid-extract tissue should collect muscle and blubber in separate sampling containers during field work and storage to avoid a potential influence of blubber lipids on muscle $\delta^{13}\text{C}$ values.

To our knowledge, this is the first study to assess the effects of lipid extraction on muscle $\delta^{34}\text{S}$ of marine mammals, and our results indicate that at least for seal species, lipid extraction can significantly bias $\delta^{34}\text{S}$ values. Sulfur ratios have been suggested as a promising new tool to separate benthic and pelagic feeding patterns and as markers of migration in marine species (Hoekstra et al. 2002, Connolly et al. 2004, Szapak & Buckley 2020). To do so, the effects of lipid extraction on $\delta^{34}\text{S}$ must be assessed. Recent studies have found mixed results on the effects of lipid extraction on $\delta^{34}\text{S}$ in various tissues, finding no effect for brown bear tissues (Javornik et al. 2019), significant effects for shark liver and muscle but not pinniped skin (Riverón et al. 2022), and mixed effects on salmon muscle and seabird eggs (Oppel et al. 2010, Elliott et al. 2014, Larocque et al. 2021). Effects are likely caused by the

co-extraction of sulfolipids or sulfur-containing proteins during lipid extraction (Oppel et al. 2010) and could affect the interpretations of $\delta^{34}\text{S}$ values. Because there are only small amounts of sulfur in muscle and liver samples, the removal of even small quantities of these compounds could explain the effects observed. In this study, the total observed range of $\delta^{34}\text{S}$ values was smaller than those of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, while the effect sizes of lipid extraction are comparable across elements. Therefore, the effect of lipid extraction is proportionally greater for $\delta^{34}\text{S}$, potentially obscuring ecologically significant patterns from $\delta^{34}\text{S}$. The cetacean species often showed intraspecific variation in the direction and magnitude of effects of lipid extraction without overall significant species-level effects, suggesting that lipid extraction may result in unreliable $\delta^{34}\text{S}$ values for these species as well as for seals. Interestingly, long-finned pilot whales showed lower values becoming more enriched and higher values becoming more depleted, but the cause of this pattern is unclear. Consequently, we recommend using non-lipid-extracted tissue for $\delta^{34}\text{S}$ of marine mammal muscle in future studies.

4.2. Inter-species comparisons of stable isotope patterns

After these observed effects were used to inform the choice of treatment for each element for inter-species comparisons, Arctic species generally had more enriched or depleted $\delta^{13}\text{C}$ values than sub-Arctic species. Bearded seal had the highest $\delta^{13}\text{C}$ of all 11 species analyzed, while ringed seal, walrus, and narwhal had values lower than almost all sub-Arctic species. While few studies of these species' diets have been done in Greenland specifically, bearded seal is generally known for benthic foraging patterns (Hjelset et al. 1999), and higher $\delta^{13}\text{C}$ is associated with benthic feeding (France 1995), likely explaining these high values. However, the low $\delta^{13}\text{C}$ of all other Arctic species is somewhat surprising, as ringed seal and particularly walrus are also known to feed benthically at least occasionally (Hobson et al. 2002). There is a documented difference in $\delta^{13}\text{C}$ between the ice-associated food web and pelagic food webs, with ice-associated carbon sources having higher $\delta^{13}\text{C}$ than pelagic carbon (Kohlbach et al. 2016); however, this interpretation does not match our data showing ringed seal, narwhal, and walrus all having lower $\delta^{13}\text{C}$ than the sub-Arctic species.

A more likely explanation for the low $\delta^{13}\text{C}$ values of ringed seal, narwhal, and walrus relative to sub-

Arctic species may be baseline $\delta^{13}\text{C}$ variation around Greenland; these species were primarily collected from central East Greenland near the Kangertittivaq fjord system (Scoresby Sound) and the municipality of Ittoqqortoormiit during the winter when extensive ice allows limited access to, e.g. *Mya* spp., *Hiatella* spp., and *Serripes* spp. While variation in $\delta^{13}\text{C}$ baseline around Greenland has been documented (Hansen et al. 2012), clear geographic patterns are not evident, and baseline values have not been reported in central East Greenland near this fjord. Carbon ratios of the bearded seal in this study are reasonably consistent with values found in other locations (Hoekstra et al. 2002, Young et al. 2010, MacKenzie et al. 2022), while ringed seal values are low compared to other ringed seals (Young et al. 2010, Young & Ferguson 2014, MacKenzie et al. 2022). Ringed seal teeth from near Ittoqqortoormiit have also shown lower $\delta^{13}\text{C}$ values than those from central West Greenland (Aubail et al. 2010), which was interpreted as colder Arctic waters brought southward to East Greenland via the East Greenland current causing a lower $\delta^{13}\text{C}$ baseline in that area compared to West Greenland waters, which are influenced by the warmer, more saline Irminger Current (Aubail et al. 2010). Furthermore, the narwhal and ringed seals in this study showed relative isotopic niche positions similar to that found in West Greenland (Linnebjerg et al. 2016), but with $\delta^{13}\text{C}$ values shifted $\sim 2\%$ lower. Therefore, the $\delta^{13}\text{C}$ baseline in central East Greenland, specifically near Kangertittivaq fjord, warrants further study, particularly as climate change continues to rapidly shift dynamics in East Greenland (Heide-Jørgensen et al. 2023). Going forward, compound-specific carbon isotope analysis could help disentangle the influence of baseline variation versus feeding habitat on $\delta^{13}\text{C}$ values of East Greenland marine mammals (McKinney et al. 2013, Whiteman et al. 2019, McMahon & Newsome 2019, Larsen et al. 2020). Specifically, patterns in the relative $\delta^{13}\text{C}$ values of diet-derived ('essential') amino acids can identify carbon originating from pelagic, sea-ice-associated, and benthic sources (Chen et al. 2022, Vane et al. 2023). These patterns are often maintained across regions with different $\delta^{13}\text{C}$ baselines (Larsen et al. 2013, Elliott Smith et al. 2018) and could therefore clarify differences in base carbon resource use, as well as baseline $\delta^{13}\text{C}$ variation, among species. Until then, the evidence for a particularly low $\delta^{13}\text{C}$ baseline in this area suggests that the low $\delta^{13}\text{C}$ values of ringed seal, narwhal, and walrus relative to sub-Arctic species may largely reflect baseline variation, obscuring possible evidence of distinct carbon resource use.

Excluding walrus, Arctic species had higher $\delta^{15}\text{N}$ values than sub-Arctic species, particularly than sub-Arctic cetaceans, suggesting that ringed seal, bearded seal, and narwhal feed at a higher trophic position than sub-Arctic species (Post 2002). Alternatively, these high $\delta^{15}\text{N}$ signatures could also be due to increases in baseline $\delta^{15}\text{N}$ with latitude (Hansen et al. 2012), and the fact that the Arctic species feed year-round at high latitude, whereas the sub-Arctic species only spend part of the year feeding in Greenland. Other studies have found relatively similar $\delta^{15}\text{N}$ values for bearded seal, ringed seal, and walrus (Dehn et al. 2007, Young et al. 2010, Aubail et al. 2011, MacKenzie et al. 2022). Harp and hooded seals had similar $\delta^{15}\text{N}$ values to the Arctic species, which is consistent with other areas of the Arctic (Ogloff et al. 2019). These sub-Arctic seals had higher $\delta^{15}\text{N}$ values than sub-Arctic cetaceans, though, which may be due to sub-Arctic seals having greater seasonal reliance on Arctic food webs than sub-Arctic cetaceans (Folkow et al. 2004, Haug et al. 2004, Laidre et al. 2008, Hamilton et al. 2021) and/or to sub-Arctic seals feeding on higher trophic position prey, at least compared to the baleen whales, which may partially feed on krill and pelagic fish (Laidre et al. 2010, Haug et al. 2017). The baleen whales also showed the largest ranges in $\delta^{15}\text{N}$ values, which could be influenced by fasting during migration, known to alter $\delta^{15}\text{N}$ ratios (Hobson et al. 1993, Newsome et al. 2010, Aguilar et al. 2014).

There were no clear patterns in $\delta^{34}\text{S}$ either by Arctic–sub-Arctic grouping or taxa. Sulfur ratios may reflect migration patterns, as sulfur baselines change with latitude (García-Vernet et al. 2022), and this could explain why migratory white-beaked dolphin had by far the largest range of $\delta^{34}\text{S}$ values, although the same pattern was not seen for the other migratory species. Long-finned pilot whale samples collected in similar locations in 2017 and 2018 showed differences in $\delta^{34}\text{S}$, but not in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$, possibly suggesting 2 groups of animals with different movement patterns. In Arctic studies, further investigation of drivers of variation in $\delta^{34}\text{S}$ (e.g. with latitude, migration, or habitat type—ice-associated vs. pelagic vs. benthic) is needed to increase the value of this tool.

4.3. Inter-species comparisons of fatty acid patterns

The PUFAs 20:5n3 and 22:6n3 were generally higher in Arctic species, while the opposite pattern was found for the monounsaturated fatty acids

(MUFAs) 20:1n9 and 22:1n11. The exceptions were narwhal, which had proportions of these fatty acids more similar to sub-Arctic species, and harp and hooded seals, which had proportions more similar to Arctic species. The variation in these signatures is evident on PC1, as species separated along a gradient from toothed whales to baleen whales to seals. Fatty acids 20:1n9 and 22:1n11 are *Calanus* copepod markers, indicating that sub-Arctic cetaceans and narwhals rely more on a pelagic, copepod-based food web (Dalsgaard et al. 2003). By contrast, higher levels of 20:5n3 in the other Arctic species and in the sub-Arctic seals are characteristic of feeding on the sea ice-associated food web with carbon from diatom-dominated ice algae (Dalsgaard et al. 2003), again consistent with greater use of Arctic food webs by harp and hooded seals than the other sub-Arctic species. Although 22:6n3 is generally considered to be a dinoflagellate marker and less indicative of sea ice (Dalsgaard et al. 2003), ice algae communities can vary in composition (Ratkova & Wassmann 2005, Lund-Hansen et al. 2020, Kunisch et al. 2021), and the higher levels of PUFAs relative to *Calanus*-marker MUFAs support less reliance on a pelagic food web. Bearded seals and walrus are specialized benthic feeders, and ringed seal occasionally feed benthically as well (Hjelset et al. 1999, Moore & Huntington 2008). In some areas of the Arctic, there is coupling of the benthic and ice-associated food webs (McMahon et al. 2006, Søreide et al. 2013, Kohlbach et al. 2019), so the close clustering of all Arctic pinnipeds could indicate reliance on common base carbon resources in both the benthic and ice-associated food webs, which is consistent with the high contributions of sea ice carbon to bearded seal, ringed seal, and walrus diets demonstrated in other areas of the Arctic (Koch et al. 2023). The clustering of baleen whales closer to the seals may reflect the presence of krill species in the whales' diet, which also have higher levels of 22:6n3 (Meier et al. 2016). Meanwhile, the clustering of narwhal firmly between all sub-Arctic species suggests vulnerability to competition for food resources.

The contrast of native Arctic species relying on sea ice and benthic resources while many increasingly present sub-Arctic species rely on pelagic resources reflects a broader trend observed across the Arctic in recent decades; as sea ice has decreased, ecosystems have transitioned from primarily benthic and sea ice-associated food webs to a higher dominance of pelagic food webs (Grebmeier et al. 2006, Meier et al. 2014, Brown et al. 2017, Florke et al. 2021). Future studies could use highly branched isoprenoid bio-

markers to further assess the coupling of sea ice-associated and benthic food webs in Greenland and to monitor changes in Greenland marine mammals' reliance on sea ice carbon as climate change progresses (Brown et al. 2014, Koch et al. 2023).

4.4. Niche breadth and overlap

Several sub-Arctic species had the highest niche breadths as determined using stable isotopes and fatty acids. Minke whales, humpback whales, and harp and hooded seals, which had the largest isotope SEA_C , are all generalist feeders, and their flexibility likely makes them more capable of exploiting novel areas and food resources as the Arctic warms (Kovacs et al. 2011, Moore et al. 2019). Harbor porpoise, which have been shown to feed on a variety of crustaceans, fish, and squid in Greenland (Teilmann & Dietz 1998, Lockyer et al. 2003) and have large home ranges in the North Atlantic (Nielsen et al. 2018), likewise showed large fatty acid niches, as did minke whales. While the patterns for species with smaller niche sizes were less clear, long-finned pilot whale had small niches using both tracers, consistent with their diet of primarily cephalopods (Santos et al. 2014). Native Arctic species had generally smaller niches, and the isotope SEA_C of narwhal and bearded seal were similar to those calculated using $\delta^{13}C$ and $\delta^{15}N$ in other regions, while ringed seal isotopic niche size was smaller than was found for conspecifics in Svalbard (1.17 vs. 1.96) (Zhao et al. 2022, MacKenzie et al. 2022). Small feeding niches emphasize the potential vulnerability of Arctic species, particularly narwhal, to ecosystem changes (Laidre et al. 2008, Chambault et al. 2020).

Patterns in niche overlap differed somewhat between the 2 tracer types, but sub-Arctic seals showed overlap with Arctic species when either tracer type was considered. The isotopic niches suggest that sub-Arctic cetaceans feed on similar prey resources to one another and overlap little with Arctic species, although there is likely some confounding influence of baseline variation on both $\delta^{13}C$ and $\delta^{15}N$. This could indicate that sub-Arctic cetaceans feed on shared sub-Arctic prey, such as capelin and other boreal fish that are also increasingly present in Greenland (Heide-Jørgensen et al. 2023). However, because baseline variation is likely biasing both $\delta^{13}C$ and $\delta^{15}N$ signatures and exaggerating separation between Arctic and sub-Arctic species, true feeding niche overlap of sub-Arctic and Arctic species may be higher than isotopic niches suggest. Even so, the

sub-Arctic seals showed high probabilities of overlapping native Arctic species (specifically ringed seal and narwhal), and in other locations, ringed seal and harp and hooded seals showed niche overlap as climate change has caused more geographic overlap as well (Ogloff et al. 2019). While controlled feeding trials are not feasible for many marine mammals, studies from other large mammals suggest that stable isotopes in muscle tissue have turnover rates of >3 mo to 1 yr (Sponheimer et al. 2006, Newsome et al. 2010, Vander Zanden et al. 2015), while blubber fatty acids likely integrate diet signatures on a scale of weeks to months (Budge et al. 2006, Watt & Ferguson 2015), so muscle stable isotopes may represent diet from a larger portion of the year, including when the migratory sub-Arctic species are at lower latitudes. Therefore, in addition to the effects of baseline variation on stable isotopes, differences between isotope and fatty acid niche overlap could represent species interactions on 2 different time scales, with fatty acids being more representative of the period in which Arctic and all sub-Arctic species overlap geographically. Fatty acids are also higher resolution tracers and may more clearly identify niche separation caused by prey with similar stable isotope signatures (i.e. among sub-Arctic cetaceans) (Budge et al. 2006), while stable isotopes can show differences in prey trophic levels not reflected in fatty acids. Despite these differences, fatty acid niches of harp and hooded seals also showed overlap with Arctic species (in this case, ringed seal and bearded seal), emphasizing that if food resources are limited, these seals may be the most likely to compete for food with Arctic species as climate-induced range shifts continue.

Fatty acid niches suggested moderate overlap of narwhal by multiple sub-Arctic species: harbor porpoise, white-beaked dolphin, long-finned pilot whale, and minke whale. While it is not clear exactly what prey these species may share, they seem to be feeding on a similar pelagic food web with a strong influence of *Calanus* copepods. Narwhal are already considered among the most vulnerable Arctic species to the effects of climate change because of their close associations with pack ice in winter, limited distributions, high site fidelity, specialized feeding, and possible increasing predation by killer whales (Laidre et al. 2008, Kovacs et al. 2011, Breed et al. 2017, Chambault et al. 2020). Although overlap probabilities on narwhal are moderate, the vulnerability of this species, and the likelihood of further community composition shifts as temperatures continue to rise, warrant particular attention. As climate change continues, competition for food resources

could be a significant, if indirect, negative effect of climate change on this important Arctic species.

4.5. Conclusions

This study provides a representation of the relationships between species' feeding patterns during the last decade, but as climate change continues to progress rapidly in the Arctic, and species' ranges and interactions continue to shift (Storrie et al. 2018, Hansen et al. 2019, Heide-Jørgensen et al. 2023), ongoing study of these inter-species relationships will be essential to understanding their effects on native Arctic species. Bulk stable isotopes currently demonstrate little niche overlap between Arctic and sub-Arctic species, but baseline isotopic variation likely masks true feeding niche segregation or overlap, and future studies using complimentary methods such as compound-specific stable isotope analysis are necessary to fully understand species' feeding dynamics. Fatty acids also generally demonstrate limited niche overlap between Arctic and sub-Arctic marine mammals, but together, both tracers point toward clear areas of potential niche overlap. Specifically, sub-Arctic seal species overlap the feeding niches of Arctic species the most of all range-shifting species, and narwhal appear to be the Arctic species most vulnerable to niche overlap by range-shifting species. This study demonstrates that as the Arctic continues to warm, some sub-Arctic and Arctic species may have the capacity to coexist through feeding niche segregation, while other may be vulnerable to niche overlap and potential competition. Although changing interspecific relationships can be challenging to observe, this project exemplifies how changing species interactions could serve as a potent threat of climate change to native species in the Arctic.

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