

RESEARCH ARTICLE

Fatty acids and stable isotope signatures of first-year and multiyear sea ice in the Canadian High Arctic

Doreen Kohlbach^{1,2*}, Steven W. Duerksen¹, Benjamin A. Lange^{1,2}, Joannie Charette¹, Anke Reppchen¹, Pascal Tremblay¹, Karley L. Campbell^{3,4}, Steven H. Ferguson¹, and Christine Michel¹

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 ($\delta^{15}\text{N}$) in bottom-ice samples of FYI ($\delta^{15}\text{N} = 6.4 \pm 0.7\%$) compared to MYI ($\delta^{15}\text{N} = 5.0 \pm 0.4\%$) 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 ($\delta^{13}\text{C}$) were not significantly different between bottom FYI (bulk $\delta^{13}\text{C}$: -28.4% to -26.7% , FA average $\delta^{13}\text{C}$: -34.4% to -31.7%) and MYI (bulk $\delta^{13}\text{C}$: -27.6% to -27.2% , FA average $\delta^{13}\text{C}$: -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 support the view that 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 MYI 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; Duerksen 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 (Timco 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

¹ Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, Manitoba, Canada

² Norwegian Polar Institute, Fram Centre, Tromsø, Norway

³ Department of Arctic and Marine Biology, University of Tromsø, The Arctic University of Norway, Tromsø, Norway

⁴ Bristol Glaciology Centre, University of Bristol, Bristol, United Kingdom

* Corresponding author:

Email: doreen.kohlbach@npolar.no

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; Rózańska et al., 2009), and 22:6n-3 is specific to dinoflagellates (reviewed in Dalsgaard et al., 2003). As indicated by FA compositions (e.g., Fahl 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 ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) stable isotope signatures of the bulk organic content (bulk stable isotope analysis, BSIA), as well as $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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; Tamelander et al., 2009).

Logistical challenges with accessing and sampling of MYI (typical thickness $> 2\text{m}$) 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/tuvaijuittuq/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: $n = 2$,

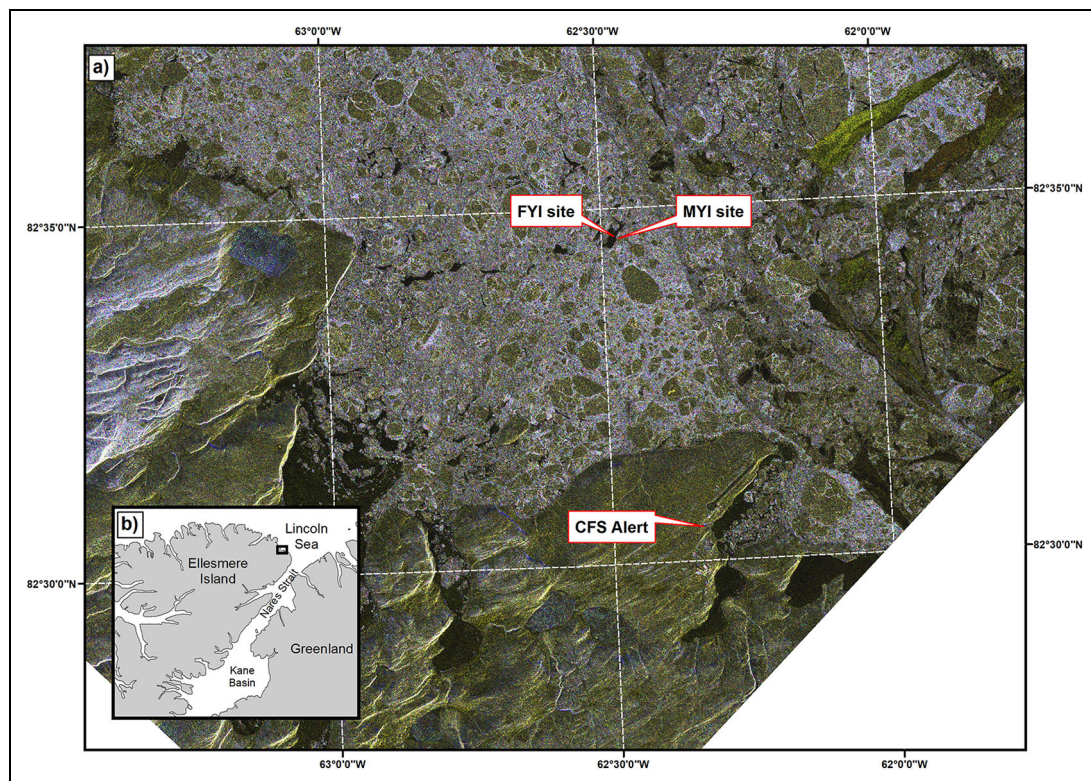


Figure 1. RADARSAT-2 (RS-2) imagery of the study area in the Lincoln Sea in spring 2018. (A) SAR Fine Quad-Pol overview image of the land-fast sea ice in the Lincoln Sea off the coast of Canadian Forces Station Alert (acquired March 31, 2018) with inset (B) showing Ellesmere Island, Canada, NW Greenland, and the Lincoln Sea (© MacDonald, Dettwiler and Associates Ltd. 2018—All Rights Reserved). Sampling was carried out as part of the Multidisciplinary Arctic Program—Last Ice 2018 field campaign (<https://www.dfo-mpo.gc.ca/oceans/mpa-zpm/tuvaijuittuq/index-eng.html>). DOI: <https://doi.org/10.1525/elementa.2020.054.f1>

and bottom: $n = 6$) between May 3, 2018, and May 23, 2018 (**Figure 1** and **Table 1**). For more details on the sampling region and ice conditions, see Lange et al. (2019).

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 ($SD \leq 0.1 \text{ mg m}^{-3}$) 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

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 ^a (# of Pooled Sections)	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) ^c	03	82.5760	62.4724	165 ± 3	12 ± 1	8 ± 2
T4-1	M (6) ^c	15	82.5758	62.4749	166 ± 2	12 ± 1	5 ± 1
T4-1	B (1) ^{c,d,e}	17	82.5758	62.4749	167 ± 5	14 ± 4	9 ± 2
T5-1	B (6) ^{c,e}	19	82.5756	62.4774	174 ± 1	13 ± 1	7 ± 1
T6-1	T (4) ^c , M (4) ^c , B (4) ^c	23	82.5756	62.4771	176 ± 1	12 ± 1	18 ± 1
M0	B (3) ^{c,e}	22	82.5757	62.4712	153 ± 2	6 ± 1	48 ± 3
M1	B (3) ^c	22	82.5757	62.4717	145 ± 1	7 ± 1	36 ± 0
M2	B (3) ^{c,e}	22	82.5757	62.4724	153 ± 1	7 ± 1	20 ± 1
M3	B (3) ^c	22	82.5757	62.4730	169 ± 1	11 ± 1	20 ± 2
M4	B (3) ^{c,e}	22	82.5757	62.4738	154 ± 1	9 ± 1	24 ± 1
M5	B (3) ^d	22	82.5757	62.4744	151 ± 1	7 ± 0	23 ± 1
M6	B (3) ^{c,e}	22	82.5756	62.4751	170 ± 3	11 ± 1	14 ± 2
M7	B (3) ^d	22	82.5756	62.4758	157 ± 2	12 ± 0	23 ± 2
M8	B (3) ^{c,e}	22	82.5756	62.4765	170 ± 2	14 ± 1	16 ± 1
MYI							
T4-2	M (6) ^c	15	82.5759	62.4626	396 ± 27	68 ± 5	2 ± 2
T4-2	B (1) ^{c,d,e}	17	82.5759	62.4626	410 ± 17	56 ± 9	8 ± 6
T5-2	T (6) ^c	19	82.5758	62.4653	378 ± 5	58 ± 4	7 ± 1
T6-2	T (4) ^c , M (4) ^c , B (4) ^{c,e}	23	82.5761	62.4632	458 ± 1	70 ± 1	4 ± 1
M15	B (3) ^{c,e}	22	82.5759	62.4679	348 ± 7	4 ± 2	59 ± 1
M16	B (3) ^{c,e}	22	82.5759	62.4672	389 ± 8	43 ± 4	32 ± 2
M19	B (3) ^{c,e}	22	82.5759	62.4652	236 ± 8	19 ± 7	15 ± 0
M23	B (3) ^d	22	82.5760	62.4625	358 ± 12	28 ± 2	33 ± 2

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

^bAverage ± SD, $n = 3-7$ stations.

^cSamples analyzed for fatty acids.

^dSamples analyzed for bulk stable isotopes.

^eSamples analyzed for compound-specific stable isotopes.

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, Nu-Check 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, $\Sigma C16/\Sigma C18$, 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

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 ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) 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 ($\delta^{15}\text{N} = -4.52\%$, $\delta^{13}\text{C} = -26.39\%$) and USGS41a ($\delta^{15}\text{N} = 47.55\%$, $\delta^{13}\text{C} = 36.55\%$). True $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were obtained after two-point normalization (Paul et al., 2007).

For compound-specific stable isotope measurements, $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ compositions of the individual FAs were calibrated with the certified standard FAMES 14:0 ($\delta^{13}\text{C} = -29.8\%$) and 20:0 ($\delta^{13}\text{C} = -30.68\%$), 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 (δ) notation ($\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$) 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 $\alpha = .05$ 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, $n = 22$, $df = 7.1$, $t = 3.8$, $P \leq 0.01$). 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 ($\leq 0.05 \text{ mg m}^{-3}$, $\leq 0.01 \text{ mg m}^{-2}$) and middle sections ($\leq 0.1 \text{ mg m}^{-3}$, $\leq 0.01 \text{ mg m}^{-2}$; 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-associated 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

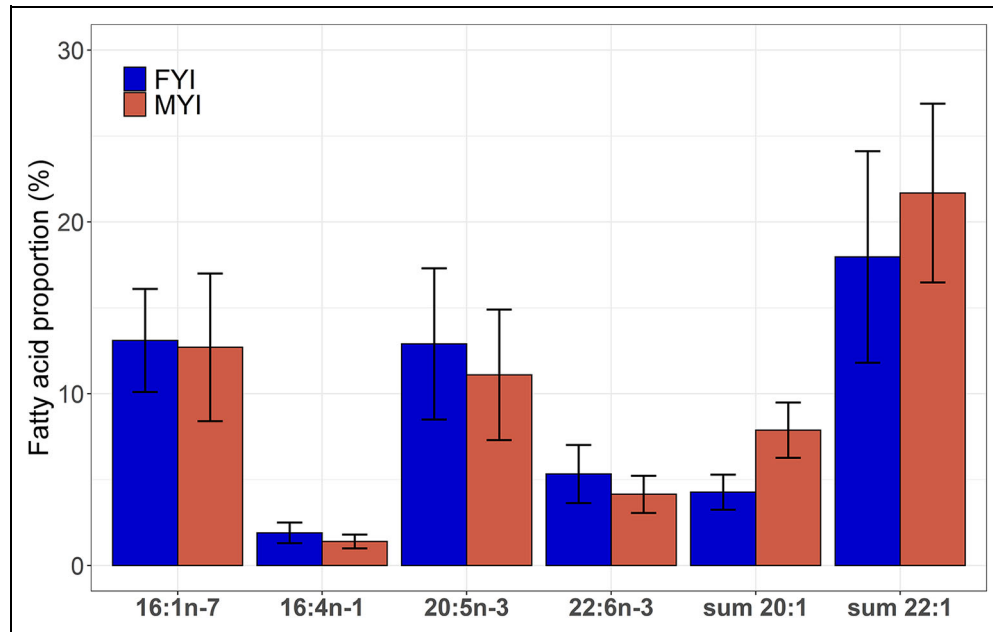


Figure 3. Relative proportions of selected fatty acids (FAs) in the bottom sections of sea ice. Individual FA proportions (average \pm SD%) are related to the total FA content in first-year ice (FYI) and multiyear ice (MYI). The FAs 16:1n-7, 16:4n-1, and 20:5n-3 represent diatom-associated FAs; 22:6n-3 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>

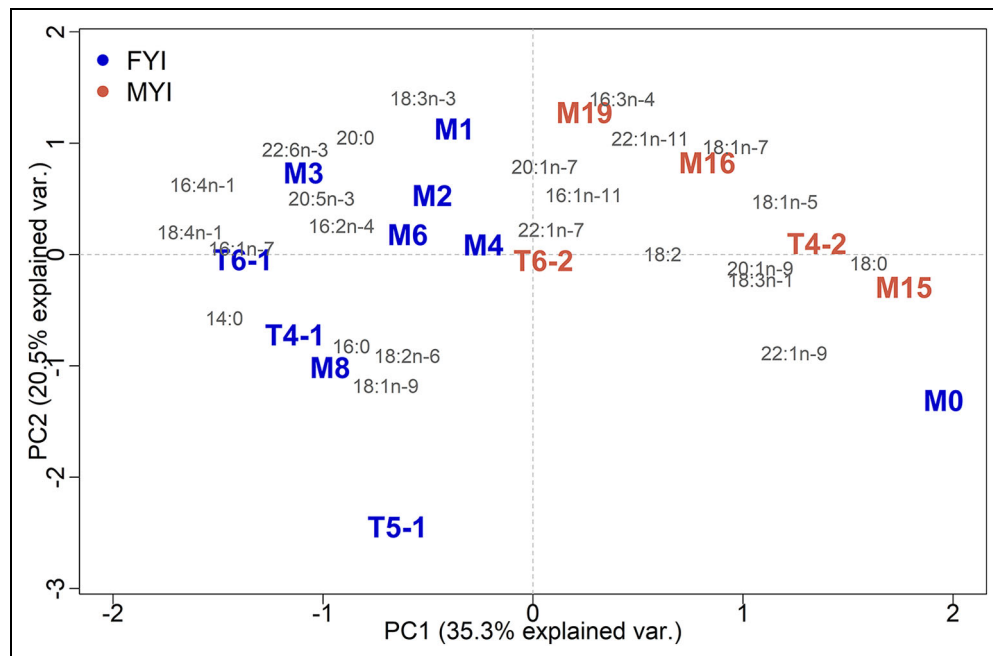


Figure 4. Principal component analysis of the most abundant fatty acids (FAs) in bottom sea-ice sections. Variability of the relative proportions of FAs in the bottom sections of first-year ice (FYI) versus multiyear ice (MYI). The first two principal components explained 55.8% of the variance in the 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>

Table 2. Bulk nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) stable isotope values, and compound-specific $\delta^{13}\text{C}$ values (average \pm $SD^{\text{‰}}$) 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 (‰)	n	FYI	n	MYI	t Test		
					df	t	P
bulk $\delta^{15}\text{N}$	5	6.4 \pm 0.7	3	5.0 \pm 0.4	6.0	3.8	≤ 0.01
bulk $\delta^{13}\text{C}$	5	-27.5 \pm 0.8	3	-27.4 \pm 0.2		ns ^a	
$\delta^{13}\text{C}$ 16:1n-7	7	-31.7 \pm 1.1	5	-31.9 \pm 0.8		ns	
$\delta^{13}\text{C}$ 20:5n-3	7	-33.3 \pm 0.9	5	-33.6 \pm 1.0		ns	
$\delta^{13}\text{C}$ 22:6n-3	7	-34.4 \pm 1.7	5	-32.7 \pm 0.7	8.7	2.3	≤ 0.05

^aNot significantly different between FYI and MYI.

the other two FAs in both FYI and MYI. Values for $\delta^{13}\text{C}$ in the dinoflagellate-associated FA 22:6n-3 (FYI: -36.2% to -31.0%, MYI: -33.7% to -31.7%) were significantly higher in MYI compared to FYI. Bulk $\delta^{13}\text{C}$ (FYI: -28.4% to -26.7%, MYI: -27.6% to -27.2%), $\delta^{13}\text{C}$ 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).

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 $\delta^{13}\text{C}$ between bottom FYI and MYI, with no significant differences in bulk $\delta^{13}\text{C}$ and $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$: -17.2‰ in Eclipse Sound during May) or in the Northeast Water Polynya during June/July (Hobson et al., 1995; average $\delta^{13}\text{C}$: -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; $\delta^{13}\text{C}$: approximately -27% to -20%) and June/July (Hobson et al., 1995; average $\delta^{13}\text{C}$: -27.9%). Phytoplankton $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$: -24.9%; beginning of June, average $\delta^{13}\text{C}$: -13.2%). Algal $\delta^{13}\text{C}$ 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 $\delta^{15}\text{N}$ 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. Charrette, unpublished data).

Differences in timing of ice productivity are likely to cause alterations in spring food-web dynamics (e.g., Sør-eide 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, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ 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).

Acknowledgments

We would like to thank Polar Continental Shelf Program (PCSP), Natural Resources Canada, Department of National Defense at Canadian Forces Station (CFS) Alert, Defense Research and Development Canada (DRDC), Environment and Climate Change Canada (ECCC), and the communities and Hunters and Trappers Associations of Resolute Bay and Grise Fjord. Special thanks to A. Platt (ECCC), C. Brown, J. Milne, J. Higgins, and M. Simms at DRDC; T. McCagherty, T. Platt, J. MacGregor, and T. Lemieux at PCSP; and Major C. Stiles, (Commanding Officer), R. Hansen, (Senior Warrant Officer), and R. Lutz (Alta Senior Warrant Officer) at CFS Alert. We thank the Biotracer Laboratory (Fisheries and Oceans Canada, Freshwater Institute) under the direction of Lisa Loseto and Bruno Rosenberg for his help with laboratory analyses.

Funding

The Multidisciplinary Arctic Program—Last Ice is funded by Fisheries and Oceans Canada (DFO) Science in support of Tuvaijuittuq. Additional support was provided by Polar Continental Shelf Program (Project 10718) and the Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Funds to CM. DK and BAL received a Visiting Fellowship from NSERC supported by DFO's International Governance Strategy to CM. Currently, DK and BAL are supported by the Norwegian Polar Institute (NPI) and funding from the Research Council of Norway (The Nansen Legacy [276730], CAATEX [280531], and HAVOC [280292]). This work is a contribution to DFO Science and the Marine Productivity Laboratory Program, and the Diatom ARCTIC project (NE/R012849/1; 03F0810A), part of the Changing Arctic Ocean program, jointly funded by the UKRI Natural Environment Research Council and the German Federal Ministry of Education and Research (BMBF).

Competing interests

All listed authors have declared that no competing interests exist.

CM is an associate editor in the knowledge domain "Ocean Science."

Author contributions

Contributed to conception and design: DK, SHF, and CM.

Contributed to acquisition of data: All authors.

Contributed to analysis and interpretation of data: DK, SWD, BAL, AR, KLC, SHF, and CM.

Drafted and/or revised the article: All authors.

Approved the submitted version for publication: All authors.

References

- Arctic Monitoring and Assessment Programme (AMAP).** 2017. *Snow, Water, Ice and Permafrost in the Arctic 2017 (SWIPA)*. Oslo, Norway. Xiv + 269 pp. Available at <https://swipa.amap.no/>. Accessed 3 February 2020.
- Arndt, CE, Swadling, KM.** 2006. Crustacea in Arctic and Antarctic sea ice: Distribution, diet and life history strategies. *Adv Mar Biol* **51**: 197–315. DOI: [http://dx.doi.org/10.1016/S0065-2881\(06\)51004-1](http://dx.doi.org/10.1016/S0065-2881(06)51004-1).
- Arrigo, KR.** 2014. Sea ice ecosystems. *Ann Rev Mar Sci* **6**: 439–467. DOI: <http://dx.doi.org/10.1146/annurev-marine-010213-135103>.
- Arrigo, KR, Mock, TM, Lizotte, MP.** 2003. Primary production in sea ice, in Thomas, DN, Dieckmann, GS eds., *Sea ice: An introduction to its physics, chemistry, biology and geology*. Oxford, UK: Blackwell Science: 143–183.
- Arrigo, KR, Mock, TM, Lizotte, MP.** 2010. Primary producers and sea ice, in Thomas, DN, Dieckmann, GS eds., *Sea ice: An introduction to its physics, chemistry, biology and geology*. 2nd edn. Oxford, UK: Wiley-Blackwell: 283–326.
- Aumack, CF, Juhl, AR, Krembs, C.** 2014. Diatom vertical migration within land-fast Arctic sea ice. *J Mar Syst* **139**: 496–504. DOI: <http://dx.doi.org/10.1016/j.jmarsys.2014.08.013>.
- Bergé, J-P, Barnathan, G.** 2005. Fatty acids from lipids of marine organisms: Molecular biodiversity, roles as biomarkers, biologically active compounds, and economical aspects. *Adv Biochem Engin/Biotechnol* **96**: 49–125. DOI: <http://dx.doi.org/10.1007/b135782>.
- Bluhm, BA, Gradinger, RR, Schnack-Schiel, SB.** 2010. Sea ice meio- and macrofauna, in Thomas, DN, Dieckmann, GS eds., *Sea ice: An introduction to its physics, chemistry, biology and geology*. 2nd edn. Oxford, UK: Wiley-Blackwell: 357–393.
- Boetius, A, Albrecht, S, Bakker, K, Bienhold, C, Felden, J, Fernández-Méndez, M, Hendricks, S, Katlein, C, Lalande, C, Krumpfen, T, Nicolaus, M, Peeken, I, Rabe, B, Rogacheva, A, Rybakoba, E, Somavilla, R, Wenzhöfer, F, Polarstern, RV, ARK27-3 Shipboard Science Party.** 2013. Export of algal biomass from the melting Arctic sea ice. *Science*

- 339(6126): 1430–1432. DOI: <http://dx.doi.org/10.1126/science.1231346>.
- Boetius, A, Anesio, AM, Deming, JW, Mikucki, J, Rapp, JZ.** 2015. Microbial ecology of the cryosphere: Sea ice and glacial habitats. *Nat Microbiol Rev* **13**: 677–690. DOI: <http://dx.doi.org/10.1038/nrmicro3522>.
- Bowman, JS, Rasmussen, S, Blom, N, Deming, JW, Rysgaard, S, Scheritz-Ponten, T.** 2012. Microbial community structure of Arctic multiyear sea ice and surface seawater by 454 sequencing of the 16S RNA gene. *ISME J* **6**: 11–20. DOI: <http://dx.doi.org/10.1038/ismej.2011.76>.
- Brett, MT, Müller-Navarra, DC.** 1997. The role of highly unsaturated fatty acids in aquatic foodweb processes. *Freshwater Biol* **38**(3): 483–499. DOI: <http://dx.doi.org/10.1046/j.1365-2427.1997.00220.x>.
- Budge, SM, Parrish, CC, McKenzie, CH.** 2001. Fatty acid composition of phytoplankton, settling particulate matter and sediments at a sheltered bivalve aquaculture site. *Mar Chem* **76**(4): 285–303. DOI: [http://dx.doi.org/10.1016/S0304-4203\(01\)00068-8](http://dx.doi.org/10.1016/S0304-4203(01)00068-8).
- Campbell, K, Mundy, CJ, Gosselin, M, Landy, JC, Delaforge, A, Rysgaard, S.** 2017. Net community production in the bottom of first-year sea ice over the Arctic spring bloom. *Geophys Res Lett* **44**(17): 8971–8978. DOI: <http://dx.doi.org/10.1002/2017GL074602>.
- Comiso, JC.** 2012. Large decadal decline of the Arctic multiyear ice cover. *J Clim* **25**(4): 1176–1193. DOI: <http://dx.doi.org/10.1175/JCLI-D-11-00113.1>.
- Conover, RJ, Herman, AW, Prinsenberg, SJ, Harris, LR.** 1986. Distribution of and feeding by the copepod *Pseudocalanus* under fast ice during the Arctic spring. *Science* **232**(4755): 1245–1247. DOI: <http://dx.doi.org/10.1126/science.232.4755.1245>.
- Conover, RJ, Huntley, M.** 1991. Copepods in ice-covered seas—distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. *J Mar Sys* **2**(1–2): 1–41. DOI: [http://dx.doi.org/10.1016/0924-7963\(91\)90011-1](http://dx.doi.org/10.1016/0924-7963(91)90011-1).
- Dalsgaard, J, John, MS, Kattner, G, Müller-Navarra, D, Hagen, W.** 2003. Fatty acid trophic markers in the pelagic marine environment. *Adv Mar Biol* **46**: 225–340. DOI: [http://dx.doi.org/10.1016/S0065-2881\(03\)46005-7](http://dx.doi.org/10.1016/S0065-2881(03)46005-7).
- David, C, Lange, BA, Krumpfen, T, Schaafsma, FL, van Franeker, JA, Flores H.** 2016. Under-ice distribution of polar cod *Boreogadus saida* in the central Arctic Ocean and their association with sea-ice habitat properties. *Polar Biol* **39**(6): 981–994. DOI: <http://dx.doi.org/10.1007/s00300-015-1774-0>.
- David, C, Lange, BA, Rabe, B, Flores, H.** 2015. Community structure of under-ice fauna in the Eurasian central Arctic Ocean in relation to environmental properties of sea-ice habitats. *Mar Ecol Prog Ser* **522**: 15–32. DOI: <http://dx.doi.org/10.3354/meps11156>.
- Derksen, C, Smith, SL, Sharp, M, Brown, L, Howell, S, Copland, L, Mueller, DR, Gauthier, Y, Fletcher, CG, Tivy, A, Bernier, M, Bourgeois, J, Brown, R, Burn, CR, Duguay, C, Kushner, P, Langlois, A, Lewkowicz, AG, Royer, A, Walker, A.** 2012. Variability and change in the Canadian cryosphere. *Clim Change* **115**(1): 59–88. DOI: <http://dx.doi.org/10.1007/s10584-012-0470-0>.
- Duffaud, C.** 2020. Structure et fonctionnement des communautés microbiennes dans la glace annuelle et pluriannuelle de la mer de Licoln au printemps [M.Sc. Thesis]. Université du Québec à Rimouski, xxvii + 74 p.
- Dunstan, GA, Volkman, JK, Barrett, SM, Leroi, J-M, Jeffrey, S.** 1993. Essential polyunsaturated fatty acids from 14 species of diatom (Bacillariophyceae). *Phytochem* **35**(1): 155–161. DOI: [http://dx.doi.org/10.1016/S0031-9422\(00\)90525-9](http://dx.doi.org/10.1016/S0031-9422(00)90525-9).
- Fahl, K, Kattner, G.** 1993. Lipid content and fatty acid composition of algal communities in sea-ice and water from the Weddell Sea (Antarctica). *Polar Biol* **13**(6): 405–409. DOI: <http://dx.doi.org/10.1007/BF01681982>.
- Falk-Petersen, S, Sargent, JR, Henderson, J, Hegseth, EN, Hop, H, Okolodkov, YB.** 1998. Lipids and fatty acids in ice algae and phytoplankton from the Marginal Ice Zone in the Barents Sea. *Polar Biol* **20**(1): 41–47. DOI: <http://dx.doi.org/10.1007/s003000050274>.
- Folch, J, Lees, M, Sloane Stanley, GHS.** 1957. A simple method for the isolation and purification of total lipids from animal tissues. *J Biol Chem* **226**(1): 497–509.
- Fry, B.** 1996. ¹³C/¹²C fractionation by marine diatoms. *Mar Ecol Prog Ser* **134**: 283–294. DOI: <http://dx.doi.org/10.3354/meps134283>.
- Gradinger, RR.** 1999a. Integrated abundance and biomass of sympagic meiofauna in Arctic and Antarctic pack ice. *Polar Biol* **22**(3): 169–177. DOI: <http://dx.doi.org/10.1007/s003000050407>.
- Gradinger, RR.** 1999b. Vertical fine structure of the biomass and composition of algal communities in Arctic pack ice. *Mar Biol* **133**(4): 745–754. DOI: <http://dx.doi.org/10.1007/s002270050516>.
- Gradinger, RR, Bluhm, BA.** 2020. First analysis of an Arctic sea ice meiofauna food web based on abundance, biomass and stable isotope ratios. *Mar Ecol Prog Ser* **634**: 29–43. DOI: <http://dx.doi.org/10.3354/meps13170>.
- Gradinger, RR, Bluhm, BA, Iken, K.** 2010. Arctic sea-ice ridges—Safe heavens for sea-ice fauna during periods of extreme ice melt? *Deep Sea Res (II): Top Stud Oceanogr* **57**(1-2): 86–95. DOI: <http://dx.doi.org/10.1016/j.dsr2.2009.08.00>
- Gradinger, RR, Meiners, K, Plumley, G, Zhang, Q, Bluhm, BA.** 2005. Abundance and composition of the sea-ice meiofauna in off-shore pack ice of the Beaufort Gyre in summer 2002 and 2003. *Polar Biol* **28**(3): 171–181. DOI: <http://dx.doi.org/10.1007/s00300-004-0674-5>.
- Gradinger, RR, Schnack-Schiel, SB.** 1998. Potential effect of ice formation on Antarctic pelagic

- copepods: Salinity induced mortality of *Calanus propinquus* and *Metridia gerlachei* in comparison to sympagic acoel turbellarians. *Polar Biol* **20**(2): 139–142. DOI: <http://dx.doi.org/10.1007/s003000050288>.
- Gradinger, RR, Spindler, M, Henschel, D.** 1991. Development of Arctic sea-ice organisms under graded snow cover. *Polar Res* **10**(1): 295–308 doi: 10.3402/polar.v10i1.6748.
- Graeve, M, Kattner, G, Hagen, W.** 1994. Diet-induced changes in the fatty acid composition of Arctic herbivorous copepods: Experimental evidence of trophic markers. *J Exp Mar Biol Ecol* **182**: 97–110. DOI: [http://dx.doi.org/10.1016/0022-0981\(94\)90213-5](http://dx.doi.org/10.1016/0022-0981(94)90213-5).
- Graeve, M, Kattner, G, Piepenburg, D.** 1997. Lipids in Arctic benthos: Does the fatty acid and alcohol composition reflect feeding and trophic interactions? *Polar Biol* **18**(1): 53–61. DOI: <http://dx.doi.org/10.1007/s003000050158>.
- Grant, WS, Horner, RA.** 1976. Growth responses to salinity variation in four Arctic ice diatoms. *J Phycol* **12**(2): 180–185. DOI: <http://dx.doi.org/10.1111/j.1529-8817.1976.tb00498.x>.
- Haas, C, Hendricks, S, Doble, M.** 2006. Comparison of the sea-ice thickness distribution in the Lincoln Sea and adjacent Arctic Ocean in 2004 and 2005. *Ann Glaciol* **44**: 247–252. DOI: <http://dx.doi.org/10.3189/172756406781811781>.
- Haas, C, Hendricks, S, Eicken, H, Herber, A.** 2010. Synoptic airborne thickness surveys reveal state of Arctic sea ice cover. *Geophys Res Lett* **37**(9): L09501. DOI: <http://dx.doi.org/10.1029/2010GL042652>.
- Hardge, K, Peeken, I, Neuhaus, S, Lange, BA, Stock, A, Stoeck, T, Weinisch, L, Metfies, K.** 2017. The importance of sea ice for exchange of habitat-specific protist communities in the Central Arctic Ocean. *J Mar Sys* **165**: 124–138. DOI: <http://dx.doi.org/10.1016/j.jmarsys.2016.10.004>.
- Hatam, I, Charchuk, R, Lange, B, Beckers, J, Haas, C, Lanoil, B.** 2014. Distinct bacterial assemblages reside at different depths in Arctic multiyear sea ice. *FEMS Microbiol Ecol* **90**(1–2): 1–11. DOI: <http://dx.doi.org/10.1111/1574-6941.12377>.
- Hatam, I, Lange, BA, Beckers, J, Haas, C, Lanoil, B.** 2016. Bacterial communities from Arctic seasonal sea ice are more compositionally variable than those from multi-year sea ice. *ISME J* **10**(10): 2543–2552. DOI: <http://dx.doi.org/10.1038/ismej.2016.4>.
- Hays, GC, Richardson, AJ, Robinson, C.** 2005. Climate change and marine plankton. *Trends Ecol Evol* **20**(6): 337–344. DOI: <http://dx.doi.org/10.1016/j.tree.2005.03.004>.
- Henderson, RJ, Hegseth, EN, Park, MT.** 1998. Seasonal variation in lipid and fatty acid composition of ice algae from the Barents Sea. *Polar Biol* **20**(1): 48–55. DOI: <http://dx.doi.org/10.1007/s003000050275>.
- Hobson, KA, Ambrose Jr, WG, Renaud, PE.** 1995. Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: Insights from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Mar Ecol Prog Ser* **128**: 1–10. DOI: <http://dx.doi.org/10.3354/meps128001>.
- Hop, H, Vihtakari, M, Bluhm, BA, Assmy, P, Poulin, M, Gradinger RR, Peeken, I, von Quillfeldt, C, Olsen, LM, Zhitina L, Melnikov, IA.** 2020. Changes in sea-ice protist diversity with declining sea ice in the Arctic Ocean from the 1980s to 2010s. *Front Mar Sci* **7**: 243. DOI: <http://dx.doi.org/10.3389/fmars.2020.00243>.
- Intergovernmental Panel on Climate Change.** 2019. IPCC special report on the ocean and cryosphere in a changing climate. Pörtner, HO, Roberts, DC, Masson-Delmotte, V, Zhai, P, Tignor, M, Poloczanska, E, Mintenbeck, K, Alegriña, A, Nicolai, M, Okem, A, Petzold, J, Rama, B, Weyer, NM eds. Available at <https://www.ipcc.ch/srocc/cite-report/>.
- Ji, R, Jin, M, Varpe, Ø.** 2013. Sea ice phenology and timing of primary production pulses in the Arctic Ocean. *Glob Change Biol* **19**(3): 734–741. DOI: <http://dx.doi.org/10.1111/gcb.12074>.
- Kattner, G, Gercken, G, Eberlein, K.** 1983. Development of lipids during a spring plankton bloom in the northern North Sea: I. Particulate fatty acids. *Mar Chem* **14**(2): 149–162. DOI: [http://dx.doi.org/10.1016/0304-4203\(83\)90039-7](http://dx.doi.org/10.1016/0304-4203(83)90039-7).
- Kauko, HM, Olsen, LM, Duarte, P, Peeken, I, Granskog, MA, Johnsen, G, Fernández-Méndez, M, Pavlov, AK, Mundy, CJ, Assmy, P.** 2018. Algal colonization of young Arctic sea ice in spring. *Front Mar Sci* **5**. DOI: <http://dx.doi.org/10.3389/fmars.2018.00199>.
- Kirst, GO, Wiencke, C.** 1995. Ecophysiology of polar algae. *J Phycol* **31**: 181–199. DOI: <http://dx.doi.org/10.1111/j.0022-3646.1995.00181.x>.
- Kohlbach, D, Ferguson, SH, Brown, TA, Michel, C.** 2019a. Landfast sea ice-benthic coupling during spring and potential impacts of system changes on food web dynamics in Eclipse Sound, Canadian Arctic. *Mar Ecol Prog Ser* **627**: 33–48. DOI: <http://dx.doi.org/10.3354/meps13071>.
- Kohlbach, D, Graeve, M, Lange, BA, David, C, Peeken, I, Flores, H.** 2016. The importance of ice algae-produced carbon in the central Arctic Ocean ecosystem: Food web relationships revealed by lipid and stable isotope analyses. *Limnol Oceanogr* **61**(6): 2027–2044. DOI: <http://dx.doi.org/10.1002/lno.10351>.
- Kohlbach, D, Graeve, M, Lange, BA, David, C, Schaafsma, FL, van Franeker, JA, Vortkamp, M, Brandt, A, Flores, H.** 2018. Dependency of Antarctic zooplankton species on ice algae-produced carbon suggests a sea ice-driven pelagic ecosystem during winter. *Glob Change Biol* **24**(10): 4667–4681. DOI: <http://dx.doi.org/10.1111/gcb.14392>.
- Kohlbach, D, Lange, BA, Graeve, M, Vortkamp, M, Flores, H.** 2019b. Varying dependency of Antarctic euphausiids on ice algae- and phytoplankton-derived carbon sources during summer. *Mar Biol* **166**(6): 79. DOI: <http://dx.doi.org/10.1007/s00227-019-3527-z>.

- Krembs, C, Gradinger, RR, Spindler, M.** 2000. Implications of brine channel geometry and surface area for the interaction of sympagic organisms in Arctic sea ice. *J Exp Mar Biol Ecol* **243**(1): 55–80. DOI: [http://dx.doi.org/10.1016/S0022-0981\(99\)00111-2](http://dx.doi.org/10.1016/S0022-0981(99)00111-2).
- Kukert, H, Riebesell, U.** 1998. Phytoplankton carbon isotope fractionation during a diatom spring bloom in a Norwegian fjord. *Mar Ecol Prog Ser* **173**: 127–138. DOI: <http://dx.doi.org/10.3354/meps173127>.
- Lange, BA, Flores, H, Michel, C, Beckers, JF, Bublit, A, Casey, JA, Castellani, G, Hatam, I, Reppchen, A, Rudolph, SA, Haas, C.** 2017. Pan-Arctic sea ice-algal chl *a* biomass and suitable habitat are largely underestimated for multiyear ice. *Glob Change Biol* **23**(11): 4581–4597. DOI: <http://dx.doi.org/10.1111/gcb.13742>.
- Lange, BA, Haas, C, Charette, J, Katlein, C, Campbell, K, Duerksen, S, Coupel, P, Anhaus, P, Jutila, A, Tremblay, POG, Carlyle, CG, Michel, C.** 2019. Contrasting ice algae and snow-dependent irradiance relationships between landfast first-year and multi-year sea ice. *Geophys Res Lett* **46**(19): 10834–10843. DOI: <http://dx.doi.org/10.1029/2019GL082873>.
- Lange, BA, Michel, C, Beckers, JF, Casey, JA, Flores, H, Hatam, I, Meisterhans, G, Niemi, A, Haas, C.** 2015. Comparing springtime ice-algal chlorophyll *a* and physical properties of multi-year and first-year sea ice from the Lincoln Sea. *PLoS One* **10**(4): e0122418. DOI: <http://dx.doi.org/10.1371/journal.pone.0122418>.
- Lee, RF, Hagen, W, Kattner, G.** 2006. Lipid storage in marine zooplankton. *Mar Ecol Prog Ser* **307**: 273–306. DOI: <http://dx.doi.org/10.3354/meps307273>.
- Legendre, P, Legendre, LF.** 2012. *Numerical ecology*. 3rd edn., vol. 24. Oxford, UK: Elsevier.
- Leu, E, Falk-Petersen, S, Kwaśniewski, S, Wulff, A, Edwardsen, K, Hessen, DO.** 2006. Fatty acid dynamics during the spring bloom in a High Arctic fjord: Importance of abiotic factors versus community changes. *Can J Fish Aquat Sci* **63**(12): 2760–2779. DOI: <http://dx.doi.org/10.1139/f06-159>.
- Leu, E, Søreide, JE, Hessen, DO, Falk-Petersen, S, Berge, J.** 2011. Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: Timing, quantity, and quality. *Prog Oceanogr* **90**(1–4): 18–32. DOI: <http://dx.doi.org/10.1016/j.pocean.2011.02.004>.
- Lizotte, MP.** 2003. The microbiology of sea ice, in Thomas, DN, Dieckmann, DN eds., *Sea ice: An introduction to its physics, chemistry, biology and geology*. Oxford: Blackwell Science: 184–210.
- Macdonald, RW, Kuzyk, ZA, Johannessen, SC.** 2015. It is not just about the ice: A geochemical perspective on the changing Arctic Ocean. *J Environ Stud Sci* **5**(3): 288–301. DOI: <http://dx.doi.org/10.1007/s13412-015-0302-4>.
- Meier, WN, Hovelsrud, GK, van Oort, BEH, Key, JR, Kovacs, KM, Michel, C, Haas, C, Granskog, MA, Gerland, S, Perovich, DK, Makshtas, A, Reist, JD.** 2014. Arctic sea ice in transformation: A review of recent observed changes and impacts on biology and human activity. *Rev Geophys* **52**(3): 185–217. DOI: <http://dx.doi.org/10.1002/2013RG000431>.
- Melnikov, IA.** 2009. Recent sea ice ecosystem in the Arctic Ocean: A review, in Nihoul J, Kostianoy AG eds., *Influence of climate change on the changing Arctic and sub-Arctic conditions*. Dordrecht: Springer: 57–71 (NATO Science for Peace and Security Series C: Environmental Security).
- Melnikov, IA, Kolosova EG, Welch, HE, Zhitina, LS.** 2002. Sea ice biological communities and nutrient dynamics in the Canada Basin of the Arctic Ocean. *Deep Sea Res I: Oceanogr Res Pap* **49**(9): 1623–1649. DOI: [http://dx.doi.org/10.1016/S0967-0637\(02\)00042-0](http://dx.doi.org/10.1016/S0967-0637(02)00042-0).
- Melnikov, IA, Zhitina, LS, Kolosova, HG.** 2001. The Arctic sea ice biological communities in recent environmental changes (scientific note). *Mem Natl Inst of Polar Res Spec Issue* **54**: 409–416.
- Michel, C, Legendre, L, Ingram, RG, Gosselin, M, Levasseur, M.** 1996. Carbon budget of sea-ice algae in spring: Evidence of a significant transfer to zooplankton grazers. *J Geophys Res Oceans* **101**(C8): 18345–18360. DOI: <http://dx.doi.org/10.1029/96JC00045>.
- Michel, C, Nielsen, TG, Nozais, C, Gosselin, M.** 2002. Significance of sedimentation and grazing by ice micro- and meiofauna for carbon cycling in annual sea ice (northern Baffin Bay). *Aquat Microb Ecol* **30**(1): 57–68. DOI: <http://dx.doi.org/10.3354/ame030057>.
- Mintenbeck, K, Brey, T, Jacob, U, Knust, R, Struck, U.** 2008. How to account for the lipid effect on carbon stable-isotope ratio ($\delta^{13}\text{C}$): Sample treatment effects and model bias. *J Fish Biol* **72**(4): 815–830. DOI: <http://dx.doi.org/10.1111/j.1095-8649.2007.01754.x>.
- Mundy, CJ, Gosselin, M, Ehn, JK, Belzile, C, Poulin, M, Alou, E, Roy, S, Hop, H, Lessard, S, Papakyriakou, TN, Barber, DG, Stewart, J.** 2011. Characteristics of two distinct high-light acclimated algal communities during advanced stages of sea ice melt. *Polar Biol* **34**(12): 1869–1886. DOI: <http://dx.doi.org/10.1007/s00300-011-0998-x>.
- Nichols, DS, McMeekin, TA.** 2002. Biomarker techniques to screen for bacteria that produce polyunsaturated fatty acids. *J Microbiol Meth* **48**(2-3): 161–170. DOI: [http://dx.doi.org/10.1016/S0167-7012\(01\)00320-7](http://dx.doi.org/10.1016/S0167-7012(01)00320-7).
- Olsen, LM, Laney, SR, Duarte, P, Kauko, HM, Fernández-Méndez, M, Mundy, CJ, Rösel, A, Meyer, A, Itkin, P, Cohen, L, Peeken, I, Tatarek, A, Rózańska-Pluta, M, Wiktor, JM, Taskjelle, T, Pavlov, AK, Hudson, SR, Granskog, MA, Hop, H, Assmy, P.** 2017. The seeding of ice algal blooms in Arctic pack ice: The multiyear ice seed repository hypothesis. *J Geophys Res: Biogeosci* **122**(7): 1529–1548. DOI: [10.1002/2016JG003668](http://dx.doi.org/10.1002/2016JG003668).
- Ostrom, NE, Macko, SA, Deibel, D, Thompson, RJ.** 1997. Seasonal variation in the stable carbon and nitrogen isotope biogeochemistry of a coastal cold ocean

- environment. *Geochim Cosmochim Acta* **61**(14): 2929–2942.
- Parrish, CC, Thompson, RJ, Deibel, D.** 2005. Lipid classes and fatty acids in plankton and settling matter during the spring bloom in a cold ocean coastal environment. *Mar Ecol Prog Ser* **286**: 57–68. DOI: <http://dx.doi.org/10.3354/meps286057>.
- Parsons TR, Maita, Y, Lalli, CM.** 1984. *A manual of chemical and biological methods for seawater analysis*. 1st edn. New York: Pergamon Press.
- Paul, D, Skrzypek, G, Fórizs, I.** 2007. Normalization of measured stable isotopic compositions to isotope reference scales—a review. *Rap Commun Mass Spectrom* **21**(18): 3006–3014. DOI: <http://dx.doi.org/10.1002/rcm.3185>.
- Polyakov, IV, Walsh, JE, Kwok, R.** 2012. Recent changes of Arctic multiyear sea ice coverage and the likely causes. *Bull Amer Meteorol Soc* **93**(2): 145–151. DOI: <http://dx.doi.org/10.1175/BAMS-D-11-00070.1>.
- Poulin, M, Daugbjerg, N, Gradinger, RR, Ilyash, L, Ratkova, T, von Quillfeldt, C.** 2011. The pan-Arctic biodiversity of marine pelagic and sea-ice unicellular eukaryotes: A first-attempt assessment. *Mar Biodiv* **41**(1): 13–28. DOI: <http://dx.doi.org/10.1007/s12526-010-0058-8>.
- R Core Team.** 2017. *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Reitan, KI, Rainuzzo, JR, Olsen Y.** 1994. Effect of nutrient limitation on fatty acid and lipid content of marine microalgae 1. *J Phycol* **30**(6): 972–979. DOI: <http://dx.doi.org/10.1111/j.0022-3646.1994.00972.x>.
- Renaud, PE, Riedel, A, Morata, N, Gosselin, M, Michel, C, Juul-Pedersen, T, Chiuchiolo, A.** 2007. Seasonal variation in the benthic community oxygen demand: A response to an ice algal bloom in the Beaufort Sea, Canadian Arctic? *J Mar Syst* **67**(1–2): 1–12. DOI: <http://dx.doi.org/10.1016/j.jmarsys.2006.07.006>.
- Reuss, N, Poulsen, L.** 2002. Evaluation of fatty acids as biomarkers for a natural plankton community. A field study of a spring bloom and a post-bloom period off West Greenland. *Mar Biol* **141**(3): 423–434. DOI: <http://dx.doi.org/10.1007/s00227-002-0841-6>.
- Riedel, A, Michel, C, Gosselin, M.** 2006. Seasonal study of sea-ice exopolymeric substances on the Mackenzie shelf: Implications for transport of sea-ice bacteria and algae. *Aquat Microb Ecol* **45**(2): 195–206. DOI: <http://dx.doi.org/10.3354/ame045195>.
- Riedel, A, Michel C, Gosselin M, LeBlanc, B.** 2008. Winter spring dynamics in sea-ice carbon cycling on the Mackenzie shelf, Canadian Arctic. *J Mar Syst* **74**(3–4): 918–932. DOI: <http://dx.doi.org/10.1016/j.jmarsys.2008.01.003>.
- Roy, V, Iken, K, Gosselin, M, Tremblay, J-É, Bélanger, S, Archambault, P.** 2015. Benthic faunal assimilation pathways and depth-related changes in food-web structure across the Canadian Arctic. *Deep Sea Res I: Oceanogr Res Pap* **102**: 55–71. DOI: <http://dx.doi.org/10.1016/j.dsr.2015.04.009>.
- Róžańska, M, Gosselin, M, Poulin, M, Wiktor, JM, Michel, C.** 2009. Influence of environmental factors on the development of bottom landfast ice protists in the Canadian Beaufort Sea during the winter-spring transition. *Mar Ecol Prog Ser* **386**: 43–59. DOI: <http://dx.doi.org/10.3354/meps08092>.
- Sargent, JR, Bell, JG, Bell, MV, Henderson, RJ, Tocher, DR.** 1995. Requirement criteria for essential fatty acids. *J Appl Ichthyol* **11**(3/4): 183–198. DOI: <http://dx.doi.org/10.1111/j.1439-0426.1995.tb00018.x>.
- Sargent, JR, Whittle, KJ.** 1981. Lipids and hydrocarbons in the marine food web, in Longhurst, AR ed., *Analysis of marine ecosystems*. London, UK: Academic Press: 491–533.
- Serreze, MC, Meier, WN.** 2019. The Arctic's sea ice cover: Trends, variability, predictability, and comparisons to the Antarctic. *Ann N Y Acad Sci* **1436**(1): 36–53. DOI: <http://dx.doi.org/10.1111/nyas.13856>.
- Søreide, JE, Leu, E, Berge, J, Graeve, M, Falk-Petersen, S.** 2010. Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. *Glob Change Biol* **16**(11): 3154–3163. DOI: <http://dx.doi.org/10.1111/j.1365-2486.2010.02175.x>.
- Spindler, M.** 1990. A comparison of Arctic and Antarctic sea ice and the effects of different properties on sea ice biota, in Bleil U, Thiede J eds., *Geological history of the polar oceans: Arctic versus Antarctic*. Dordrecht: Springer: 173–186 (NATO ASI Series: Series C: Mathematical and Physical Sciences, vol. 308).
- Tameland, T, Kivimäe, C, Bellerby, RGJ, Renaud, PE, Kristiansen, S.** 2009. Base-line variations in stable isotope values in an Arctic marine ecosystem: Effects of carbon and nitrogen uptake by phytoplankton. *Hydrobiol* **630**(1): 63–73. DOI: <http://dx.doi.org/10.1007/s10750-009-9780-2>.
- Thomas, DN, Lara, RJ, Eicken, H, Kattner, G, Skoog, A.** 1995. Dissolved organic matter in Arctic multi-year sea ice during winter: Major components and relationship to ice characteristics. *Polar Biol* **15**(7): 477–483. DOI: <http://dx.doi.org/10.1007/BF00237461>.
- Thompson, PA, Calvert, SE.** 1994. Carbon-isotope fractionation by a marine diatom: The influence of irradiance, daylength, pH, and nitrogen source. *Limnol Oceanogr* **39**(8): 1835–1844. DOI: <http://dx.doi.org/10.4319/lo.1994.39.8.1835>.
- Timco, GW, Burden, RP.** 1997. An analysis of the shapes of sea ice ridges. *Cold Reg Sci Technol* **25**(1): 65–77. DOI: [http://dx.doi.org/10.1016/S0165-232X\(96\)00017-1](http://dx.doi.org/10.1016/S0165-232X(96)00017-1).
- Tremblay, JE, Michel, C, Hobson, KA, Gosselin, M, Price, NM.** 2006. Bloom dynamics in early opening waters of the Arctic Ocean. *Limnol Oceanogr* **51**(2):

- 900–912. DOI: <http://dx.doi.org/10.4319/lo.2006.51.2.0900>.
- van Leeuwe, MA, Tedesco, L, Arrigo, KR, Assmy, P, Campbell, K, Meiners, KM, Rintala, J-M, Selz, V, Thomas, DN, Stefels, J.** 2018. Microalgal community structure and primary production in Arctic and Antarctic sea ice. *Elem Sci Anth* **6**: 4. DOI: <http://dx.doi.org/10.1525/elementa.267>.
- Wang, SW, Budge, SM, Gradinger, RR, Iken, K, Wooller, MJ.** 2014. Fatty acid and stable isotope characteristics of sea ice and pelagic particulate organic matter in the Bering Sea: Tools for estimating sea ice algal contribution to Arctic food web production. *Oecologia* **174**(3): 699–712. DOI: <http://dx.doi.org/10.1007/s00442-013-2832-3>.
- Wang, SW, Budge, SM, Iken, K, Gradinger, RR, Springer, AM, Wooller, MJ.** 2015. Importance of sympagic production to Bering Sea zooplankton as revealed from fatty acid-carbon stable isotope analyses. *Mar Ecol Prog Ser* **518**: 31–50. DOI: <http://dx.doi.org/10.3354/meps11076>.
- Wassmann, P, Duarte, CM, Agusti, S, Sejr, MK.** 2011. Footprints of climate change in the Arctic marine ecosystem. *Glob Change Biol* **17**(2): 1235–1249. DOI: <http://dx.doi.org/10.1111/j.1365-2486.2010.02311.x>.

How to cite this article: Kohlbach, D, Duerksen, SW, Lange, BA, Charette, J, Reppchen, A, Tremblay, P, Campbell, KL, Ferguson, SH, Michel, C. 2020. Fatty acids and stable isotope signatures of first-year and multiyear sea ice in the Canadian High Arctic. *Elem Sci Anth*. 8: 1. DOI: <https://doi.org/10.1525/elementa.2020.054>

Domain Editor-in-Chief: Jody W. Deming, University of Washington, Seattle, WA, USA

Associate Editor: Kevin Arrigo, Stanford University, Stanford, CA, USA

Knowledge Domain: Ocean Science

Part of an *Elementa* Special Feature: Multidisciplinary Arctic Program—Last Ice

Published: December 21, 2020 **Accepted:** October 31, 2020 **Submitted:** May 20, 2020

Copyright: © 2020 The Author(s). This is an open-access article distributed under the terms of the Creative Commons Attribution 4.0 International License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. See <http://creativecommons.org/licenses/by/4.0/>.



Elem Sci Anth is a peer-reviewed open access journal published by University of California Press.

OPEN ACCESS