Ice algae are critical components to the lipid-driven Arctic marine food web, particularly early in the spring. As little is known about these communities in multiyear ice (MYI), we aimed to provide a baseline of fatty acid (FA) and stable isotope signatures of sea-ice communities in MYI from the Lincoln Sea and compare these biomarkers to first-year ice (FYI). Significant differences in the relative proportions of approximately 25% of the identified FAs and significantly higher nitrogen stable isotope values ($\delta^{15}$N) in bottom-ice samples of FYI ($\delta^{15}$N = 6.4 ± 0.7%) compared to MYI ($\delta^{15}$N = 5.0 ± 0.4%) reflect different community compositions in the two ice types. Yet, the relative proportion of diatom- and dinoflagellate-associated FAs, as well as their bulk and most of the FA-specific carbon stable isotope compositions ($\delta^{13}$C) were not significantly different between bottom FYI (bulk $\delta^{13}$C: −28.4% to −26.7%, FA average $\delta^{13}$C: −34.4% to −31.7%) and MYI (bulk $\delta^{13}$C: −27.6% to −27.2%, FA average $\delta^{13}$C: −33.6% to −31.9%), suggesting at least partly overlapping community structures and similar biochemical processes within the ice. Diatom-associated FAs contributed, on average, 28% and 25% to the total FA content of bottom FYI and MYI, respectively, indicating that diatoms play a central role in structuring sea-ice communities in the Lincoln Sea. The differences in FA signatures of FYI and MYI suggest different ice types harbor different inhabitants and that the loss of Arctic MYI will impact complex food web interactions with ice-associated ecosystems. Comparable nutritional quality of FAs, however, as indicated by similar average levels of polyunsaturated FAs in bottom FYI (33%) and MYI (28%), could help to ensure growth and reproduction of ice-associated grazers despite the shift from a FYI to FYI-dominated sea-ice cover with ongoing climate warming.

**Keywords:** Last Ice Area, Tuvaijuittuq Marine Protected Area, Lincoln Sea, Climate change, Sea ice algae, Biomarkers

1. **Introduction**

Both Arctic and Antarctic sea ice offer a unique habitat for sea-ice-related organisms, yet environmental responses to climate warming can vary substantially between the polar regions due to fundamental structural differences in sea-ice properties (Serreze and Meier, 2019). Over the past decades, climate warming has caused a large-scale decrease in Arctic sea-ice extent, led to earlier melt, and driven the replacement of thick old multiyear ice (MYI) with a younger first-year ice (FYI) cover (Comiso, 2012; Derksen et al., 2012; Polyakov et al., 2012; Arctic Monitoring and Assessment Programme [AMAP], 2017; Intergovernmental Panel on Climate Change [IPCC], 2019). Besides differences between Arctic FYI and MYI in age (MYI > FYI), thickness (MYI > FYI), and biochemical properties (e.g., salinity FYI > MYI; Comiso, 2012), high elevation undulations of the MYI surface, called hummocks, have been described as common features of MYI (Lange et al., 2017). The importance of MYI as suitable habitat for ice algae may have been underestimated, as thick MYI hummocks may allow more light penetration than previously thought (Lange et al., 2015, 2017). Furthermore, the highly variable under-ice topography of MYI compared to FYI (Timko and Burden, 1997) may enable richer biodiversity and species abundances (Melnikov et al., 2002) and offers an attractive feeding ground and refuge for ice-associated species year-round (Gradinger et al., 2010). A loss of ecosystem resilience may thus be expected as MYI...
is being replaced with a more uniform FYI cover (Meier et al., 2014). The different characteristics of MYI and FYI provide evidence that known ecosystem structures are not only threatened by the general reduction of available sea-ice habitat but also by changes in the occurrence of different ice types. Potential differences in their support of different algal assemblages (e.g., Hop et al., 2020) might yield important consequences for highly specialized sea-ice grazers, the entire dependent ecosystem, and the flow of energy within it.

In the Arctic, the bulk of the sea-ice algal biomass is typically found within the bottom ice layer near the ice–water interface (e.g., Arrigo, 2014). In MYI, internal algal layers identified as remnants from bottom-ice communities of previous years have also been documented (Thomas et al., 1995; Lange et al., 2015) and could play a role in seeding the spring bottom-ice algal communities in following years (Olsen et al., 2017). Primary production by sea-ice-associated microalgae can support key ecological species, including copepods, amphipods, and benthic fauna, in Arctic regions with perennial or seasonal sea-ice cover (Michel et al., 1996, 2002; Wang et al., 2015; Kohlbach et al., 2016, 2019a). Sea-ice-derived carbon serves as an important food resource for organisms feeding at the ice–water interface (under-ice fauna) and those inhabiting the sea ice itself (in-ice fauna; Melnikov et al., 2002; Michel et al., 2002; Arndt and Swadling, 2006; Bluhm et al., 2010) and is subsequently channeled into pelagic and benthic food webs (Renaud et al., 2007; Boetius et al., 2013; Kohlbach et al., 2019a). During spring, ice algal-derived carbon is essential for the maturation and reproduction of pelagic grazers, for example, Calanus spp., before phytoplankton is available for their offspring (Søreide et al., 2010). The overall tight sea-ice trophic coupling in Arctic marine ecosystems highlights their vulnerability to climate-associated changes in sea-ice algal biomass and its availability to grazers (AMAP, 2017). These changes will affect interactions between sea ice and pelagic and benthic components of the food webs across a wide range of trophic levels (e.g., Hays et al., 2005; Wassmann et al., 2011; Roy et al., 2015) and can create a mismatch between availability of food sources and occurrence of grazers (Michel et al., 1996; Leu et al., 2011).

Investigating fatty acid (FA) signatures of ice-associated particulate organic matter can provide information on the composition of communities and ecological processes within sea ice (Søreide et al., 2010; Kohlbach et al., 2016). Microalgae can be distinguished by their FA composition, as certain FAs are indicative of algal taxonomic groups (marker FAs). Notably, the FAs 16:1n-7, 16:4n-1, and 20:5n-3 are specific to diatoms, which are known to dominate spring sea-ice communities (Melnikov et al., 2002; Różańska et al., 2009), and 22:6n-3 is specific to dinoflagellates (reviewed in Dalsgaard et al., 2003). As indicated by FA compositions (e.g., Fahli and Kattner, 1993; Kohlbach et al., 2018, 2019b). Antarctic sea-ice algal communities are also often dominated by diatoms during different seasons (Arrigo et al., 2010; van Leeuwe et al., 2018). However, biodiversity and community composition of algae and in-ice fauna can largely differ between the hemispheres (Spindler, 1990; Gradinger, 1999a). These differences can be attributed to differences in ice formation, thickness, age, and structure between Arctic and Antarctic sea ice (Spindler, 1990) and varying interactions with surrounding land masses and thus the input of terrestrial material, which was found to be higher in Arctic ecosystems (Arrigo et al., 2010). The presence of calanoid copepods in sea-ice communities can be identified by high proportions of the long-chain FAs 20:1 and 22:1 (all isomers; Sargent and Whittle, 1981; Lee et al., 2006). Polyunsaturated FAs (PUFAs; more than 2 double bonds) are biosynthesized predominantly by primary producers (Dunstan et al., 1993), and high proportions of long-chain Omega-3 and Omega-6 PUFAs translate into a high food quality for the food web, where they are essential for successful growth and reproduction of marine organisms (Sargent et al., 1995; Brett and Müller-Navarra, 1997; Søreide et al., 2010). In addition to FA fingerprints, nitrogen (δ15N) and carbon (δ13C) stable isotope signatures of the bulk organic content (bulk stable isotope analysis, BSIA), as well as δ13C in specific marker FAs (compound-specific stable isotope analysis, CSIA), can inform about the composition of sea-ice communities and biological processes within the sea ice (Wang et al., 2014; Kohlbach et al., 2019a). Typically, Arctic sea-ice algae show δ13C values between ~22% and ~13%, which can be distinguished from those of pelagic algae (~28% to ~20%; Hobson et al., 1995; Tremblay et al., 2006; Tämelaender et al., 2009).

Logistical challenges with accessing and sampling of MYI (typical thickness > 2m) have limited the number of studies on MYI and sea-ice communities within this ice type (e.g., Melnikov et al., 2002; Bowman et al., 2012; Hatam et al., 2016). What effect the replacement of MYI with FYI will have on Arctic food-web processes in areas previously dominated by MYI is unclear. In this study, we compared FA and stable isotope signatures of adjacent FYI and MYI to evaluate ecological components and processes within the two ice types in the Lincoln Sea during spring. We hypothesized that FA and stable isotope signatures would differ between FYI and MYI, indicative of different sea-ice community composition between the two adjacent ice types. With FYI becoming the dominant ice type in the Arctic, this study fulfills important knowledge gaps on the potential ecological consequences of the reduction in MYI for food webs in the Arctic Ocean.

2. Materials and methods
2.1. Sample collection
Samples were collected on the consolidated pack ice in the Lincoln Sea off the coast of Northern Ellesmere Island, Nunavut, offshore the Canadian Forces Station Alert (Figure 1) as part of the Multidisciplinary Arctic Program—Last Ice 2018 field campaign (https://www.dfo-mpo.gc.ca/oceans/mpa-zpm/taujuittuq/index-eng.html). The study area is generally dominated by thick MYI, interspersed with patches of thinner FYI (Haas et al., 2006, 2010; Lange et al., 2019). For this study, samples were collected from 14 FYI cores (top: n = 2, mid: n = 2, and bottom: n = 12) and 8 MYI cores (top: n = 2, mid: n = 2,
Ice cores were collected with a 9-cm inner diameter Mark II ice corer (Kovacs Enterprise). Cores were measured and sectioned with a stainless steel handsaw at the site immediately after collection. Each top and bottom section had a length of 10 cm; middle sections had a length of 20 cm. Cores were transferred into sterile Whirlpak bags, and individual sections were pooled together for subsequent analysis. Between one and six cores were collected at each site to obtain sufficient material for analysis (Table 1). For consistency between sections of the vertical ice profile with inherently unique physical properties (e.g., salinity), cores were melted in the dark without addition of seawater over a period of 24–36 h. At each sampling location, ice thickness (n = 3–7 per station), freeboard (height of the sea-ice surface above the water level; n = 3–7 per station), and snow depth (n = 3–7 per station) were measured (Table 1).

### 2.2. Chlorophyll a (chl a) concentrations

Chl a concentrations were determined fluorometrically on duplicate subsamples from the top, middle, and bottom sections of FYI and MYI. For this analysis, between 125 and 150 ml of melted top and mid sea-ice subsamples and between 25 and 50 ml of melted bottom-ice subsamples were filtered onto 25-mm Whatman GF/F filters (nominal pore size 0.7 μm). Filtrations were carried out under low vacuum pressure (5–10 psi). Pigments were extracted in 90% acetone during 20–24 h at 5 °C in the dark (Parsons et al., 1984). After extraction, chl a concentrations were measured with a Turner Designs 10AU fluorometer calibrated against pure chl a extract (Sigma Chemicals). Total chl a concentrations were calculated according to Parsons et al. (1984). Chl a values represent the average value of duplicate subsamples (SD ≤ 0.1 mg m⁻³) from pooled cores (as described above).

### 2.3. Relative FA proportions

For the analysis of FAs, between 236 and 700 ml of melted sea ice were filtered onto precombusted 47-mm Whatman GF/F filters (6 h, 450 °C) and stored at −80 °C until further processing. Prior to lipid extraction, filters were freeze-dried (−50 °C, 0.2 mbar, 24 h). Total lipids were extracted with chloroform/methanol (2:1, v/v) containing 0.01% butylated hydroxytoluene (Folch et al., 1957) and cleaned with 0.7% sodium chloride solution. Lipids were converted into fatty acid methyl esters (FAMEs) by transesterification in methanol containing 3% concentrated sulfuric acid at 50 °C overnight. FAMEs were subsequently extracted with hexane and separated on an Agilent Technologies 7890A gas chromatograph with a DB-23 capillary
column (30 m, 0.25 mm I.D., 0.15 μm film thickness) and a flame ionization detector operating at 350 °C, using a temperature program (60 °C–200 °C). Samples were injected splitless at 260 °C, and hydrogen was used as a carrier gas. Individual FAMEs were identified via FAME standard mixtures (Supelco 37 component FAME mix, NuCheck GLC 455 and 463). Samples were analyzed either individually or on duplicates (total n: FYI = 15, MYI = 10).

FAMEs were reported as the percentage of the total FA content in the shorthand nomenclature A: Bn – X, where A represents the number of carbon atoms, B refers to the number of double bonds, and n – X indicates the position of the unsaturation nearest to the methyl terminus.

Our analysis was focused mainly on four marker FAs, that is, the diatom-associated FAs 16:1n-7, 16:4n-1, and 20:5n-3 (Graeve et al., 1997; Falk-Petersen et al., 1998), and the dinoflagellate-associated FA 22:6n-3 (Graeve et al., 1994). In addition to relative proportions of FAs, we investigated marker FA ratios, in particular 16:1n-7/16:0, SC16/SC18, and 20:5n-3/22:6n-3, which may indicate a dominance of diatom-produced over dinoflagellate-produced carbon (Reuss and Poulsen, 2002; Dalsgaard et al., 2003; Bergé and Barnathan, 2005). The long-chain FAs 20:1 and 22:1 (all isomers) were used to indicate the presence of calanoid copepods as part of the in-ice fauna. The importance of FAs of bacterial and terrestrial origin

### Table 1. Sampling information for first-year ice (FYI) and multiyear ice (MYI) collected in the Lincoln Sea during May 2018. DOI: https://doi.org/10.1525/elementa.2020.054.t1

| Sample ID | Ice Core Section* | Collection Date (Day in May) | Latitude (°N) | Longitude (°W) | Sea Ice Thickness (cm)b | Freeboard (cm)b | Snow Depth (cm)b |
|-----------|-------------------|-----------------------------|---------------|---------------|------------------------|----------------|-----------------|
| FYI       |                   |                             |               |               |                        |                |                 |
| T1-1      | T (6) f           | 03                          | 82.5760       | 62.4724       | 165 ± 3                | 12 ± 1         | 8 ± 2           |
| T4-1      | M (6) f           | 15                          | 82.5758       | 62.4749       | 166 ± 2                | 12 ± 1         | 5 ± 1           |
| T4-1      | B (1)e           | 17                          | 82.5758       | 62.4749       | 167 ± 5                | 14 ± 4         | 9 ± 2           |
| T5-1      | B (6)e           | 19                          | 82.5756       | 62.4744       | 174 ± 1                | 13 ± 1         | 7 ± 1           |
| T6-1      | T (4), M (4), B (4) | 23                          | 82.5756       | 62.4771       | 176 ± 1                | 12 ± 1         | 18 ± 1          |
| M0        | B (3)e           | 22                          | 82.5757       | 62.4712       | 153 ± 2                | 6 ± 1          | 48 ± 3          |
| M1        | B (3)e           | 22                          | 82.5757       | 62.4717       | 145 ± 1                | 7 ± 1          | 36 ± 0          |
| M2        | B (3)e           | 22                          | 82.5757       | 62.4724       | 153 ± 1                | 7 ± 1          | 20 ± 1          |
| M3        | B (3)e           | 22                          | 82.5757       | 62.4730       | 169 ± 1                | 11 ± 1         | 20 ± 2          |
| M4        | B (3)e           | 22                          | 82.5757       | 62.4738       | 154 ± 1                | 9 ± 1          | 24 ± 1          |
| M5        | B (3)e           | 22                          | 82.5757       | 62.4744       | 151 ± 1                | 7 ± 0          | 23 ± 1          |
| M6        | B (3)e           | 22                          | 82.5756       | 62.4751       | 170 ± 3                | 11 ± 1         | 14 ± 2          |
| M7        | B (3)e           | 22                          | 82.5756       | 62.4758       | 157 ± 2                | 12 ± 0         | 23 ± 2          |
| M8        | B (3)e           | 22                          | 82.5756       | 62.4765       | 170 ± 2                | 14 ± 1         | 16 ± 1          |
| MYI       |                   |                             |               |               |                        |                |                 |
| T4-2      | M (6) f           | 15                          | 82.5759       | 62.4626       | 396 ± 27               | 68 ± 5         | 2 ± 2           |
| T4-2      | B (1)e           | 17                          | 82.5759       | 62.4626       | 410 ± 17               | 56 ± 9         | 8 ± 6           |
| T5-2      | T (6) f           | 19                          | 82.5758       | 62.4653       | 378 ± 5                | 58 ± 4         | 7 ± 1           |
| T6-2      | T (4), M (4), B (4) | 23                          | 82.5761       | 62.4632       | 458 ± 1                | 70 ± 1         | 4 ± 1           |
| M15       | B (3)e           | 22                          | 82.5759       | 62.4679       | 348 ± 7                | 4 ± 2          | 59 ± 1          |
| M16       | B (3)e           | 22                          | 82.5759       | 62.4672       | 389 ± 8                | 43 ± 4         | 32 ± 2          |
| M19       | B (3)e           | 22                          | 82.5759       | 62.4652       | 236 ± 8                | 19 ± 7         | 15 ± 0          |
| M23       | B (3)e           | 22                          | 82.5760       | 62.4625       | 358 ± 12               | 28 ± 2         | 33 ± 2          |

* T indicates top section (10-cm length); M, middle section (20-cm length); B, bottom section (10-cm length).

*Average ± SD, n = 3–7 stations.

*Samples analyzed for fatty acids.

*Samples analyzed for bulk stable isotopes.

*Samples analyzed for compound-specific stable isotopes.
was estimated from the relative proportions of iso- and anteiso-branched chain FAs and unbranched 15:0 and 17:0 (bacterial), and the proportions of 18:2n-6 and 18:3n-3 (terrestrial), respectively (Budge et al., 2001; Dalsgaard et al., 2003).

2.4. Bulk and compound-specific stable isotopes in bottom ice
For the analysis of bulk nitrogen ($\delta^{15}$N) and carbon ($\delta^{13}$C) stable isotopes, between 250 and 600 ml of melted sea ice was filtered onto precombusted 47-mm Whatman GF/F filters (6 h, 450 °C) and stored at –80 °C until further processing. Prior to bulk stable isotope analysis, filters were freeze-dried (–50 °C, 0.2 mbar, 24 h). Lipids were not removed prior to measurements in order to avoid inducing changes to the stable isotope compositions (Mintenbeck et al., 2008). Bulk samples were analyzed with a continuous flow isotope ratio mass spectrometer (Delta V Plus, Thermo Scientific) interfaced with an elemental analyzer (Costech Instruments ECS 4010) and connected via a Conflo IV interface (Thermo Scientific). Accuracy and precision of isotopic measurements were verified by the certified reference material (International Atomic Energy Agency, Vienna) USGS40 ($\delta^{15}$N = –4.52%, $\delta^{13}$C = –26.39%) and USGS41a ($\delta^{15}$N = 47.55%, $\delta^{13}$C = 36.55%). True $\delta^{13}$C and $\delta^{15}$N values were obtained after two-point normalization (Paul et al., 2007).

For compound-specific stable isotope measurements, $\delta^{13}$C signatures of the diatom-associated FAs 16:1n-7 and 20:5n-3 and the dinoflagellate-associated FA 22:6n-3 were determined from the FA extracts of bottom FYI and MYI using a Thermo GC-c-IRMS system, equipped with a Trace GC Ultra gas chromatograph, connected to the mass spectrometer via the Conflo IV interface. FAMES were injected in splitless mode at 260 °C and separated on a DB-FFAP column (30 m, 0.25 mm I.D., 0.25 μm film thickness), using a temperature program from 60 °C to 240 °C. The $\delta^{13}$C compositions of the individual FAs were calibrated with the certified standard FAMEs 14:0 ($\delta^{13}$C = –29.8%) and 20:0 ($\delta^{13}$C = –30.68%), supplied by Indiana University. Bulk stable isotope samples were analyzed either individually or on duplicates (total n: FYI = 6, MYI = 4); compound-specific stable isotope samples were analyzed individually (total n: FYI = 7, MYI = 5).

Stable isotope ratios are presented in the delta ($\delta$) notation ($\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$) as % deviation from the primary (calibration) standard atmospheric nitrogen for nitrogen measurements and Vienna Pee Dee Belemnite for carbon measurements.

2.5. Statistical analyses
Differences in physical properties of FYI and MYI and in FA and stable isotope signatures between bottom sections of FYI and MYI were assessed using unpaired Student’s t tests. Variability in FA data sets was visualized with principal component analysis (PCA). Results with a statistical threshold of $\alpha = 0.05$ were considered significant. Prior to statistical analysis, the data were verified for normality of distribution with histogram plots and Shapiro–Wilk normality tests. FA data were transformed applying an arcsine square root function to meet normality requirements for parametric statistics (Legendre and Legendre, 2012). All statistical analyses were run with the Software R, Version 3.4.3 (R Core Team, 2017).

3. Results
3.1. Physical properties of FYI and MYI
MYI was significantly thicker (236–458 cm) than FYI (145–176 cm; Table 1; t test, n = 22, df = 7.2, t = 9.1, $P \leq 0.001$). MYI freeboard was more variable (4–70 cm) compared to FYI (6–14 cm) and was also significantly higher associated with MYI compared to FYI (Table 1; t test, n = 22, df = 7.1, t = 3.8, $P < 0.01$). Snow depth varied from 4 to 48 cm on FYI and from 2 to 59 cm on MYI; average values were similar between FYI (19.4 ± 11.7 cm) and MYI types (20.0 ± 19.8 cm; Table 1) at our sampling sites.

3.2. Chl a concentrations
In both ice types, chl a concentrations were very low in the top ($\leq 0.05$ mg m$^{-3}$, $\leq 0.01$ mg m$^{-2}$) and middle sections ($\leq 0.01$ mg m$^{-3}$, $\leq 0.01$ mg m$^{-2}$; exception T4-1: 1.9 mg m$^{-3}$, 0.2 mg m$^{-2}$). Bottom-ice chl a concentrations ranged between 2.6 and 27.0 mg m$^{-3}$ (0.2–2.7 mg m$^{-2}$) in FYI and were significantly higher compared to MYI (2.1–14.4 mg m$^{-3}$, 0.2–1.3 mg m$^{-2}$; t test, n = 18, df = 13.6, t = 2.6, $P \leq 0.05$).

3.3. Relative FA proportions
In both ice types, the PCAs showed a clear distinction in FA compositions between the top, middle, and bottom-ice sections, explaining 78.6% and 83.9% of the variability within FYI and MYI with the first two axes, respectively (Figure 2). As shown by the proximity of data points in Figure 2, the proportion of FAs in the top and middle sections of the ice were more similar to each other than to FAs in the bottom ice for both ice types. Based on higher proportions of all four algal marker FAs (i.e., 16:1n-7, 16:4n-1, 20:5n-3, and 22:6n-3), the relative importance of microalgal-produced FAs increased from the top to the bottom sections in both FYI and MYI (Figure 2 and Table S1). Based on the marker FA ratios, the dominance of diatoms over dinoflagellates also increased from the top to the bottom layer in both ice types. The dinoflagellate-associate marker FA 22:6n-3 was not detected in the top layers of FYI or MYI. In both ice types, proportions of calanoid copepod-associated FAs were generally high in all three ice sections, but the sum of all 20:1 and 22:1 isomers was somewhat higher in the top and middle sections compared to the bottom sections. PUFA levels were higher in the bottom ice compared to the middle and top sections in both FYI and MYI (Table S1).

Relative proportions of 18:1n-9 were significantly higher in bottom FYI, whereas proportions of 18:1n-7 were significantly higher in bottom MYI compared to bottom FYI (Figure 3 and Table S1). Most copepod-associated FAs were significantly higher in bottom MYI compared to FYI (Table S1). Relative contributions of terrestrial marker FAs (sum 18:2n-6 + 18:3n-3) were significantly higher in the bottom sections of FYI compared to MYI. PUFAs were not
significantly different between the ice type bottoms (t test, \( n = 15, \text{df} = 9.5, t = 1.9, P = 0.07 \)), whereas monounsaturated FAs (MUFA) were significantly higher in bottom MYI compared to bottom FYI (Table S1).

Among the FYI bottom sections, sample M0 (Table 1) was clearly separated from the other samples in the PCA and overlapping in FA composition with MYI samples (Figure 4). This result was based mainly on higher relative proportions of 18:0, copepod-associated FAs and bacterial FAs, with lower proportions of all four marker FAs and terrestrial FAs, in M0 compared to the other FYI samples.

### 3.4. Stable isotope signatures in bottom ice

Values for \( \delta^{15} \text{N} \) in FYI (5.5%–7.1%) were significantly higher than in MYI (4.6%–5.3%). In both ice types, the \( \delta^{13} \text{C} \) values of all three marker FAs were more depleted compared to the bulk \( \delta^{13} \text{C} \) values, respectively (Table 2). FA 16:1n-7 had higher average \( \delta^{13} \text{C} \) values compared to

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**Figure 2.** Principal component analysis of the most abundant fatty acids (FAs) in the different sea-ice sections. (A) Variability of the relative proportions of FAs in the top, middle, and bottom sections of first-year ice (FYI). The first two principal components explained 78.6% of the variance in the FA data set between the different ice sections. (B) Variability of the relative proportions of FAs in the top, middle, and bottom sections of multiyear ice (MYI). The first two principal components explained 83.9% of the variance in the FA data set between the different ice sections. The FAs 16:1n-7, 16:4n-1, and 20:5n-3 represent diatom-associated FAs; 22:6n-3 represents a dinoflagellate-associated FA; 20:1 and 22:1 represent calanoid copepod-associated FAs; 15:0, 15:0 iso, and 17:0 iso represent bacterial FAs; and 18:2n-6 and 18:3n-3 represent terrestrial FAs. Samples were collected in the Lincoln Sea during May 2018. DOI: https://doi.org/10.1525/elementa.2020.054.f2
Figure 3. Relative proportions of selected fatty acids (FAs) in the bottom sections of sea ice. Individual FA proportions (average ± SD%) are related to the total FA content in first-year ice (FYI) and multiyear ice (MYI). The FAs 16:1n-7, 16:4n-1, and 20:5n-3 represent diatom-associated FAs; 22:6n-3 represents a dinoflagellate-associated FA; and 20:1 and 22:1 represent calanoid copepod-associated FAs. Samples were collected in the Lincoln Sea during May 2018. DOI: https://doi.org/10.1525/elementa.2020.054.f3

Figure 4. Principal component analysis of the most abundant fatty acids (FAs) in bottom sea-ice sections. Variability of the relative proportions of FAs in the bottom sections of first-year ice (FYI) versus multiyear ice (MYI). The first two principal components explained 55.8% of the variance in the FA data set between bottom FYI and MYI. The FAs 16:1n-7, 16:4n-1, and 20:5n-3 represent diatom-associated FAs; 22:6n-3 represents a dinoflagellate-associated FA; 20:1 and 22:1 represent calanoid copepod-associated FAs; and 18:2n-6 and 18:3n-3 represent terrestrial FAs. Information about individual samples can be found in Table 1. Samples were collected in the Lincoln Sea during May 2018. DOI: https://doi.org/10.1525/elementa.2020.054.f4
Based on the relative proportions of the algal marker FAs in both FYI and MYI, the values for \( \delta^{13}C \) in the dinoflagellate-associated FA 22:6n-3 (FYI: –36.2% to –31.7%, MYI: –33.3% to –31.7%) were significantly higher in MYI compared to FYI. Bulk \( \delta^{13}C \) (FYI: –28.4% to –26.7%, MYI: –27.6% to –27.2%), \( \delta^{13}C \) in 16:1n-7 (FYI: –32.9% to –30.4%, MYI: –32.7% to –30.6%), and in 20:5n-3 (FYI: –34.4% to –32.1%, MYI: –35.3% to –32.8%) were not significantly different between the ice types (Table 2).

### Table 2: Bulk nitrogen (\( \delta^{15}N \)) and carbon (\( \delta^{13}C \)) stable isotope values, and compound-specific \( \delta^{13}C \) values (average ± SD‰) in the diatom-associated fatty acids 16:1n-7 and 20:5n-3 and the dinoflagellate-associated fatty acid 22:6n-3 in first-year ice (FYI) and multiyear ice (MYI) for samples collected in the Lincoln Sea during May 2018. DOI: https://doi.org/10.1525/elementa.2020.054.t2

| Stable Isotopes (%) | FYI | MYI | \( t \) Test |
|---------------------|-----|-----|-------------|
| \( \delta^{15}N \) | 5.4 ± 0.7 | 5.0 ± 0.4 | df 6.0, t 3.8, P \( \leq 0.01 \) |
| \( \delta^{13}C \) 16:1n-7 | –31.7 ± 0.8 | –31.9 ± 0.8 | ns<sup>a</sup> |
| \( \delta^{13}C \) 20:5n-3 | –33.3 ± 0.9 | –33.6 ± 1.0 | ns |
| \( \delta^{13}C \) 22:6n-3 | –34.4 ± 1.7 | –32.7 ± 0.7 | df 8.7, t 2.3, P \( \leq 0.05 \) |

<sup>a</sup>Not significantly different between FYI and MYI.

### 4. Discussion

Based on the relative proportions of the algal marker FAs and all marker FA ratios, bottom-ice algal communities in both FYI and MYI were dominated by diatom species rather than dinoflagellates, a commonly documented pattern of taxonomic structure in sea-ice algal communities (Kirst and Wiencke, 1995; Henderson et al., 1998; Poulin et al., 2011; van Leeuwe et al., 2018; Kohlbach et al., 2019a). This finding is consistent with taxonomic analyses confirming the dominance of pennate diatoms in the bottom section of both ice types (K. Campbell and J. Charette, unpublished data). Generally, algae, bacteria, and other (heterotrophic) organisms are not evenly distributed within the ice (Gradinger, 1999b; Mundy et al., 2011), as a result of gradients in environmental conditions (e.g., light, temperature, salinity, and nutrients) throughout the ice and the vertical movement of sea-ice inhabitants (Aumack et al., 2014; van Leeuwe et al., 2018). The finding of lower relative proportions of both diatom- and dinoflagellate-associated FAs in the top and middle compared to the bottom-ice sections in both ice types is attributed to the accumulation of ice algae near the sea-ice interface where conditions are most favorable for algal growth (Gradinger et al., 1991; Duffaud, 2020).

FA proportions and stable isotope compositions in FYI and MYI not only reflect the biomarker signatures of primary producers associated with sea ice but also those of grazers (e.g., copepods) and a diverse community of heterotrophic protists which also contribute to sea-ice carbon and its biochemical properties (e.g., Michel et al., 2002; Gradinger and Bluhm, 2020). In contrast to another study where invertebrates were scarce or even absent within the sea ice sampled from the Beaufort Gyre during October to March (Melnikov et al., 2001), high relative proportions of 20:1 and 22:1 FAs indicated the presence of calanoid copepods in both FYI and MYI, contributing on average 21% and 29% to the FYI and MYI bottom total FAs, respectively. Elevated levels of 20:1n-9 (approximately 9%) were also found in the neutral lipid fraction of an ice-algal sample collected during May in the Barents Sea (Henderson et al., 1998), and invertebrates were part of the sea-ice community in MYI during summer in the Beaufort Sea (Gradinger et al., 2005). Most calanoid copepod-associated FAs had significantly higher relative proportions in MYI, attributing to significantly higher MUFA levels in comparison to FYI. This result is not necessarily indicative of a higher absolute abundance of copepods in MYI but could simply be due to the lower algal biomass in bottom MYI (chl \( a \) up to 14.4 mg m\(^{-3}\)) compared to bottom FYI (chl \( a \) up to 27.0 mg m\(^{-3}\)). In other regions of the Canadian Arctic, such as Eclipse Sound (Kohlbach et al., 2019a), Franklin Bay (Riedel et al., 2006), and Resolute Passage (Michel et al., 1996), chl \( a \) values in bottom landfast ice during spring can be more than two orders of magnitude higher than those observed in this study, and the contribution of copepod-associated FAs to the FA content of bottom FYI from Eclipse Sound was found to be negligible (Kohlbach et al., 2019a). Seasonality in sea-ice parameters (e.g., melting conditions) and thus in-ice fauna living conditions, as well as regional variability, might offer an explanation for the differences between the studies. Moreover, sea-ice communities in pack ice have been found to differ from the composition of protists in landfast ice (Mundy et al., 2011; van Leeuwe et al., 2018).

The available brine channel volume for ice inhabitants is controlled by ice temperature and bulk salinities (Kirst and Wiencke, 1995; Lizotte, 2003; Bluhm et al., 2010), which then determines species sizes and abundances and thus in-ice fauna taxonomic compositions (Krembs et al., 2000). Low salinities and temperatures particularly in the upper layers of the ice usually counteract the accumulation of ice fauna due to more narrow brine channels, and high salinities in the bottom ice can restrict the upward movement of algae (Grant and Horner, 1976). Yet, we
found high relative proportions of the copepod-associated FAs also in the upper parts of the ice. The presence of calanoid copepods in our study could be ascribed to the introduction of these taxa during ice formation and ice growth, as calanoid copepods can occur in high concentrations at the ice–water interface (Conover et al., 1986; Conover and Huntley, 1991; Bluhm et al., 2010; David et al., 2015). The organisms might have been damaged during ice formation processes (Bluhm et al., 2010), as described for the Antarctic copepod *Calanus propinquus* due to its sensitivity to brine salinity during ice formation (Gradinger and Schnack-Schiel, 1998).

Terrestrial FAs contributed <3% to the total FA content in all layers of both ice types, indicating that carbon originating from vascular plants was not abundant in the sea ice, similar to landfast ice from Eclipse Sound during spring (Kohlbach et al., 2019a). Similarly, the relative contributions of bacterial FAs in both FYI and MYI were low. As bacteria are capable of biosynthesizing PUFAs, including bacterial species from sea ice (Nichols and McMeekin, 2002; Boetius et al., 2015), a bacterial contribution to the PUFA proportions in our study cannot be excluded, although it would likely be minimal based on the overall low proportions of bacterial FAs. Relative proportions of PUFAs were not significantly different between bottom FYI (average 33%) and MYI (average 28%), suggesting a similar nutritional quality of algae in both ice types. Typically, PUFA levels of >30% are indicative of exponential algal growth (Parrish et al., 2005; Leu et al., 2006), as the majority of FAs biosynthesized during the spring bloom are polyunsaturated and utilized for cell stabilization in polar lipids (Kattner et al., 1983; Reitan et al., 1994; Henderson et al., 1998).

The general resemblance in $\delta^{13}$C between bottom FYI and MYI, with no significant differences in bulk $\delta^{13}$C and $\delta^{13}$C in 16:1n-7 and 20:5n-3, suggests that similar biochemical processes had occurred within the two sea-ice communities. In both ice types, bulk and FA-specific $\delta^{13}$C values were strongly depleted (mean $<-27.4\%$) compared to ice-associated particulate organic matter in other regions of the Canadian Arctic (e.g., Kohlbach et al., 2019a; average $\delta^{13}$C: $-17.2\%$ in Eclipse Sound during May) or in the Northeast Water Polynya during June/July (Hobson et al., 1995; average $\delta^{13}$C: $-18.6\%$) but were similar to isotopic values of phytoplankton communities, for example, in the North Water Polynya in May/June (Tremblay et al., 2006; $\delta^{13}$C: approximately $-27\%$ to $-20\%$) and June/July (Hobson et al., 1995; average $\delta^{13}$C: $-27.9\%$). Phytoplankton $\delta^{13}$C compositions have been found to be more depleted in early bloom stages compared to peak and late bloom stages (Ostrom et al., 1997; Kukert and Riebesell, 1998), which can also apply to dynamics of ice-algal isotopic compositions as documented by Tremblay et al. (2006) in the North Water Polynya (beginning to mid-May, average $\delta^{13}$C: $-24.9\%$; beginning of June, average $\delta^{13}$C: $-13.2\%$). Algal $\delta^{13}$C values also exhibit strong spatiotemporal variability, driven by a variety of factors including gradients in CO$_2$ concentrations, nutrient concentrations, irradiance, and algal-specific growth rates (Thompson and Calvert, 1994; Fry, 1996; Kukert and Riebesell, 1998; Arrigo et al., 2003).

Relative proportions of 18:1n-9 and 18:1n-7 were generally low in the bottom ice, yet these FAs were different in their proportional contributions between the two ice types. Ratios of 18:1n-9/18:1n-7 were higher in bottom FYI (2.5) compared to MYI (0.8), based on significantly higher proportions of 18:1n-9 in FYI compared to MYI and significantly higher proportions of 18:1n-7 in MYI compared to FYI. This ratio is often used in food web studies as a proxy for carnivory in a consumer (e.g., Graeve et al., 1997) and could reflect differences in the concentration of heterotrophic organisms between the two ice types in our study. In accordance with higher bottom FYI $\delta^{15}$N values, the higher ratio of 18:1n-9/18:1n-7 could indicate a higher abundance of heterotrophic species (i.e., dinoflagellates, with slightly higher relative proportions in FYI compared to MYI) or perhaps higher respiratory requirements in FYI compared to MYI. Continued heterotrophic conditions have been reported during ice-algal blooms, switching to net autotrophy as the bloom transitioned toward greater dominance of diatoms (Riedel et al., 2008; Campbell et al., 2017). These differences could be further explained by differences in composition of the ice-algal and protist community in the two ice types (K. Campbell and J. Charlette, unpublished data).

Differences in timing of ice productivity are likely to cause alterations in spring food-web dynamics (e.g., Soriede et al. 2010) as MYI continues to be replaced by FYI in the Arctic. FYI might provide more favorable conditions for algal growth when light penetrates the thinner ice pack early in the season (Macdonald et al., 2015; Lange et al., 2019), but an earlier onset of the ice-associated and pelagic blooms is likely to create a mismatch in carbon source availability and grazer occurrence (Leu et al., 2011; Ji et al., 2013). MYI is considered a potential refuge for Arctic species (e.g., Gradinger et al., 2010; David et al., 2016), with ubiquitous habitats (Lange et al., 2017) and communities (e.g., Hatam et al., 2014, 2016). Furthermore, MYI can act as long-term storage for carbon and other elements, given internal biomass layers (e.g., Lange et al., 2015) and its potential for seeding spring bottom-ice algal communities in the following year (Olsen et al., 2017; Kauko et al., 2018), compared to FYI that undergoes a complete annual cycle of growth and melt. The different biochemical signatures of the upper and bottom layers of the ice and the partly contrasting signatures of bottom FYI and MYI found in our study (25% of identified FAs, $\delta^{15}$N and $\delta^{13}$C in 22:6n-3 with significant differences) support our hypothesis that FYI and MYI can host different sea-ice inhabitants and are consistent with previous studies reporting differences in community composition between the two ice types (Hardge et al., 2017; Hop et al., 2020). MYI protist communities are particularly rich in species diversity (Melnikov, 2009; Hop et al., 2020), suggesting that the loss of Arctic MYI will impact the complex interaction between primary producers, immediate consumers, and consequently top predators. Yet, bottom-ice layers in both ice types had comparable levels of PUFAs, indicating similar nutritional food quality, and based on high relative
proportions of diatom-associated FAs, diatoms played a major role in the taxonomic composition of both sea-ice communities. This similarity in biochemical composition between ice types has the potential to benefit ice-dependent grazers during a time of changing ice conditions in the Lincoln Sea. Our results highlight the need to pinpoint the ecological consequences of a shift from MYI to FYI to trophic structure and interactions within and associated with sea ice and to overall marine ecosystem resilience in the changing Arctic.

Data accessibility statement
All data used for all analyses in this report are publically available from the Government of Canada Open Data Portal https://open.canada.ca/en/open-data (https://open.canada.ca/data/en/dataset/c1533828-bde9-46d4-84a3-937b28fadd68).

Supplemental files
Table S1. Relative proportions of fatty acids in top, middle, and bottom sections of first- and multiyear ice collected in the Lincoln Sea during May 2018 (DOCX).

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