



## Article

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# Carbon and nitrogen uptake rates and macromolecular compositions of bottom-ice algae and phytoplankton at Cambridge Bay in Dease Strait, Canada

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**Abstract**

Our understanding of ice algal responses to the recent changes in Arctic sea ice is impeded by limited field observations. In the present study, environmental characteristics of the landfast sea-ice zone as well as primary production and macromolecular composition of ice algae and phytoplankton were studied in the Kitikmeot Sea near Cambridge Bay in spring 2017. Averaged total chlorophyll-*a* (Chl-*a*) concentration was within the lower range reported previously for the same region, while daily carbon uptake rates of bottom-ice algae were significantly lower in this study than previously reported for the Arctic. Based on various indicators, the region's low nutrient concentrations appear to limit carbon uptake rates and associated accumulation of bottom-ice algal biomass. Furthermore, the lipids-dominant biochemical composition of bottom-ice algae suggests strong nutrient limitation relative to the distinctly different carbohydrates-dominant composition of phytoplankton. Together, the results confirm strong nitrate limitation of the local marine system.

**Introduction**

Ice algae within or attached to the sea-ice bottom provide an important food source in arctic marine food webs from sympagic and pelagic zooplankton to marine mammals as well as seabirds (Søreide and others, 2010; Daase and others, 2013; Van Leeuwe and others, 2018; others therein). Although their contributions as primary producers appear to vary regionally from <1% in seasonal ice-covered shelf areas up to ~60% in the central deep Arctic Ocean (Gosselin and others, 1997; Lee and others, 2015; Song and others, 2016), ice algae play an ecologically critical role as a primary food source for the arctic marine ecosystem in spring (Lee and others, 2011; Leu and others, 2015). Ice algal blooms are prominent prior to the pelagic spring bloom in the early arctic summer (Apollonio, 1965; Legendre and others, 1992; Michel and others, 1996; Lee and others, 2008; Leu and others, 2015). A potential fall bloom after the phytoplankton blooms in late summer can also extend the short arctic summer production period and provide late-season food complements before the long dark winter (Lee and others, 2011). These spring and fall blooms of ice algae prolong the production season of overwintering grazers in the Arctic Ocean (Michel and others, 1996; Lee and others, 2008, 2011; Fernández-Méndez and others, 2014). Moreover, the diatom-dominant ice algal community contains large amounts of high-quality polyunsaturated fatty acids which can be critical for successful egg production, hatching and larval development of sympagic herbivores (Leu and others, 2010).

The bottom-ice algal community is generally the most productive sea-ice community in landfast ice zone fringing the Arctic Ocean (e.g., Smith and others, 1987; Renaud and others, 2007; Lee and others, 2008; Campbell and others, 2016). Greater than 90% of chlorophyll-*a* (Chl-*a*) biomass of ice algae can be accumulated at the bottommost 0.03–0.05 m of the landfast sea ice (Smith and others, 1990; Lee and others, 2008, 2010; Campbell and others, 2016).

Recent changes in sea-ice conditions could have negative or positive impacts on ice-related organisms in the Arctic Ocean (Barber and others, 2015; Tedesco and others, 2019). Moreover, greater precipitation and earlier snow-melt onset projected for the Arctic (Lynch and others, 2004) could change the timing of ice algal spring blooms (Lavoie and others, 2005; Lee and others, 2008). However, the response of the bottom-ice algae to these changes in sea-ice and snow conditions could be diverse with latitudinal dependency (Castellani and others, 2017; Tedesco and others, 2019). Currently, a relatively sparse number of in situ field observations of ice algal production hinder our understanding of their responses to the current and ongoing environmental changes in previously ice-covered regions (Gradinger, 2009; Lee and others, 2010). The objectives of this study are to: (1) describe the environmental characteristics of the landfast sea-ice zone near Cambridge Bay in Dease Strait, Canada; (2) estimate the primary production and the relative contribution of bottom-ice algae and pelagic phytoplankton

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during spring; and (3) evaluate the characteristics in macromolecular composition of ice algae and phytoplankton.

## Material and methods

### Study area

Ice and water samples were collected from the first year sea ice near the Finlayson islands located in Kitikmeot Sea of the Canadian Arctic from 26 April to 12 May 2017. Four stations were selected for regular sampling along a transect crossing a narrow constricted waterway based on Dalman and others (2019), who observed evidence for an enhanced ocean-ice nutrient supply towards the centre of the Finlayson Islands (Fig. 1). However, due to logistical issues, not all stations were sampled consistently throughout the program. Sampling stations 1 through 4 started at a 33 km distance from Cambridge Bay, Nunavut (Fig. 1).

### Sampling

A hyperspectral cosine sensor (Satlantic HyperOCR) was employed to measure under-ice transmitted spectral irradiance. The sensor was positioned 1.5 m south of a 25 cm auger hole using an under-ice arm and snow was placed in the hole to minimize stray light contamination of the measurements. Spectral irradiance was integrated over 400–700 nm to obtain the estimates of transmitted photosynthetically active radiation. Because we did not measure light intensity at our incubation sites, the measured intensities were only used as a relative reference. Snow depths were measured from ten different locations around our sampling sites before collecting ice core samples. Sea-ice samples were extracted using a Mark II Kovacs core barrel (inner diameter = 9 cm) and sea-ice thickness was measured from the ice core hole. Bottom 0.1 m sections were collected in dark-insulated cooler jugs and transported to the laboratory for further processing and analyses. Two ice core bottoms collected from each sampling station were melted together slowly (without the addition of filtered sea water) in the dark at room temperature overnight. Surface water samples for phytoplankton were collected from the auger hole with a polypropylene bucket after removing all the fragments of the ice and stored in sterile LDPE collapsible water collection bottles. All the bottles were transported to the laboratory in a dark insulated box. Salinities of melted ice and sea water samples were measured with a YSI model 30 salinity meter (YSI, Yellow Springs, Ohio). The instrument was calibrated with 50 mS cm<sup>-1</sup> conductivity standard (YSI Catalog# 3169) with an accuracy of ±0.1. To measure bulk nutrient concentrations (ammonium, nitrate + nitrite, phosphate and silicate), 500 mL of melted ice and water samples were filtered through 47 mm GF/F filters (nominal pore size = 0.7 µm). A total of 50 mL of each filtrate was placed in labelled conical tubes and stored in a -20°C freezer until analysis within 2 months using an Auto analyser (Quattro, Bran + Luebbe, Germany) in the National Institute of Fisheries Science, South Korea.

### Chl-*a* analysis

To measure the total Chl-*a* concentration of ice algae and phytoplankton, 50–200 mL of melted ice and water samples were filtered onto 25 mm GF/F filters. To determine size-fractionated Chl-*a* concentration, samples were passed sequentially through 20 and 2 µm Nucleopore filters (47 mm) and Whatman GF/F filters. Filters were stored in a freezer (below -80°C) until analysis using a Turner Designs model 10-AU fluorometer calibrated with commercially purified Chl-*a* standard after a 24 h extraction in 90% acetone at 4°C (Parsons and others, 1984).

### Analysis of macromolecular components in ice algae and phytoplankton

Subsamples of 100–150 mL melted ice and 1 L surface water samples were filtered onto 47 mm GF/F filters for the determination of macromolecular components of bottom-ice algae and phytoplankton samples. Filtered samples were stored at -60°C for later analysis at the Pusan National University in South Korea following methods from Bhavya and others (2019).

### Carbon and nitrogen uptake measurements of ice algae and phytoplankton using stable isotope tracers (<sup>13</sup>C and <sup>15</sup>N)

Immediately after extraction, the bottom 0.1 m sections of two additional ice cores were cut into several pieces and placed in 1 L polycarbonate incubation bottles for in situ incubation using stable isotope tracers following the method of Lee and others (2008). Each bottle containing one bottom core was topped up with 400 mL of cold filtered (GF/F) sea water for buffering and labelled carbon (NaH<sup>13</sup>CO<sub>3</sub>) with either nitrate (K<sup>15</sup>NO<sub>3</sub>) or ammonium (<sup>15</sup>NH<sub>4</sub>Cl) substrates was added. The uptake rates of ice algae were corrected for the volume of added filtered sea water. After isotope inoculations, the bottles were put back to the original position through the auger hole and then the incubation hole was covered with ice chunks and snow. In situ field incubations were performed for 3–4 h during the daytime. After the field incubation, incubation bottles were transported and the ice samples were thawed in the dark at room temperature within a couple of hours without adding any inhibitor. No significant uptake under the dark condition before filtering samples was observed based on the previous results from incubation experiments conducted at Barrow, Alaska (Lee and others, 2008). Immediately after the samples were completely melted, 100 mL of incubated samples were filtered onto 25 mm GF/F filters. The filters were immediately frozen and stored in the freezer at -20°C until the preparation for mass spectrometric analysis at the Alaska Stable Isotope Facility (ASIF).

For phytoplankton incubation, water samples from underneath the sea ice were collected from the auger hole. After the inoculation of each stable isotope (NaH<sup>13</sup>CO<sub>3</sub> and K<sup>15</sup>NO<sub>3</sub> or <sup>15</sup>NH<sub>4</sub>Cl), polycarbonate incubation bottles were tied to an anchor rope and lowered 1 m below the ice bottom for 3–4 h incubation. After in situ incubation, the bottles were transported to the laboratory in a dark insulated box and 150 mL of incubated water samples were filtered onto 25 mm GF/F filters. The filters were immediately frozen and stored in the freezer at -20°C for mass spectrometric analysis at the ASIF. The carbon and nitrogen uptake rates of bottom-ice algae and phytoplankton were calculated according to Hama and others (1983) and Dugdale and Goering (1967).

## Results

### Environmental factors

Snow depth and sea-ice thickness at sample sites averaged (±SD) 0.04 ± 0.01 and 1.49 ± 0.17 m, respectively, over the study period (Table 1). Generally, a thinner sea-ice thickness was observed at st.1 (1.34 ± 0.02 m) relative to that at the other stations. The average salinity of melted ice samples and surface waters were 7.4 ± 2.6 and 26.7 ± 2.5, respectively, with low variation over the study period. Light intensity below the sea ice ranged from 15.5 to 48.4 µmol m<sup>-2</sup> s<sup>-1</sup> with an average of 29.3 ± 8.1 µmol m<sup>-2</sup> s<sup>-1</sup>. The average concentrations of ammonium, nitrate + nitrite, phosphate and silicate were 1.13 ± 0.33, 1.79 ± 0.42, 1.14 ± 0.36, and 2.18 ± 0.72 µM at the bottom section of sea-ice samples, respectively (Fig. 2). Surface sea water ammonium, nitrate + nitrite, phosphate

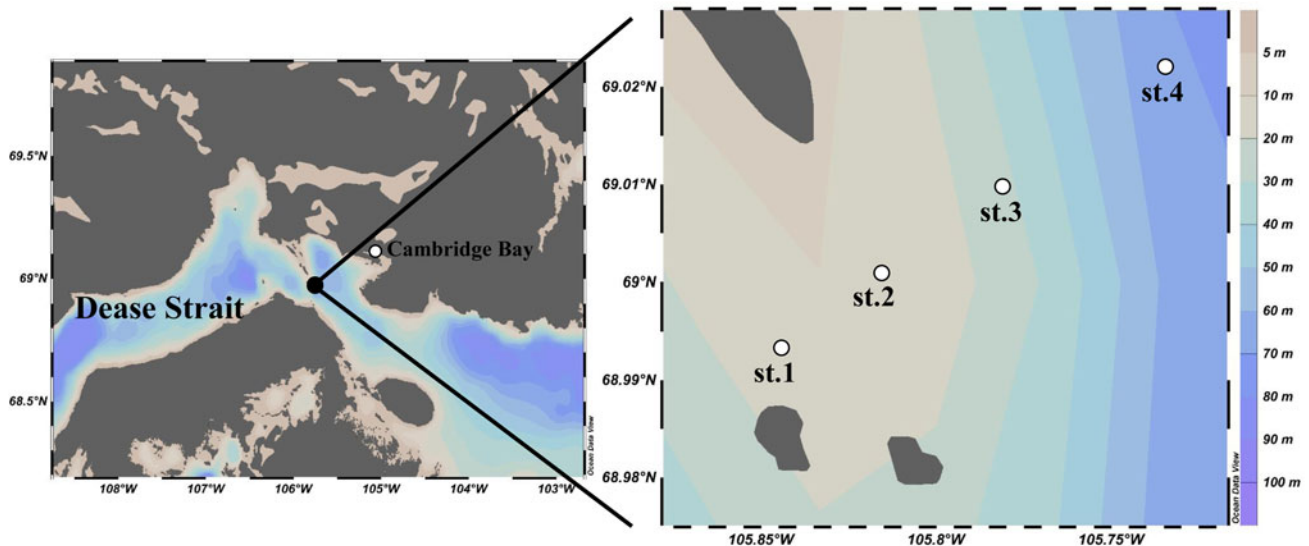


Fig. 1. Location of study area in Dease Strait, 2017.

Table 1. Environmental conditions of each sampling station over the study period in Dease Strait in 2017

Station	Date	Sea ice thickness (m)	Snow depth (m)	Bulk salinity in bottom ice (0.1 m)	Salinity in surface sea water	Light intensity under the ice ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
st.1	26 Apr.	–	–	–	–	–
	28 Apr.	1.32	0.04	7.3	–	15.46
	01 May	1.35	0.04	7.2	27	19.37
	03 May	1.3	0.06	6.8	27.5	19.74
	06 May	1.33	0.06	6.3	28.7	22.1
	09 May	1.36	0.04	6.8	28.1	31.77
	12 May	1.36	0.04	6.7	–	35.59
st.2	26 Apr.	–	–	–	–	–
	28 Apr.	1.37	0.05	7.3	–	31.01
	01 May	1.36	0.04	7.8	25.6	21.57
	03 May	1.43	0.04	6.5	28	32.81
	06 May	1.36	0.04	7.1	28.2	28.85
	09 May	1.37	0.04	6.9	28.3	38.8
	12 May	–	–	–	–	–
st.3	26 Apr.	–	–	–	–	–
	28 Apr.	1.55	0.04	7.7	–	20.57
	01 May	–	–	–	–	–
	03 May	1.55	0.05	6.7	28.1	30.44
	06 May	–	–	–	–	–
	09 May	1.57	0.05	6	20.8	23.72
	12 May	–	–	–	–	–
st.4	26 Apr.	1.9	0.04	18	–	28.43
	28 Apr.	1.64	0.03	8	25.6	31.15
	01 May	1.67	0.02	4.8	21.2	48.42
	03 May	1.68	0.03	6.4	27.1	35.77
	06 May	1.64	0.03	6.8	28.5	31.72
	09 May	1.71	0.03	6.9	28.2	38.82
	12 May	–	–	–	–	–

and silicate concentrations averaged  $0.96 \pm 0.83$ ,  $2.96 \pm 0.50$ ,  $0.74 \pm 0.11$  and  $7.31 \pm 1.38 \mu\text{M}$ , respectively (Fig. 3). Overall, higher phosphate concentrations were observed in the bottom 0.1 m section, whereas higher nitrate + nitrite and silicate concentrations were found in the water samples. However, no statistically significant difference of nutrients among the sampling stations was found in the bottom 0.1 m section of sea ice and surface sea water during this study period.

#### Chl-*a* concentrations of bottom-ice algae and phytoplankton

Total Chl-*a* concentration of bottom-ice algae in the lowermost 0.1 m ranged from 8.95 to  $65.33 \mu\text{g L}^{-1}$  with a mean of  $31.78 \pm 16.28 \mu\text{g L}^{-1}$  in this study (Fig. 4). Relatively higher Chl-*a*

concentrations were observed at st.1 over the study, except on 28 April. In comparison, total Chl-*a* concentration of phytoplankton ranged from 0.29 at st.1 to  $6.72 \mu\text{g L}^{-1}$  at st.3 with a mean of  $1.27 \pm 1.55 \mu\text{g L}^{-1}$ , which was substantially lower than those of bottom-ice algae (Fig. 4). The different size-fractionated Chl-*a* composition of bottom-ice algae was not distinctly different among the four stations during this study. Overall, microalgal cells ( $>20 \mu\text{m}$ ) accounted for  $72 \pm 8\%$  of the bottom-ice algal community, followed by nanoalgal cells ( $2\text{--}20 \mu\text{m}$ ,  $26 \pm 8\%$ ) and picoalgal cells ( $0.7\text{--}2 \mu\text{m}$ ,  $2 \pm 1\%$ ) based on the size-fractionated Chl-*a* concentrations (Fig. 5). For the surface phytoplankton community, microalgal cells accounted for  $51 \pm 13\%$ , followed by nanoalgal ( $43 \pm 11\%$ ) and picoalgal cells ( $6 \pm 6\%$ ) (Fig. 5).

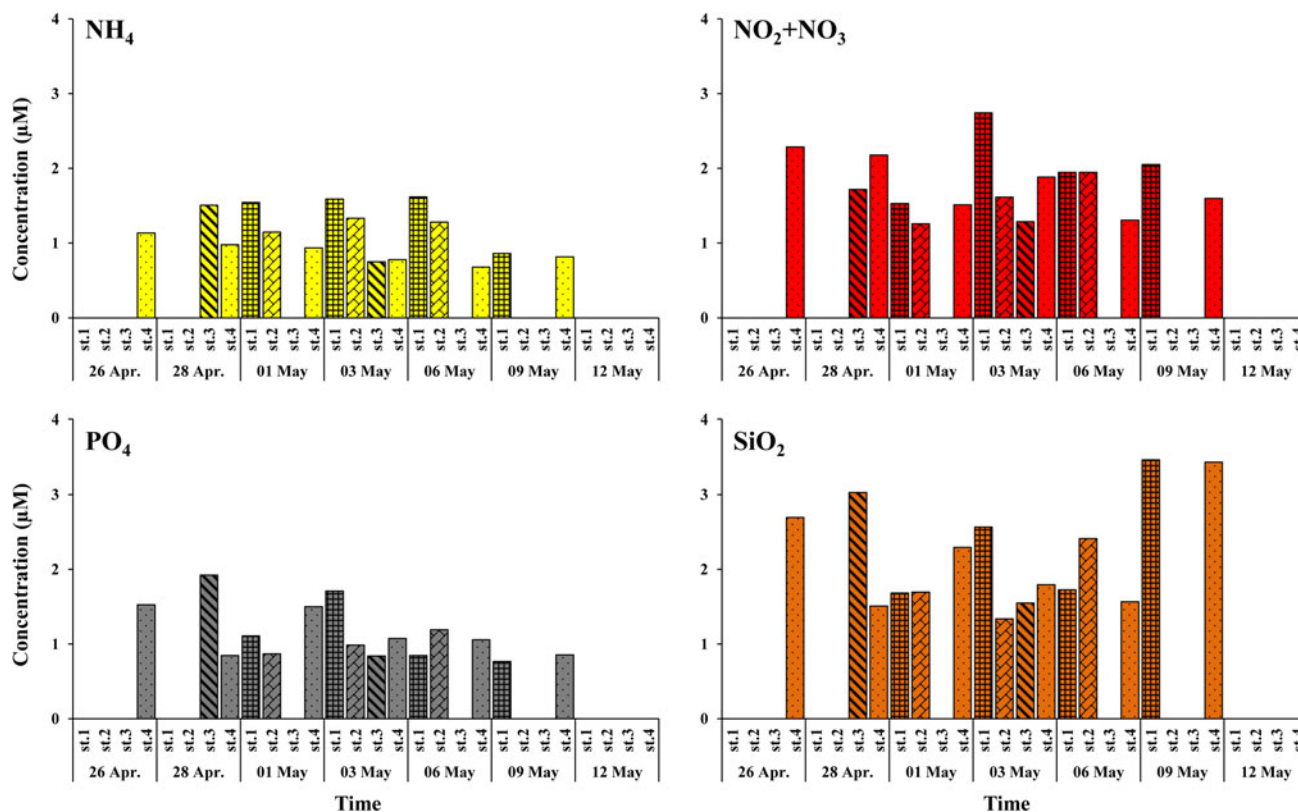


Fig. 2. The bulk nutrient concentrations at the bottom 0.1 m section of the sea ice at each sampling day in Dease Strait, 2017.

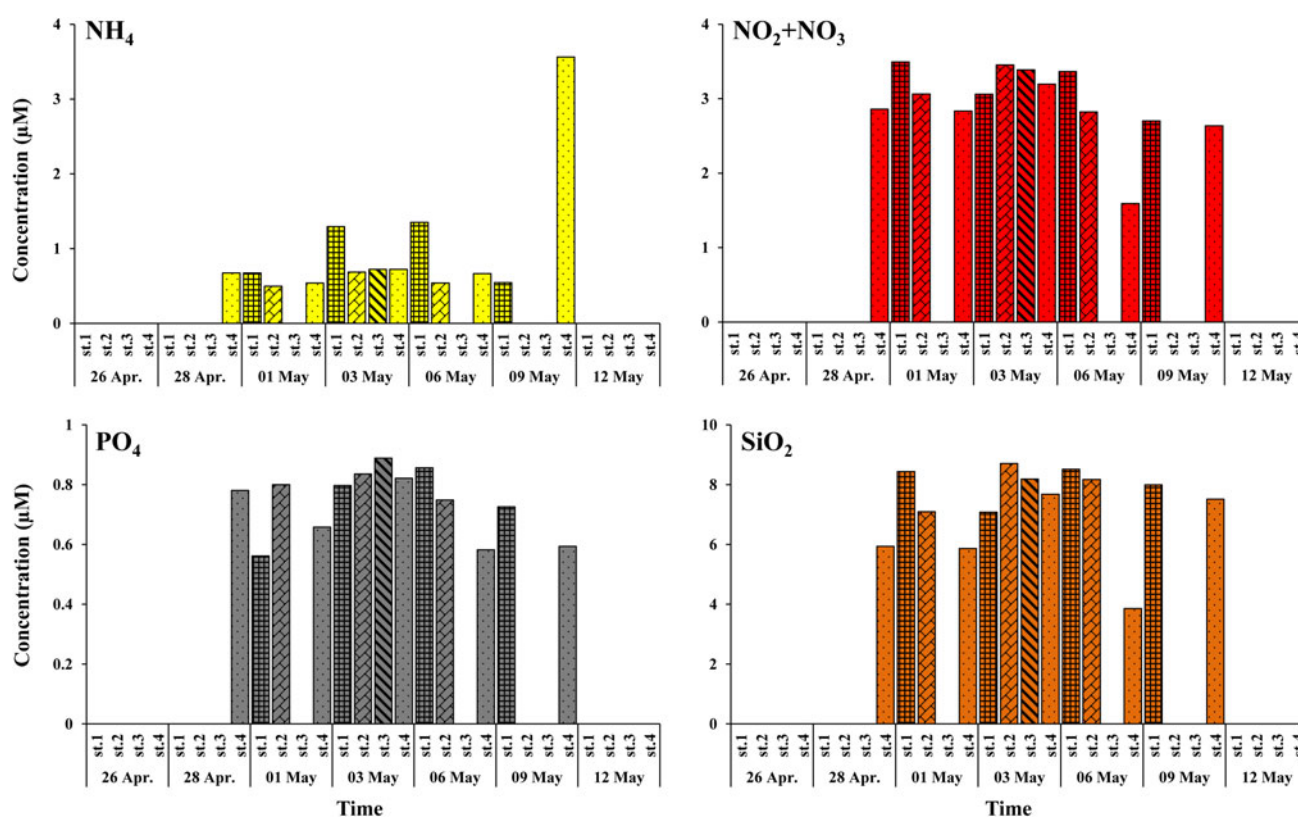


Fig. 3. The nutrient concentrations in surface water at each sampling day in Dease Strait, 2017.

### Carbon and nitrogen uptake rates of bottom-ice algae and phytoplankton

The hourly carbon uptake rate of bottom-ice algae ranged from 0.21 to 2.17 mg C m<sup>-3</sup> h<sup>-1</sup> with an average of 0.97 ± 0.60 mg C

m<sup>-3</sup> h<sup>-1</sup> from our productivity stations during the study period from 28 April to 12 May 2017 (Fig. 6). The maximum rate of bottom-ice algae at st.4 on 6 May (i.e., the 2.17 mg C m<sup>-3</sup> h<sup>-1</sup>) appears to be an outlier. Without this outlier, there is a clear

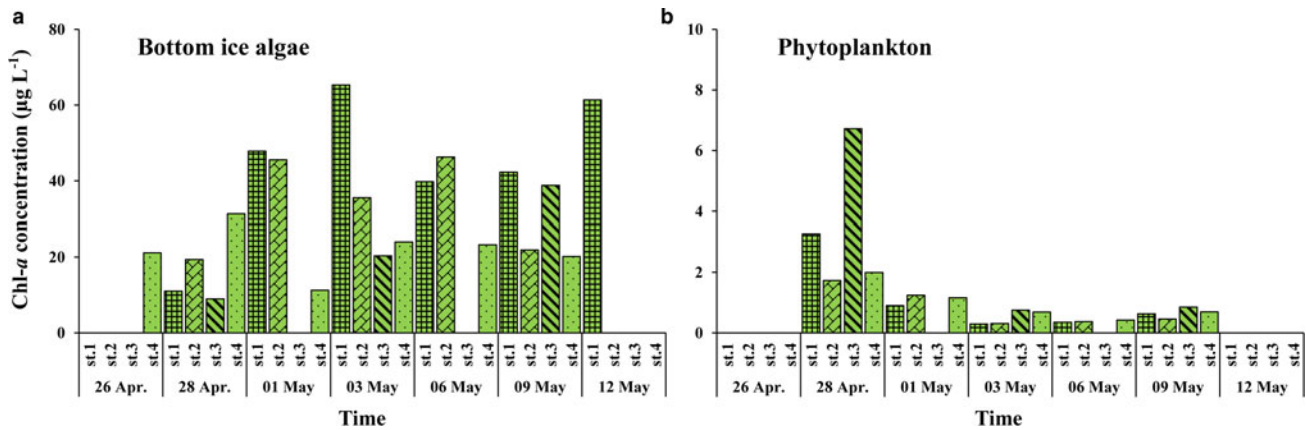


Fig. 4. The Chl-*a* concentrations for bottom-ice algae (a) and phytoplankton (b) at each sampling day in Dease Strait, 2017.

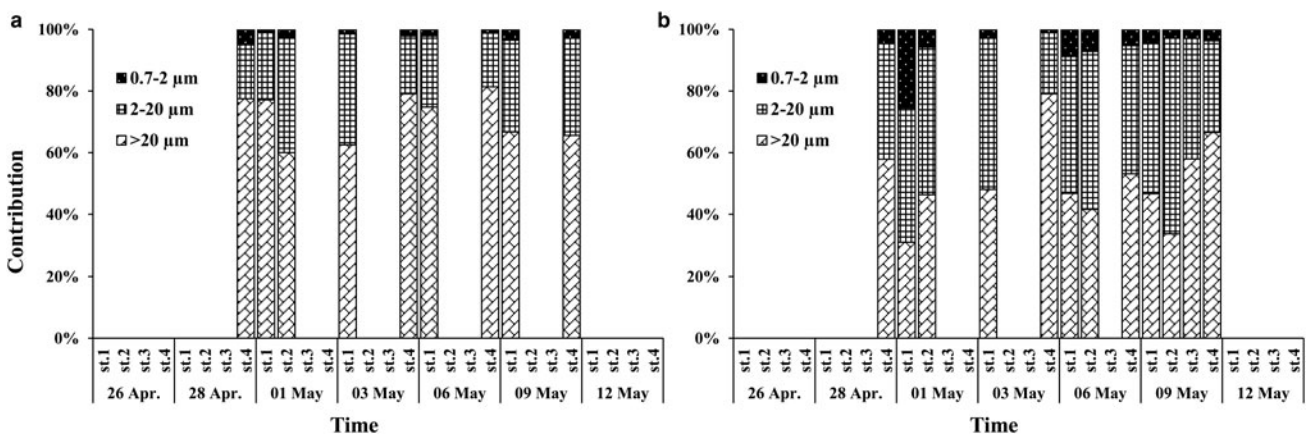


Fig. 5. The contributions of size-fractionated Chl-*a* concentration to the total Chl-*a* concentration of bottom-ice algae (a) and phytoplankton (b) at each sampling day in Dease Strait, 2017.

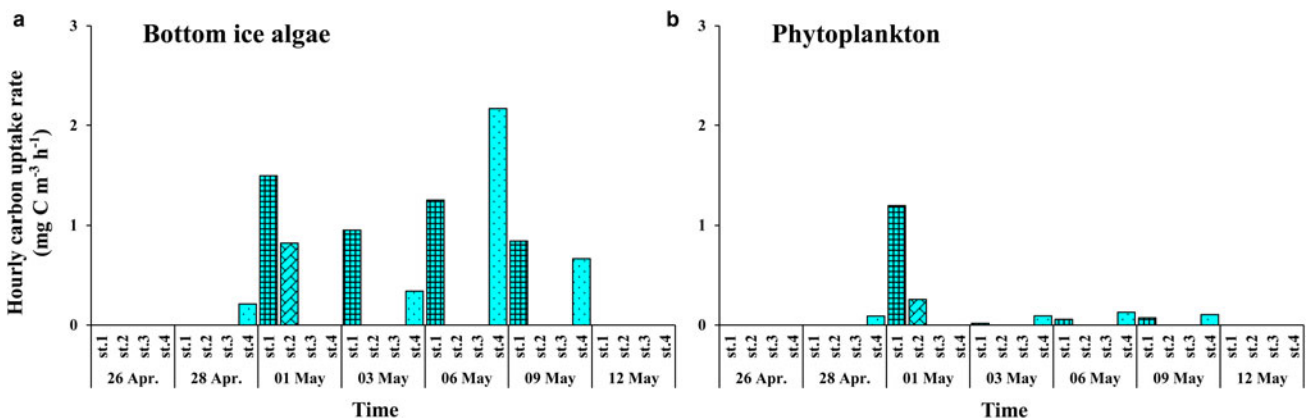


Fig. 6. The hourly carbon uptake rates for bottom-ice algae (a) and phytoplankton (b) at each sampling day in Dease Strait, 2017.

trend in the carbon uptake rate of bottom-ice algae from within the tidal strait to outside the tidal strait. In comparison, the rate of phytoplankton production ranged from 0.02 to 1.19 mg C m<sup>-3</sup> h<sup>-1</sup> with an average of 0.22 ± 0.37 mg C m<sup>-3</sup> h<sup>-1</sup> (Fig. 6b). Carbon uptake rates of bottom-ice algae were significantly (*t* test, *p* < 0.05, *df* = 16) higher than those of phytoplankton during the study. However, the assimilation rates for bottom-ice algae were relatively lower than those of phytoplankton. The assimilation rates for bottom-ice algae ranged from 0.01 to 0.09 mg C mg<sup>-1</sup> Chl-*a*<sup>-1</sup> h<sup>-1</sup> (0.03 ± 0.03 mg C mg<sup>-1</sup> Chl-*a*<sup>-1</sup> h<sup>-1</sup>).

In comparison, the assimilation rates of phytoplankton ranged from 0.01 to 0.30 mg C mg<sup>-1</sup> Chl-*a*<sup>-1</sup> h<sup>-1</sup> (0.14 ± 0.09 mg C mg<sup>-1</sup> Chl-*a*<sup>-1</sup> h<sup>-1</sup>).

Nitrate and ammonium uptake rates of bottom-ice algae ranged from 0.38 to 4.31 mg N m<sup>-3</sup> h<sup>-1</sup> with an average of 2.22 ± 1.38 mg N m<sup>-3</sup> h<sup>-1</sup> and 1.09 to 3.41 mg N m<sup>-3</sup> h<sup>-1</sup> with an average of 2.80 ± 0.92 mg N m<sup>-3</sup> h<sup>-1</sup>, respectively (Fig. 7). Generally, nitrate uptake rates of bottom-ice algae were different among stations, whereas the ammonium uptake rates did not greatly differ. The nitrate and ammonium uptake rate of phytoplankton ranged

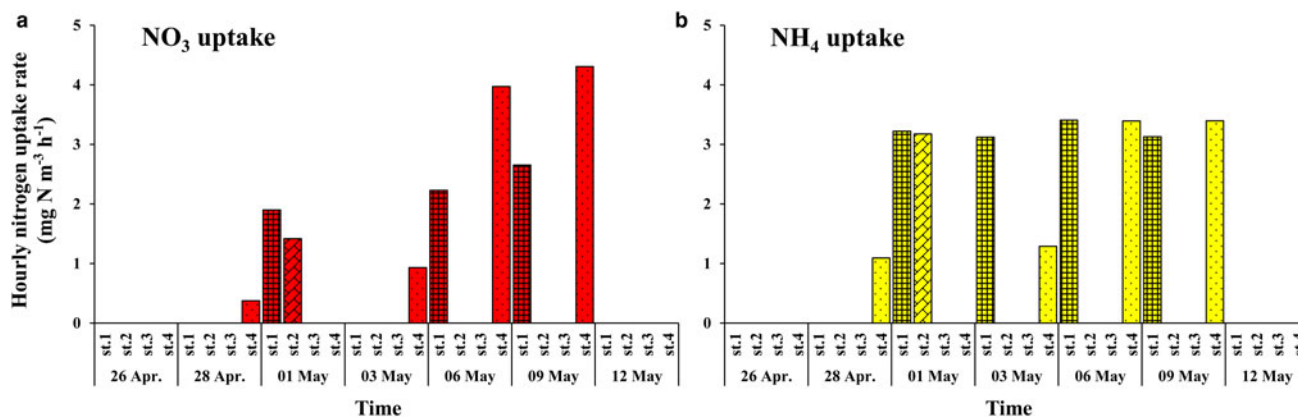


Fig. 7. The nitrate (a) and ammonium (b) uptake rates for bottom-ice algae at each sampling day in Dease Strait, 2017.

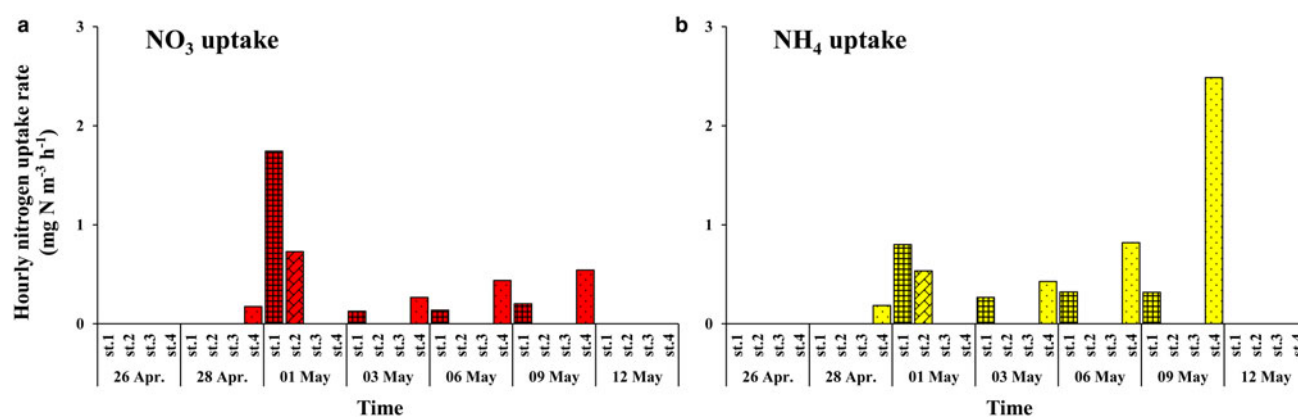


Fig. 8. The nitrate (a) and ammonium (b) uptake rates for phytoplankton at each sampling day in Dease Strait, 2017.

from 0.13 to 1.74 mg N m<sup>-3</sup> h<sup>-1</sup> with an average of  $0.48 \pm 0.51$  mg N m<sup>-3</sup> h<sup>-1</sup> and 0.19 to 2.49 mg N m<sup>-3</sup> h<sup>-1</sup> with an average of  $0.68 \pm 0.71$  mg N m<sup>-3</sup> h<sup>-1</sup>, respectively (Fig. 8). Based on the nitrate and ammonium uptake rates measured in this study, relative nitrogen preference index (RPI; McCarthy and others, 1977) and *f*-ratios (nitrate uptake/sum of nitrate and ammonium uptake; Dugdale and Goering, 1967) were calculated for the bottom-ice algae and phytoplankton. The RPI<sub>NH<sub>4</sub></sub> averaged  $1.7 \pm 0.5$  and  $2.6 \pm 0.7$ , and the mean *f*-ratios were  $0.41 \pm 0.11$  and  $0.41 \pm 0.15$  for bottom-ice algae and phytoplankton, respectively.

#### Macromolecular compositions of bottom-ice algae and phytoplankton

Averaged concentrations of total carbohydrates, proteins and lipids of particulate organic matter (POM) from the bottom-ice algal cores were  $1.90 \pm 0.66$ ,  $1.72 \pm 0.70$  and  $4.14 \pm 1.40$  mg L<sup>-1</sup>, respectively (Fig. 9). Similar to the Chl-*a* concentration and carbon uptake rate, the average concentration of proteins and lipids were observed to be greater at st.1 than those at other stations, with the exception of carbohydrates. However, the relative contribution of each macromolecule to bottom-ice algae composition was similar among the different stations. In comparison, the concentrations of each macromolecule of POM from the under-ice water column (phytoplankton) were  $0.34 \pm 0.18$ ,  $0.08 \pm 0.04$  and  $0.16 \pm 0.08$  mg L<sup>-1</sup> for total carbohydrates, proteins and lipids, respectively (Fig. 10). Overall, the concentrations of each macromolecule measured in bottom-ice algae were significantly (*t* test, *p* < 0.05, *df* values for carbohydrates, proteins and lipids were 24, 19 and 19, respectively) higher than those of phytoplankton. The dominant component

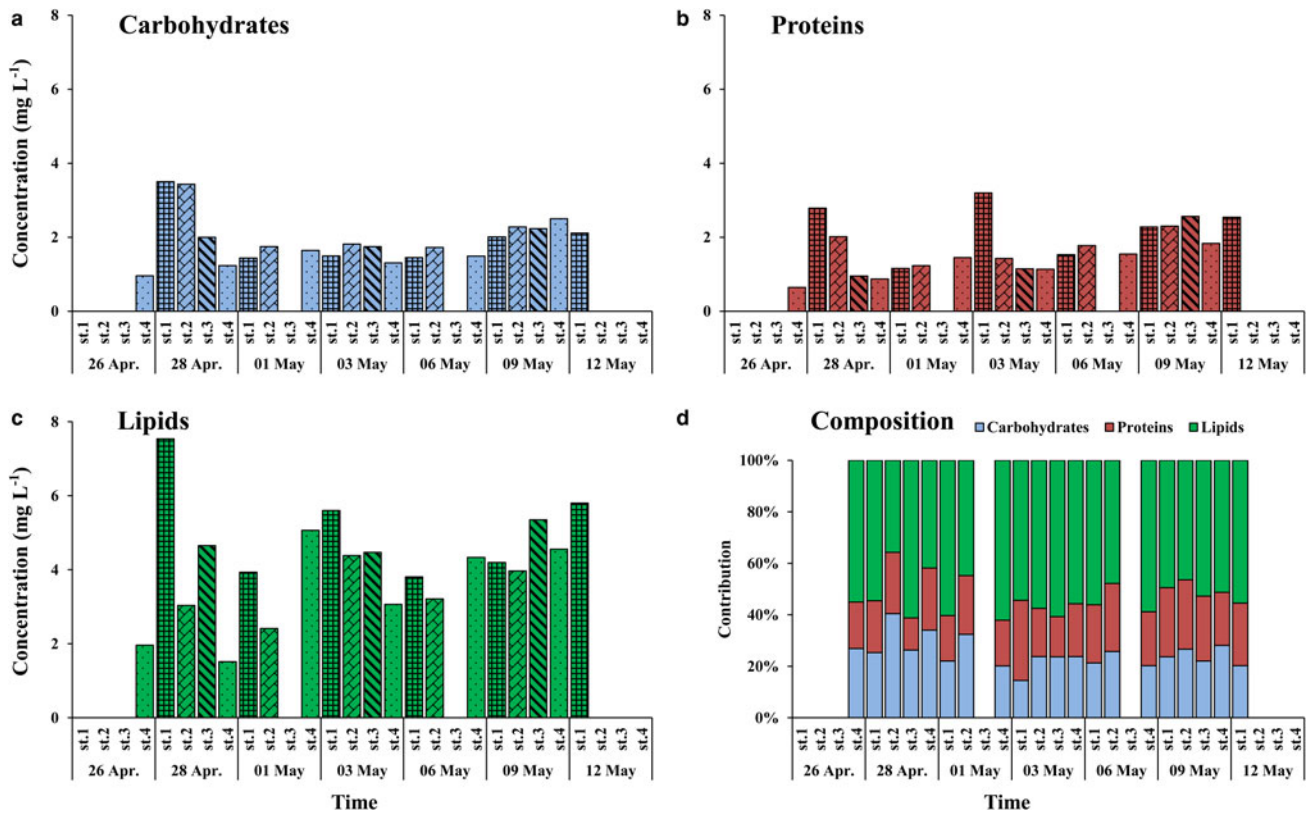
among the biochemical composition of bottom-ice algae was lipids, contributing  $53 \pm 7\%$  to the ice algal POM, followed by carbohydrates ( $25 \pm 6\%$ ) and proteins ( $22 \pm 4\%$ ) (Fig. 9), whereas carbohydrates accounted for  $59 \pm 6\%$  in phytoplankton POM, followed by lipids ( $27 \pm 5\%$ ) and proteins ( $14 \pm 5\%$ ) (Fig. 10).

#### Discussion

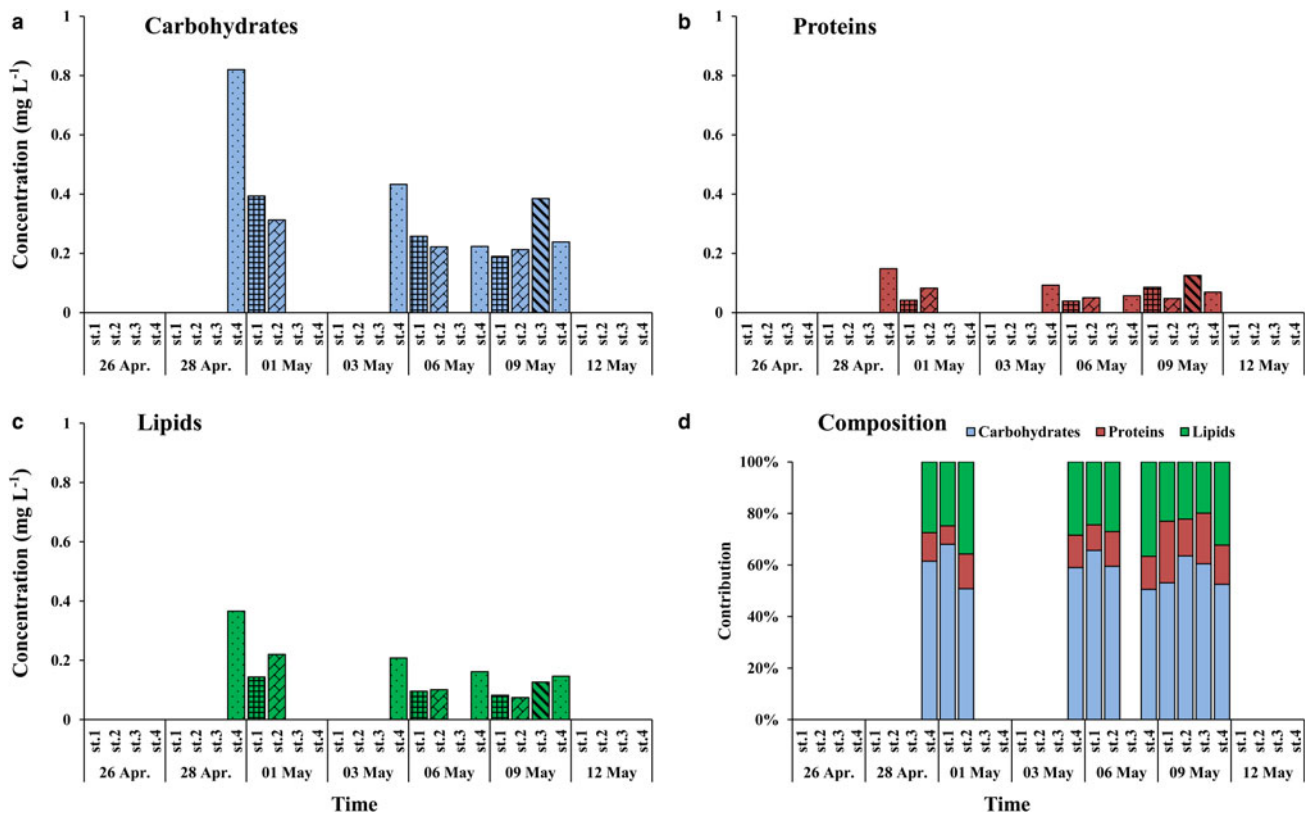
##### Chl-*a* concentrations of bottom-ice algae and phytoplankton

Microalgal cells (>20 μm) were the dominant size class ( $72 \pm 8\%$ ) contributing to ice algal Chl-*a* concentration. These results are similar to that (78% microalgal Chl-*a* contribution) observed at Barrow, Alaska during the spring season in 2003 (Lee and others, 2008), and the general case for the Arctic Ocean where the microalgal diatom *Nitzschia frigida* tends to dominate ice algal communities in numbers and biomass (Poulin and others, 2011; Van Leeuwe and others, 2018). In contrast, the relative microalgal cell abundance range of 6–38% observed in Campbell and others (2018) for the same region suggests the potential for significant interannual or spatial changes in algal community composition. Indeed, additional studies in the same region have reported a contribution of large pennate cells to the bottom-ice algal cell composition to be 45 to >80% (Dalman and others, 2019; Pogorzelec (2019)).

A large variation in bottom-ice areal Chl-*a* concentrations was observed across our sample sites, especially for st.1 and st.4 that were statistically different (*t* test, *p* < 0.05, *df* = 10). Mean Chl-*a* concentrations were  $4.46 \pm 1.94$  and  $2.19 \pm 0.65$  mg m<sup>-2</sup> at st.1 and st.4, respectively. Although st.1 and st.4 are separated by only 5 km, water depths (st.1 ≈ 33 m, st.4 ≈ 80 m) differ greatly



**Fig. 9.** The carbohydrates (a), proteins (b) and lipids (c) concentrations and the average composition of each biochemical component of ice algae (d) during this study period in Dease Strait, 2017.



**Fig. 10.** The carbohydrates (a), proteins (b) and lipids (c) concentrations and the average composition of each biochemical component of phytoplankton (d) during this study period in Dease Strait, 2017.

**Table 2.** Comparison of Chl-*a* concentration and carbon uptake rate of bottom-ice algae in the landfast sea ice among the different Arctic regions

Year	Season	Region	Bottom section (m)	Incubation method and time	Chl- <i>a</i> concentration (mg m <sup>-2</sup> )	Carbon uptake rate (mg C m <sup>-2</sup> d <sup>-1</sup> )	References
1985–1986	Mar.–Jun.	Canadian Arctic Archipelago (Resolute)	0.04	<sup>14</sup> C, 1–24 h	1.5–46 <sup>a</sup>	21–463	Smith and others (1988)
1987–1988	May–Jun.	Canadian Arctic Archipelago (Resolute)	0.05–0.06	<sup>14</sup> C, 1 h	< 350 <sup>a</sup>	20–157	Smith and Herman (1991)
1998	Apr.–May	Canadian Arctic Archipelago (Baffin Bay)	0.02–0.04	<sup>14</sup> C, 2–4 h	0.1–55.6	26–317	Nozais and others (2001)
1998	Apr.–Jun.	Canadian Arctic Archipelago (Baffin Bay, north water 6)	0.02–0.04	<sup>14</sup> C, 2–4 h	0.2–25.4	2–153	Michel and others (2002)
2003	Feb.–Jun.	Barrow, Alaska	0.03	<sup>13</sup> C, 3–4 h	<27 <sup>a</sup>	0.72–84	Lee and others (2008)
2014	Apr.–Jun.	Canadian Arctic Archipelago (Dease Strait)	0.05	–	4.0–11.7	–	Campbell and others (2016)
2016	May	Canadian Arctic Archipelago (Dease Strait)	0.05	–	1.41–9.31	–	Dalman and others (2019)
2017	Apr.–May	Canadian Arctic Archipelago (Dease Strait)	0.10	<sup>13</sup> C, 3–4 h	0.90–6.53 <sup>a</sup>	0.38–4.22	This study

<sup>a</sup>No-buffered melting procedure for Chl-*a* concentration and carbon uptake rate.

because of a sill located at st.1. The shallow sill between the islands constricts the tidal flow of water across the waterway, resulting in greater current speeds in excess of 0.2 m s<sup>-1</sup> (Dalman and others, 2019). This tidal current likely increases the exchange of nutrients to the ice bottom and potential for the bottom-ice algal biomass accumulation at st.1. Moreover, tidal effects can also increase the transfer of heat and momentum between the ocean and sea-ice bottom (Widell and others, 2006), resulting in the observed thinner ice cover at st.1.

A comparison of bottom-ice Chl-*a* concentrations from various landfast sea-ice sites in the Arctic region shows that the average bottom-ice Chl-*a* concentration observed in our study falls within the lower end of the range previously reported for the Kitikmeot Sea (Campbell and others, 2016; Dalman and others, 2019; Table 2). We note that the lower Chl-*a* concentration of bottom-ice algae in our study could be influenced by the non-buffered melting process for bottom Chl-*a* concentration. However, maximum bottom-ice areal Chl-*a* concentrations in this study were relatively lower than those previously reported for other areas of the North American Arctic (Table 2). Although light availability controls ice algal bloom onset and early bloom development in spring, nutrient access is the primary factor determining the maximum potential for ice algal biomass accumulation (Cota and others, 1987; Smith and others, 1990; Mock and Gradinger, 1999). This is particularly true for the thin snow depths examined in our study. The ranges of N:P and N:Si ratio in the ice bottom were 1.63–4.22 (2.71 ± 0.75) and 0.70–2.20 (1.44 ± 0.45), respectively, during our study period. These ratios are lower than the Redfield stoichiometric ratio (mol:mol) of 106C:16N:15Si:1P, which represents the mean cellular composition of marine diatoms (Brzezinski, 1985). Rózańska and others (2009) suggested the low N:P (1.5–2.0) and N:Si (0.3) ratios in surface waters could represent potential limiting conditions for bottom-ice algae. Moreover, Campbell and others (2016) reported the nutrient ratios of N:P and N:Si of the bottom ice at 0.20 ± 0.19 and 0.20 ± 0.15, respectively, in Dease Strait. In the studies of Rózańska and others (2009) and Campbell and others (2016), only nitrate + nitrite concentrations were considered for their N:P and N:Si ratios. The lower ratios including NH<sub>4</sub> concentrations in our study are consistent with nitrogen deficiency conditions for ice algal growth as suggested in both Campbell and others (2016) and Dalman and others (2019). The unique aspect of our study is the inclusion of ammonium concentrations to examine the role of recycled production in the system.

#### Nitrogen and carbon uptake rates of bottom-ice algae and phytoplankton

The ammonium RPI (RPI<sub>NH<sub>4</sub></sub>) of bottom-ice algae (1.7 ± 0.5) and phytoplankton (2.6 ± 0.7) in this study indicate that ammonium

was potentially preferred compared to nitrate throughout the study period (McCarthy and others, 1977). Harrison and others (1990) also found higher RPI<sub>NH<sub>4</sub></sub> (>1) of ice algae at Barrow Strait and in the Canadian Arctic. However, the RPI should be used carefully because it could be weakly related to the physiological preferences of marine algae (Dortch, 1990; Stolte and Riegman, 1996; Underwood and Kromkamp, 1999). Stolte and Riegman (1996) pointed out that the RPI could be used reasonably for comparing the utilization of a nitrogen compound under similar concentrations of ammonium and nitrate. Since the average concentrations of ammonium and nitrate in bottom ice and surface water were not considerably different during our observation period, the relative ammonium preference for bottom-ice algae and phytoplankton is assumed reasonable for our study (Stolte and Riegman, 1996; Andersson and others, 2006).

The *f*-ratio is often used to present on the fraction of new (nitrate-based) production by an algal community and can be a function of the ice algal bloom stage (Harrison and others, 1990; Lee and others, 2008). In Barrow Strait of the Canadian Arctic, Harrison and others (1990) observed a large range in *f*-ratio varying from 0.89 at an early bloom stage to 0.08 at a late to post-bloom stage of bottom-ice algae. In general, microalgae prefer ammonium because it is a readily available form of nitrogen source (Dugdale and Goering, 1967; McCarthy, 1980; Alexander and Chapman, 1981) and algae require energy to convert nitrate into ammonium in their cell bodies (Dortch and Postel, 1989). The low *f*-ratios in our study demonstrate that a considerable amount of primary production of bottom-ice algae in the Dease Strait region is based on a regenerated production rather than on new production. The stagnant circulation of the region driven by high riverine input (McLaughlin and others, 2006) and the associated limited input of new nutrients from nearby modified Pacific waters (e.g., Carmack and others, 2004) are the likely cause of the local nitrogen-deplete conditions. These depleted conditions also influenced carbon-based production.

The assimilation rates for bottom-ice algae and phytoplankton are considerably lower in this study than in earlier studies reported in Alaskan Arctic, Barents and Greenland seas (Table 3). In particular, higher assimilation rates for phytoplankton than that of ice algae were observed in this study, which is contrary to the pattern reported by Gosselin and others (1997). However, similar observations have been made for phytoplankton and bottom-ice algae near Barrow, Alaska (Lee and others, 2008). Although the Chl-*a* concentration of bottom-ice algae was substantially higher than that of phytoplankton, the significantly higher assimilation rates observed in phytoplankton imply that the photosynthetic efficiency of bottom-ice algae was less than that of phytoplankton. This lower assimilation efficiency of



**Table 3.** Comparison of assimilation rates of ice algae and phytoplankton among the different Arctic regions

Year	Season	Region	Ice type	Ice algae	Phytoplankton	References
1988	May–Jun.	Canadian Arctic Archipelago (Resolute passage)	First, multiyear sea ice	0.08–0.41	N.D.	Smith and Herman (1991)
1994	Jul.–Aug.	Chukchi sea–Eastern side of the Arctic	First, multiyear sea ice	0.17–0.95	0.04–0.42	Gosselin and others (1997)
1997	May–Jun.	Barents and Greenland Seas	First, multiyear sea ice	0.04–0.31	N.D.	Mock and Gradinger (1999)
2003	Feb.–Jun.	Barrow, Alaska	landfast sea ice	0.01–0.22	<0.01–0.28	Lee and others (2008)
2014	Apr.–Jun.	Canadian Arctic Archipelago (Dease Strait)	landfast sea ice	0.01–9.62	N.D.	Campbell and others (2016)
2017	Apr.–May	Canadian Arctic Archipelago (Dease Strait)	landfast sea ice	0.01–0.09	0.01–0.30	This study

Unit: mg C mg<sup>-1</sup> Chl-*a*<sup>-1</sup> h<sup>-1</sup>. N.D. represents no data.

bottom-ice algae also could indicate a greater nutrient limitation on their production compared to phytoplankton since a greater nutrient demand would be associated with the higher ice algal biomass (Cota and others, 1987). Indeed carbon uptake rates of bottom-ice algae were noticeably lower in our study than that of previous studies conducted from the Canadian Arctic Archipelago (Table 2). The ranges of carbon uptake rate in the high Canadian Arctic (Resolute Passage) by Smith and others (1988) and Smith and Herman (1991) were 21–463 and 20–157 mg C m<sup>-2</sup> d<sup>-1</sup> during the spring times in 1985–1986 and 1987–1988, respectively. Nozais and others (2001) and Michel and others (2002) also reported higher carbon uptake rates ranging from 26 to 317 mg C m<sup>-2</sup> d<sup>-1</sup> and 2 to 153 mg C m<sup>-2</sup> d<sup>-1</sup> at the Baffin Bay located in Canadian Arctic, respectively.

The high RPI<sub>NH4</sub> value, and low *f*-ratios, assimilation rates and carbon-based production estimates all strongly support the limitation of nitrogen in the Kitikmeot Sea, particularly for the ice algal bloom during spring. The observed lipid-dominant macromolecular composition of the bottom-ice algae further supports this conclusion. Aaronson and others (1980) reported that the total lipid content of rapidly growing ice algae varies from 1 to 45% of the cell dry weight. The quantitative lipids of ice algae are influenced by environmental factors, mainly irradiance (Iwamoto and others, 1955; Orcutt and Patterson, 1975; Fisher and Schwarzenbach, 1978) and nutrients (Werner, 1977; Shifrin and Chisholm, 1981). Temperature could be one of the major factors for the more lipid accumulation in ice algae (Smith and Morris, 1980; Guschina and Harwood, 2006) compared to phytoplankton. However, the difference in temperature between bottom ice and underneath surface water could be insignificant (Lee and others, 2008) and thus temperature was ruled out for further discussion in this study. Generally, high lipid concentrations of ice algae can be explained by nutrient limitation (Lizotte and Sullivan, 1992; Pogorzelec and others, 2017), increasing irradiance (Smith and others, 1989) or stationary growth phase (Morris, 1981). Smith and others (1997) found an increasing carbon allocation into lipids in arctic ice algae as their growth was slowed by nutrient depletion. There were no major changes in sea-ice thickness and light availability under sea ice during our short sampling period in 2017. Indeed, no strong relationship was observed between macromolecular compositions and the two environmental factors. The protein:carbohydrate ratio in ice algae can be an indication for the nitrogen availability condition. Our values, which were <1 (0.92 ± 0.35) indicate nitrogen deplete conditions (Mayzaud and others, 1989; Lizotte and Sullivan, 1992; Danovaro and others, 2000), in line with our earlier conclusions. It is noted that the lipid-dominant bottom-ice algal community observed in our study is consistent with that of Pogorzelec and others (2017) who found the transition in carbon allocation of bottom-ice algae from protein into lipid content under increasing light and depleting nutrient conditions for the same study region.

In contrast to the bottom-ice algal community, under-ice phytoplankton were carbohydrate-dominant during our study. In the northern Chukchi Sea, Kim and others (2014) and Yun

and others (2015) reported higher lipid contents (>50%) than those of other macromolecular classes in phytoplankton, while in the Laptev and East Siberian seas, Ahn and others (2019) observed carbohydrate-dominant phytoplankton. In fact, previous studies report that phytoplankton can produce more carbohydrates or lipids depending on nutrient conditions (Shifrin and Chisholm, 1981; Harrison and others, 1990; Hu, 2004; Ahn and others, 2019). Phytoplankton produce carbohydrates as a prime reserve product under nutrient-deplete conditions, whereas photosynthetic products can be diverted from the carbohydrates into lipid synthesis as secondary reserve materials under prolonged nutrient depletion conditions (Fogg and Thake, 1987; Hu, 2004; Ahn and others, 2019). Therefore, these data further support that phytoplankton were under less nitrogen-limiting conditions compared to that of the bottom-ice algal community during our springtime study.

## Summary and Conclusions

In this study, we summarized the physical, chemical and biological characteristics of the bottom landfast sea ice near Cambridge Bay in Kitikmeot Sea during the late spring season from 26 April to 12 May 2017. Our results strongly support that the region is nitrogen-deplete with low algal biomass standing stocks and a low potential for new primary production. With an averaged *f*-ratio of 0.41, ammonium was demonstrated to be a major nitrogen source for the growth demand of both bottom-ice algae and phytoplankton communities. However, lower assimilation rates and a greater lipid-dominant biochemical composition suggest bottom-ice algae were under greater nutrient limitation in a likely post-bloom state relative to the more carbohydrate-dominant phytoplankton that had yet to undergo their spring bloom. To better understand and verify these findings, more seasonal field observations with a sufficient spatial resolution and longer duration in the Kitikmeot Sea are suggested since we found a significant spatial difference in Chl-*a* concentrations and our sampling period likely encompassed a post-bloom state of the bottom-ice algal spring bloom. The distinctively different biochemical compositions of bottom-ice algae and phytoplankton could be important with respect to its nutritional content for the foodweb. It is noted that lipids-dominant bottom-ice algae could be effective for a long-term energy reserve, whereas carbohydrates-rich phytoplankton could provide a short-term energy gain to potential grazers (Taipale and others, 2016; Ahn and others, 2019).

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