Enhanced bottom-ice algal biomass across a tidal strait in the Kitikmeot Sea of the Canadian Arctic

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Sea ice algae are an important contributor of primary production in the Arctic ecosystem. Within the bottom-ice environment, access to nutrients from the underlying ocean is a major factor controlling production, phenology, and taxonomic composition of ice algae. Previous studies have demonstrated that tides and currents play an important role in driving the flux of nutrients to bottom-ice algal communities when biological demand during the spring bloom is high. In this study we investigate how surface currents under landfast first-year ice influence nutrient supply based on stoichiometric composition, algal chlorophyll a biomass and species composition during spring 2016, in Dease Strait, Nunavut. Stronger water dynamics over a shoaled and constricted strait dominated by tidal currents (tidal strait) supported turbulent flow more than 85% of the deployment duration in comparison to outside the tidal strait in an embayment where turbulent flow was only evidenced a small percentage (<15%) of the time. The system appeared to be nitrate-depleted with surface water concentrations averaging 1.3 µmol L⁻¹. Increased currents were correlated significantly with a decrease in ice thickness and an increase in ice algal chlorophyll a. Furthermore, pennate diatoms dominated the ice algal community abundance with greater contribution within the strait where currents were greatest. These observations all support the existence of a greater nutrient flux to the ice bottom where currents increased towards the center of the tidal strait, resulting in an increase of bottom ice chlorophyll a biomass by 5–7 times relative to that outside of the strait.

Therefore, expanding beyond the long identified biological hotspots of open water polynyas, this paper presents the argument for newly identified hotspots in regions of strong sub-ice currents but persistent ice covers, so called “invisible polynyas”.

Keywords: Ice algae; Fast ice; Tidal strait; Nutrients; Under-ice current

Introduction

Ice algae represent an important component of the Arctic marine ecosystem, providing a springtime pulse of primary production when other sources are at a minimum (Leu et al., 2015). Climate-induced changes to the type and extent of sea ice cover, as well as the seasonal timing of melt and ice formation, are expected to greatly affect the contribution of sea ice algae to carbon cycling in the trophic system (Arrigo et al., 2014).

Spring blooms of ice algae commence as a function of light availability, controlled by seasonal insolation, ice thickness and depth of snow cover on the ice surface (Gosselin et al., 1985; Mundy et al., 2005; Campbell et al., 2015). During the bloom, algae accumulate in the bottommost 5–10 cm of sea ice where favourable conditions of light and nutrients drive a concentrated growth of algae and an increasing demand for nutrients to facilitate continued growth (Cota et al., 1987). Without significant replenishment, this increasing demand leads to nutrient limitation in the algal community that ultimately constrains the magnitude of the bloom (Gosselin et al., 1990; Smith et al., 1997; Leu et al., 2015), while also influencing species composition, abundance and metabolite composition of cells present (Pogorzalec et al., 2017; Campbell et al., 2018; van Leeuwe et al., 2018). In particular, during the growth phase of a bloom when nutrients are replete, larger groups such as pennate diatoms tend to dominate the bottom-ice algal community (Poulin et al., 2011; van Leeuwe et al., 2018), whereas during post-bloom nutrient-deplete conditions, smaller centric diatoms (Campbell et al., 2018) and flagellates (Mundy et al., 2011) can dominate the community. After the initial bloom, studies have demonstrated that further algal accumulation is controlled by re-supply of nutrients from
the water column (e.g., Gosselin et al., 1985; Cota et al., 1987, 1991; McMinn et al., 2000).

Mechanisms of nutrient supply to bottom-ice algal communities in the Arctic can include: i) freeze-segregation of salt ions, thereby increasing salt and thus nutrient concentrations; ii) brine-driven convection forcing exchange of high salinity brine in sea ice with underlying low salinity nutrient-rich seawater; iii) re-mineralization of organic matter; and iv) diffusion from the underlying water column (Mergue et al., 1967). The dominant source of nutrient supply to support algal growth demand is from the water column while other inputs are minimal (Cota et al., 1987). During ice growth, segregation and brine drainage processes have been shown to enhance nutrient fluxes by means of convection within the skeletal layer (Rearrugh, 1984; Cota et al., 1990; Vancoppenolle et al., 2010).

Furthermore, tidal forcing and turbulence can increase instabilities, creating shear at the ice-ocean interface enhancing heat and fluid transport across the boundary layer (McPhee, 1992; Feltham and Worster, 1999; Feltham et al., 2002). This exchange can be enhanced by under-ice surface roughness that intensifies sub-ice turbulent flow (Shirasawa and Ingram, 1991, 1997; McPhee, 1992), thereby increasing friction and molecular diffusion of nutrients across the viscous sublayer (Cota et al., 1987).

Previous studies have shown how the fortnightly tidal cycle can influence a periodic increase and decrease in bottom-ice nutrient concentrations and ice algal biomass (Gosselin et al., 1985; Cota et al., 1987). Stronger currents and mixing during spring tides were hypothesized to enhance the ocean-ice flux of water column nutrients, thereby maintaining and extending the spring bloom (Gosselin et al., 1985; Cota et al., 1987). These nutrient supply-related processes have been parameterized into an ice algal growth model resulting in greater mixing of the upper water column and compression of the ocean-ice viscous sublayer thickness with increasing tidal amplitude and turbulence (Lavioie et al., 2005).

Strait constrictions and bathymetric shoals increase localized currents and associated turbulence as waters transit through the Canadian Arctic archipelago (Melling, 2002). Michel et al. (2006) suggested that this mechanism may enhance nutrient supply and primary production near Resolute Bay, Nunavut. However, strong currents can also act to erode bottom-ice algae mechanically (Mundy et al., 2007) and, if enhanced oceanic heat flux is sufficiently strong, can form small polynyas (Barber and Massom, 2007; Williams et al., 2007; Hannah et al., 2009), thus removing the ice algal habitat. More recently, Melling et al. (2015) defined the existence of “invisible polynyas”, where ice cover is thinner as a result of tidal current-enhanced ocean-ice heat flux that slows local ice growth, but does not necessarily lead to the erosion of bottom-ice habitat. These areas are distinguishable upon late freeze-up or early in the spring melt season as they are first to break-up (Melling et al., 2015). Prior to ice melt, these invisible polynyas can be stable habitats for ice algae, where we hypothesize a greater ocean-ice nutrient flux can support hotspots of ice algal activity.

The goal of the current study was to test this hypothesis through a case study focused on a constricted waterway with currents dominated by tides (hereafter referred to as a tidal strait), within Dease Strait of the Kitikmeot Sea, between Coronation Gulf and Queen Maud Gulf. Sampling took place during the Ice Covered Ecosystem – CAMbridge bay Process Study (ICE–CAMPS) in May 2016 prior to spring melt. From this dataset, we show that enhanced sub-ice current velocities characteristic of invisible polynyas within tidal straits will increase ice algal biomass and influence taxonomic composition. We also address the potential mechanisms of enhanced nutrient flux to bottom-ice algal communities.

Materials and Methods

Field site

The study was carried out by sampling six sites every other day (n = 4) along a 22-km transect between 6 and 12 May 2016 which was geographically positioned to encompass stable and dynamic water bodies protected by an embayment or constricted by the Finlayson Islands in Dease Strait, Nunavut, respectively (Figure 1). Furthermore, the transect position was selected to include a baseline site (site 6) where ice algal production had been examined previously (Campbell et al., 2016), while also extending through the Finlayson Island chain to where the sea ice is first to break-up in spring (as seen by NASA Worldview imagery not shown). The spring ice algal bloom has been shown to occur between March through the end of June in the vicinity of our study (Campbell et al., 2016). Sampling in the ICE-CAMPS 2016 project targeted the bottom-ice algal community, as previous studies in the region found cells to be concentrated in the bottommost 2–5 cm (Campbell et al., 2016). Sea ice in the study region was characterized by undeformed landfast first-year ice (FYI) overlying water depths from 79 m (site 5) within the embayment, to 33 m (site 2) centered within the tidal strait between the Finlayson Islands (Figure 1). The region experiences mixed tides with a dominating lunar semi-diurnal component. Sampling occurred during the transition from neap to spring tide in the region.

Environmental conditions

Undisturbed locations at a given transect site were chosen by selecting for a low snow depth (<5 cm) for each sampling event, followed by measurements of sea ice thickness. Although we selected for a thin snow depth, snow cover in the region was generally thin overall with few drifts. Ice cores were taken during sampling events with a 9-cm Mark II Kovacs core barrel at each site to measure bulk ice salinity (Orion 3-star salinometer) in the bottommost 5-cm section. Seawater was collected from the ice-water interface, hereafter referred to as interface water, just below the sea ice cover using a submersible pump for analysis of salinity and nutrients. Profiles of conductivity, temperature and depth (CTD) of the water column were performed at each site on May 12 using an RBR concerto CTD (RBR Ltd., Canada) sensor lowered through an auger hole.
Surface downwelling and upwelling measurements of photosynthetically active radiation (PAR, 400–700 nm) were collected using a quantum sensor (Li-Cor LI-190SA) and data logger (LI-1000). Measurements were made approximately 1 m above the snow surface varying between 09:30 and 12:30 local time on sampling days. An average of five upwelling and downwelling values at each site was used to calculate albedo as the ratio of surface upwelling to downwelling.

**Current profiles**

To measure surface current velocities (cm s\(^{-1}\)) below the fast ice, two inverted Aquadopp acoustic Doppler current profilers (ADCP) were deployed down-looking through augured holes immediately beneath the ice-ocean interface. The ADCPs were deployed for approximately 48-h periods at each of the sites to obtain currents, recording current speed and direction at 0.3 m vertical intervals every 5 min over a 6-day period. For example, an ADCP was deployed at site 1 and 4 on the first day, and after 48 h they were moved to site 2 and 5, then finally to sites 3 and 6 after an additional 48 h. The ADCPs have the following specifications: 23 Hz sampling frequency, ±0.5 cm s\(^{-1}\) in accuracy, and ± 0.01 cm s\(^{-1}\) in velocity resolution.

Two horizontal current velocity components (North and East) were first averaged vertically over the upper 10 m of the water column for every recorded 5-min ensemble. These 10-m interval averaged velocity components were then averaged over the deployment period including a calculation of standard deviation. Current speed was calculated using:

\[
\text{Current Speed} = \sqrt{u^2 + v^2}
\]  

where \(u\) and \(v\) are East and North components, respectively. Full spring-neap tidal cycle coverage was not possible; however, interpretation of the data in relation to the fortnightly tidal cycle was executed with a tidal prediction model between 2 and 17 May 2016 for site 5 produced using WebTide Tidal Prediction Model (Collins et al., 2011). A new WebTide grid for the Kitikmeot Sea that now includes bathymetry for the Finlayson Islands was used and has significantly improved the tidal prediction, correlating well with moored data in the region (L. Rotermund, personal communication). Site 5 was chosen because it was least likely to be influenced by topographic features and would be more representative for the region.

The potential for dynamic instability of sheared flow can be estimated using the Richardson number, \(Ri\), which is calculated using:

\[
Ri = \frac{N^2}{S^2} = \frac{\sqrt{\frac{g}{\rho} \frac{\partial \rho}{\partial z}}}{\left(\frac{\partial U}{\partial z}\right)^2}
\]  

where \(g\) is gravitational force, \(\rho\) is potential density, \(U\) is the raw current velocity, and \(z\) is the depth. The onset of turbulence is determined by low \(Ri\) values of <0.25 that indicate instabilities as described by Crawford et al. (1999). CTD profiles from each site were used to calculate a vertical profile of \(Ri\) numbers for every velocity profile measured by ADCPs within the top 10 m of the water column. The probability of \(Ri\) numbers <0.25 over the deployment period for every 0.3 m bin at each site were then calculated.

Figure 1: Map of Finlayson Islands in Dease Strait, Nunavut. Locations of sampling sites along the tidal strait transect within Dease Strait of the Kitikmeot Sea, Nunavut, Canada. DOI: https://doi.org/10.1525/elementa.361.f1
**Nutrients**

An independent bottom 5-cm core was collected at each site for bulk nutrient analysis, which was melted in the dark without dilution. Subsamples were taken from undiluted melted cores and interface water and filtered through a pre-combusted GF/F filter in an HCl sterilized syringe and swinnex filter holder. The filtrate was collected in two 13-mL acid washed tubes. Following filtration, samples were frozen at –20°C for approximately 7 months before analysis. Water collected from the ice-ocean interface was processed on the same day as core collection. The concentration of nitrate (NO$_3^-$) and nitrite (NO$_2^-$), phosphate (PO$_4^{3-}$) and silicic acid (Si(OH)$_4$) for interface water and the bottom 5 cm was determined using a SEAL autoanalyzer 3 (Grasshoff et al., 1999). For each sample, nutrient concentration values were corrected for the corresponding salinity value using standard curves.

Estimates of maximum algal nitrogen demand (D$_N$) were determined following the equation in Cota et al. (1987):

$$D_N = mC_aR_q$$  

(3)

where $m$ is maximum specific growth rate, $C_a$ is the algal chlorophyll a (chl a) concentration, and $R_q$ is algal cellular nitrogen to chl a mass ratio (Cota et al., 1987). Assumptions for constant average ratios for major cellular constituents of the algae for a N:Chl a ratio of 5 (gg) and an estimate of specific growth rate of 0.53 d$^{-1}$ at –1.8°C following Cota et al. (1987). Mean values of nitrogen demand for sites were determined using corresponding average chl a concentrations and maximum and minimum nitrogen demand was determined using the highest and lowest chl a concentration observed.

**Particulates**

Another three, bottom 0–5 cm sections of ice cores were collected at each sampling site and pooled. Prior to melting the pooled cores at laboratory facilities for 24 h in the dark, filtered seawater (FSW) was added at a ratio of 3:1 (three parts filtered seawater, one part ice core volume) to minimize osmotic stress. The FSW used was always filtered through a 0.2-µm hydrophilic Durapore membrane filter within 24 h of sample collection. The melted sea ice and FSW mixture was used for all measurements. Volumes filtered ranged from 5 to 20 mL depending on coloration of filter. An additional 5–10 cm section was collected at site 2 due to a visible band of ice algal biomass higher up in the core (Figure S1), a feature not present at other sites.

Pseudo-duplicate subsamples for chl a concentration from the melted pooled cores were filtered onto 0.7-µm glass fiber filters (Whatman GF/F filters). Pigments were extracted from these filters following placement into darkened vials with 10 mL of 90% acetone for 18 to 24 h at 4°C. Following extraction, chl a fluorescence was measured (Turner Designs Trilogy Fluorometer) before and after acidification with 5% HCl (Parsons et al., 1984). Chl a concentration was calculated from these measurements based on the equations of Holm-Hansen et al. (1965) and corrected for FSW dilution. Subsamples for assessment of particulate organic carbon (POC) and nitrogen (PON) were taken by filtering the melted core FSW solution onto pre-combusted (450°C for 5 h) GF/F filters, which were subsequently frozen for later analysis using a continuous-flow isotope ratio mass spectrometer (Glaz et al., 2014). An FSW blank was subtracted from measurements of POC and PON, which contributed an average of 15.1 (5.0 to 31.2)% and 37.0 (17.6 to 85.7)% prior to correcting concentration calculations for FSW dilution, respectively.

**Light microscopy**

A 100-mL subsample of the pooled core sample from each site on 6 May was preserved by addition of acidic Lugol’s solution (Parsons et al., 1984) for enumeration and identification of ice algal species. Samples were assessed using Utermöhl settling and light microscopy at 400× magnification (Leica DMII LED) within one year of sample collection. The lower limit of cell sizes during counts for pennate diatoms was >5 µm and >2 µm for centric diatoms, flagellates, and dinoflagellates. Reported cell abundance was corrected for FSW core dilution, and the percent composition of algal taxonomic groups was calculated relative to the total number of classified cells. Methods of light microscopy and taxonomic analysis used in this study are detailed further in Campbell et al. (2018).

**Statistical analyses**

The statistical analyses were executed in R Studio. A Shapiro-Wilk test was used to test for normality of the data. For normally distributed data, an analysis of variance (ANOVA) was performed to test significance between variables. If significant, a Tukey’s Post Hoc analysis was executed to assess differences or similarities between sample sites and transects. For non-normally distributed data, Spearman’s rank correlation evaluated association between variables and Mann-Whitney U tests were used to assess variation between sample sites. All values are presented as mean ± standard deviation unless otherwise stated.

**Results**

**Environmental conditions**

During the sampling period, daily averaged air temperatures ranged from –9.84 to –4.75°C and surface albedo averaged 0.81 ± 0.04 across all sites. Targeted snow depths did not vary significantly between sampling sites, averaging 2.8 ± 0.5 cm during the study (Figure 2; $p = 0.08$). Ice thickness of all sites averaged 173.7 ± 9.5 cm and did not change significantly in thickness over the sampling period. Ice thickness was thinnest at site 3, averaging 162.3 ± 3.4 cm, and thickest at site 1 averaging 184.5 ± 1.5 cm (Figure 2). Overall ice thickness decreased toward the center of the tidal strait (i.e., from sites 6 and 5 towards 4) and ice thickness at sites 2, 3 and 4 were significantly different from sites 1, 5 and 6 (Tukey’s, $p < 0.001$) with the exception of the comparison of sites 2 and 5 ($p = 0.09$). Average salinity of the interface water and bottom 5 cm of the ice was 28.8 ± 0.4 and 8.46 ± 1.29, respectively.

Bathymetry was shallowest (33 m) at site 2 and increased to depths of 65 and 78.5 m away from the center of the tidal strait at sites 1 and 5, respectively (Figure 3a).
Significant positive association was observed between ice thickness and bathymetry (Spearman’s, $p < 0.001$, $r = 0.671$). Currents through the tidal strait were dominated by the East–West ($u$) velocity component, for which the standard deviation was 6.8 times greater than that of the North-South ($v$) component at site 2 (Figure 3b). In comparison, the $u$ velocity component was 3.7 times greater at site 1, whereas at sites 3–6, the $u$ velocity component was only 1.2 to 2.3 times that of the $v$ component. Standard deviations of the components were also greatest at site 2 ($u$ component of 18 cm s$^{-1}$), slightly less at sites 1, 3 and 4 ($u$ component ranging from 10–12 cm s$^{-1}$), and least at sites 5 and 6 ($u$ component ranging from 2–4 cm s$^{-1}$). Vertical profiles of current speed illustrate that the highest current magnitudes over the 48 h deployments were observed at site 2 occurring mid-way in the tidal cycle (Figure S2).

Richardson number ($Ri$) estimates <0.25 for the upper 10 m of the water column indicating turbulent regime occurred 87.1, 86.6 and 91.3% of the deployment time at sites 1, 2 and 3, respectively (Figure 3b). The same probabilities at sites 4, 5 and 6 indicate that the turbulent regime occurred during 12.7, 11.4, and 13% of deployment time, respectively. The structure of the water column was generally more mixed at sites 2 and 3 where higher salinities were observed near the surface relative to profiles from the other sites (Figure 3a). Tidal fluctuations evolved from the beginning to the end of the study period according to the Webtide model (Figure S2a). The predicted sea level amplitudes from the tidal model between 2 and 17 May 2016 were 7.2, 9.6, 11.7, and 3.6 cm for O1, K1, M2, and S2 tidal components, respectively, showing that the M2 lunar semi-diurnal component dominates.

**Nutrients**

Bulk concentrations in the ice bottom for $\text{NO}_3 + \text{NO}_2$, $\text{Si(OH)}_4$ and $\text{PO}_4$ averaged $0.87 \pm 0.57$, $6.92 \pm 4.23$ and $3.26 \pm 2.42 \mu$mol L$^{-1}$, respectively ($n = 4$). The concentration of $\text{NO}_3 + \text{NO}_2$ generally remained below 1 $\mu$mol L$^{-1}$ although it fluctuated significantly between sampling transects specifically between 8 to 10 May, and 10 to 12 May (Mann-Whitney, $p < 0.05$, median = 0.73). $\text{Si(OH)}_4$ was abundant within the ice bottom, reaching a maximum concentration of 18.5 $\mu$mol L$^{-1}$ at the center of the tidal strait. There were no significant differences in bottom-ice bulk nutrient concentrations between sites. A significant association existed between $\text{Si(OH)}_4$ versus chl $a$ in the ice bottom (Figure 4b; Spearman’s, $p < 0.01$, $\rho = 0.615$). However, no associations existed between $\text{NO}_3 + \text{NO}_2$ (Figure 4a; Spearman’s, $p = 0.650$, $\rho = -0.010$) or $\text{PO}_4$ (Figure 4c; Spearman’s, $p = 0.383$, $\rho = 0.190$) versus chl $a$. Molar nutrient ratios for $\text{NO}_3 + \text{NO}_2$ to $\text{PO}_4$ (N:P) and $\text{NO}_3 + \text{NO}_2$ to $\text{Si(OH)}_4$ (N:Si) of this study were $1.49 \pm 0.31$ and $0.240 \pm 0.04$ for interface water, and $0.591 \pm 0.66$ and $0.167 \pm 0.11$ for bulk ice, respectively.

Dilution curves of nutrient concentrations versus salinity of all samples showed that the bottom 5 cm of ice generally had higher nutrient concentrations than the interface water except for that of $\text{NO}_3 + \text{NO}_2$ concentration (Figure 5). The average concentrations of $\text{NO}_3 + \text{NO}_2$, $\text{Si(OH)}_4$, and $\text{PO}_4$ in the interface water were $1.35 \pm 0.31$ $\mu$mol L$^{-1}$, $5.62 \pm 0.38$ $\mu$mol L$^{-1}$, and $0.90 \pm 0.03$ $\mu$mol L$^{-1}$,
respectively. Based on observed chl \(a\) concentrations (Figure 6a) and assumptions presented in the methods, estimates of algal nitrogen demand ranged from 0.21 to 2.2 mmol m\(^{-2}\) d\(^{-1}\) at the chl \(a\) concentration extremes. The highest averaged nitrogen demand was 1.76 mmol m\(^{-2}\) d\(^{-1}\) at site 2 and the lowest, 0.27 mmol m\(^{-2}\) d\(^{-1}\), was observed at site 5.

**Biotic parameters**

The highest concentration of chl \(a\) in the ice bottom was observed in the center of the tidal strait (site 2), averaging 9.31 ± 2.40 mg m\(^{-2}\), in comparison to the other five (sites 1 and 3–6) that ranged from 1.41 ± 0.47 to 4.32 ± 0.39 mg m\(^{-2}\) (Figure 6a). Chl \(a\) concentrations were significantly greater at site 2 in comparison to all other sampling sites following Mann-Whitney analysis \((p < 0.05, \text{median} = 3.29)\). Furthermore, concentrations of chl \(a\) were significantly different between sites 1 and 5, 3 and 5, and 3 and 6 (Mann-Whitney, \(p < 0.05, \text{median} = 3.38 \text{ [site 1], 4.37 [site 3], 1.22 [site 5], 1.65 [site 6]}\)).

The majority of the ice algae were in the very bottom centimeters of the skeletal layer which was present at all sites throughout the duration of the study. Interestingly, ice algae at site 2 were not only concentrated in the bottom ice layer, but were also visibly concentrated higher up with a chl \(a\) concentration of 4.54 mg m\(^{-2}\) in the 5–10 cm section. No other 5–10 cm section concentrations were sampled for comparison; however, all other sites did not exhibit any visible signs of algae further into the ice (Figure S1).
Figure 4: Relationship between nutrients and chlorophyll \( a \). Nitrate plus nitrite (a), silicic acid (b), and phosphate (c) versus chlorophyll \( a \) (chl \( a \)) concentrations in melted bulk-ice samples for all six sampling sites. The correlation coefficient is depicted by \( \rho \) for Spearman’s rank correlation. DOI: https://doi.org/10.1525/elementa.361.f4
Particulate organic carbon in the ice bottom was greatest at the westernmost site 1, decreasing eastward towards site 6, with the exception of site 5, which had the lowest concentration of POC at $328 \pm 166 \text{ mg m}^{-2}$. Concentrations of POC were significantly different at site 5 in comparison to all other sites except site 6 (Tukey’s, $p < 0.05$). Ratios of POC:chl $a$ (mg:mg) were lowest at site 2, which averaged $154 \pm 80$ (Figure 6b). East and west of site 2, POC to chl $a$ ratios increased, ranging from $254 \pm 173$ to $430 \pm 322$. The average values of POC:PON (mol:mol) ratios ranged from $16.3 \pm 14.7$ to $33.7 \pm 34.7$ and there was no significant difference between sites (Figure 6c).

**Species composition**

The relative abundance of common protist groups documented in ice samples collected on 6 May is presented for all sample sites in Figure 7. Diatoms were the dominant group during the study across all sites, accounting for over 90% of cells enumerated. Pennate diatoms were especially abundant in the bottom-ice communities for all study sites, with the exception of site 1 where pennates represented only $44.5\%$ ($5.3 \times 10^9$ cells L$^{-1}$), while centric diatoms represented $52\%$ ($6.2 \times 10^9$ cells L$^{-1}$) of the population. Excluding site 1, pennate and centric diatoms accounted for $80.6 \pm 4.4\%$ and $15.0 \pm 6.1\%$ of...
Figure 6: Concentration and ratio of biotic parameters along the transect. Averaged (± standard deviation error bars) bottom-ice chlorophyll a (chl a) concentration (a), the ratio of particulate organic carbon (POC) to chl a (b) and the ratio of POC to particulate organic nitrogen (PON) (c). The secondary x-axis illustrates the sites in relation to distance. DOI: https://doi.org/10.1525/elementa.361.f6
the bottom-ice communities, respectively. We note that sites 2 and 3 had a slightly greater relative abundance of pennate diatoms at 83% (1.1 x 10^10 cells L^-1) and 87% (4.4 x 10^9 cells L^-1), in comparison with sites 4 and 5 at 78% (5.9 x 10^9 cells L^-1) and 80% (2.1 x 10^9 cells L^-1), respectively.

Among pennate diatoms, *Nitzschia frigida* accounted for 28.2 ± 5.4% of pennates across sites, while Attheya spp. (2–10 µm) was the most abundant centric diatom at 53.9% ± 20.2% followed by Attheya spp. (10–20 µm) at 34.3% ± 20.2%. The contribution of flagellates (>2 µm) to the ice bottom community was low throughout the study at 4.0 ± 2.0% (<6.7 x 10^8 cells L^-1). The number of dinoflagellates (>2 µm) in the ice bottom was also very low across sites accounting for 0.25 ± 0.15% (<3.3 x 10^7 cells L^-1) of the community abundances during the spring. Dinoflagellate and flagellate abundances did not differ between sites, and spatial trends were not observed.

**Discussion**

**Physical oceanography of the tidal strait**

The shallow sill between the chain of islands across Dease Strait constricts the flow of water across the tidal strait, resulting in current speeds in excess of 20 cm s^-1_. The present study occurred during the transition from neap to spring tide, with the strongest currents observed at site 2 in the middle of this transition (Figure S2), demonstrating that currents were indeed strongest in the middle of the tidal strait. Thinner ice in these higher-current regions (Figure 2a) suggests that there may have also been additional oceanic heat flux at the ice-water interface, which would reduce demand for latent heat to balance energy losses at the ice-atmosphere interface, and thus slow thermodynamic growth of ice (Williams et al., 2007; Melling et al., 2015).

Flow appeared to be most dynamic at the shallow sill of the tidal strait, specifically at site 2, where variability in sub-ice currents was greatest over a 48-h measurement period (Figures 3b, S2b) and higher salinities reached surface waters (Figure 3a). The estimates of Ri at sites 1 to 3 show that the necessary conditions for turbulent flow persisted more than 85% of the time measurements were collected (Figure 3b). In comparison, sites 4 to 6 were likely dominated by a laminar flow regime, with a very small percentage (<15%) of Ri estimates that would be indicative of i) more turbulent flow (Figure 3b), ii) lower variability in current velocities (Figure 3b), and iii) a more stratified and lower salinity upper water column (Figure 3a). Figure S2 shows that tidal forcing drove semi-diurnal patterns in current speeds at sites 1–4 (Cota et al., 1987; Shirasawa and Ingram, 1997), but it was not the factor determining the absolute magnitude of currents. The timing of measurements is thus unlikely to explain the high current velocities observed at site 2, as an increase in currents at all sites would have been expected with increasing tidal amplitude were tidal cycle the dominant factor driving variability in current velocities between sites. Instead, we conclude that the presence of a sill at site 2 caused the highest current magnitudes, which were recorded in the midst of the study period on 8 to 10 May.

**Nutrient depletion**

Light is the main factor influencing algal growth at the beginning of the spring bloom, as limited downwelling irradiance from low insolation is greatly attenuated by a stable or increasing snow and ice cover (Leu et al., 2015). However, nutrients can quickly become limiting as algal biomass rapidly accumulates in the ice bottom and depletes concentrations immediately available (Cota et al., 1987). Ice algal production in Dease Strait is known to be strongly nitrogen-limited, yet evidence for diurnal light and nutrient co-limitation has also been shown for the region (Campbell et al., 2016). That is, even though nearly
24-h daylight occurred in May (time of present study), low nighttime solar angles can still lead to production differences between thin and thick snow depths. Consistent sampling of thin snow cover across the transect in this study helped minimize the potential influence of a variable light environment, where sample site snow depths averaged 2.8 ± 1.1 cm and were not significantly different between sites. It follows that differences in chl a concentration, algal composition or speciation observed between sites were driven instead by variability in nutrients associated with changes in under-ice currents rather than the availability of light.

The Redfield stoichiometric ratio (mol:mol) of 106C:16N:15Si:1P represents the average cellular composition of marine diatoms (Brzezinski, 1985), although recent studies have shown a potentially larger range for sea ice algae (Niemi and Michel, 2015). Nevertheless, deviation from the ideal Redfield composition can be used to indicate depletion or enrichment of different nutrients in the environment, a function of either biological activity under nutrient limitation, or source water mass composition. The molar nutrient ratios of N:P and N:Si are below the values of 1.5–2.0 and 0.3 reported by Różanska et al. (2009) for the month of May near to this region, but are within the range of values documented by Campbell et al. (2016) at 0.20 ± 0.19 and 0.20 ± 0.15 in Dease Strait, respectively. The lower ratio values are interpreted as strong nitrogen depletion in the ice algal environment. Dilution curves for nutrient concentrations versus salinity can also help to illustrate the impact that biological activities have on nutrients (Cota et al., 1990). In this study the concentration of NO$_3$ + NO$_2$ in the bottom ice fell closer to the salinity dilution line derived from average surface water nutrient concentrations (Figure 5a), further supporting the potential for nitrogen depletion relative to that of PO$_4$ or Si(OH)$_4$ that were well above it. The elevated concentrations of PO$_4$ and Si(OH)$_4$ in the ice bottom relative to those in the interface water suggest that algae were potentially retaining excess quantities as intracellular pools that were leaked into the bulk ice measurement due to osmotic shock during melt (Cota et al., 1990; Harrison et al., 1990; Smith et al., 1990; Pineault et al., 2013; Campbell et al., 2016; Torstensson et al., 2019). Another explanation is that sea ice diatoms and bacteria produce copious amounts of exopolymeric substances that can increase viscosity and reduce diffusion, as well as adsorption of some ions, potentially trapping nutrients within a sea ice biofilm (Krembs et al., 2002, 2011; Steele et al., 2014; Roukaerts, 2018).

The POC:PON relationship did not show any significant difference between sites; however, the relatively high averaged values of >16 have been reported before for the region (Campbell et al., 2016) and are more typical of a post-bloom scenario (Niemi and Michel, 2015). The region is thus likely nitrogen-depleted throughout the year. The algal nitrogen demand between 0.21 to 2.2 mmol m$^{-2}$ d$^{-1}$ for this study was very low in comparison to other regions across the western Arctic, where values ranging from 3 to 21 mmol m$^{-2}$ d$^{-1}$ have been reported (Cota et al., 1991). Although nitrogen demand is highly dependent on bloom magnitude, lower nitrogen demand documented in this study further illustrates how nitrogen-depleted the Dease Strait region is in relation to other areas of the western Arctic. Dividing the areal sea ice NO$_3$ concentration by these calculated nitrogen demands, a total supply of 0.21 to 2.86 h was estimated to be available in the ice bottom habitat. The nitrogen molar ratio of bottom-ice PON to interface NO$_3$ was also calculated to provide a rough estimate of water volume flux required to the ice bottom habitat to support observed bottom-ice algal biomass (Gradinger, 2009). Our values ranged from averages of 9.1 at site 5 to 15.4 at site 2 and 19.5 at site 1, compared with the ratio range of 0.4 to 19 presented in Gradinger (2009). As in Gradinger (2009), assuming a 100% uptake rate of NO$_3$, the ratio was interpreted as a requirement of 9.1 to 19.5 m$^3$ of water circulating per m$^2$ of sea ice to support the observed accumulation of algal biomass. Although the above calculations make assumptions that are likely unrealistic, they provide evidence that a greater flux of NO$_3$ from the water column was required to support the algal biomass observations across the tidal strait.

Ammonium is also understood to be an important nitrogen source for algal production, particularly during the post-bloom period when its uptake can dominate nitrogen-based metabolism, equaling regeneration rates in the ice (Harrison et al., 1990). However, nitrate was found to dominate nitrogen-based metabolism during the biomass accumulation period (Harrison et al., 1990). Similarly, high f-ratio values (NO$_3$ uptake/(NO$_3$ + NH$_4$ + urea) uptake) ranging from 0.71 to 0.92 have been documented for ice algae where ammonium and urea were concluded to be negligible sources during a bloom (Olson, 1980; Kristiansen and Farbrot, 1991). Although ammonium was not measured in this study, we surmise that enhanced accumulation of algal biomass within the tidal strait relative to other sites was largely driven by nitrate rather than ammonium.

Nutrients at the ice-ocean interface remained low throughout this study (Figure 5) despite the potential for replenishment from depth associated with increased tidal energy and turbulence along the constricted strait (Gosselin et al., 1985; Cota et al., 1987). The friction generated by fluid movement across the sea ice interface with tides also disrupts the molecular sublayer of water beneath the ice (Feltham and Worster, 1999), through which nutrients diffuse into the ice bottom (Cota et al., 1987). As a result, the velocity of sub-ice water masses may be used to indirectly represent nutrient availability to ice algal communities, and thus the potential for biomass accumulation. Following this rationale, the potential for nutrient supply and biomass accumulation along the study transect was greatest towards the center of the tidal strait (sites 1 to 3) where elevated levels of turbulence and mixing was evidenced.

**Spatial distribution of biomass**

The spatial distribution of chl a across the transect increased towards the center of the tidal strait where currents and turbulent flow were greatest. As discussed previously, this enhanced sub-ice turbulent flow in the tidal strait likely
increased the exchange of nutrients to the ice bottom and the potential for biomass accumulation. The unique observation of chl a approximately 8 cm above the ocean-ice interface at site 2 can be explained by i) mobility of solitary ice algae (e.g., Welch and Bergmann, 1989; Krembs et al., 2000), which can be up to 14.4 cm d\(^{-1}\) within the ice (Aumack et al., 2014), and/or ii) forced convection within the ice that can promote nutrient supply higher up into the ice (Feltham and Worster, 1999; Feltham et al., 2002; Vancoppenolle et al., 2013). Snow-loading experiments by Aumack et al. (2014) have demonstrated the potential for upward migration of many ice algal taxa in response to decreases in light availability or, alternatively, concentration of cells at the ice-ocean interface with greater light transmittance. Given the consistency of snow depths between sites in this study and thus light availability, light-driven cell migration was not likely responsible for the unique banding of chl a at site 2. Instead, we suggest that the responsible mechanism was forced convection.

Low POC:chl a estimates can be an indicator for algal communities acclimated to low light intensities or less nutrient limitation, relative to high POC:chl a ratios that can indicate high-light acclimation or greater nutrient limitation (Gosselin et al., 1990). Campbell et al. (2016) showed that ice algae in Dease Strait had elevated POC:chl a ratios due to strong nitrogen limitation, where ratios increased from 70 in late April to >200 in early June. Ratios observed in this study were greater than those reported in Campbell et al. (2016) with the exception of site 2 that fell within the range. It is impossible to conclude if the difference between these two studies is due to higher light access (snow depths sampled were less than those sampled in Campbell et al., 2016) or greater nutrient stress (chl a concentration and thus nutrient demand was greater in the current study). However, there were trends of increasing POC:chl a and decreasing chl a concentration and turbulence potential away from the center of the tidal strait, yet snow depth (light access) did not significantly vary. These observations highlight the potential for greater nutrient stress towards the more stagnant sub-ice conditions observed at sites 4 to 6.

Species composition

Pennate diatoms overwhelmingly dominate bottom-ice algal communities during the spring bloom, shifting towards flagellates during post bloom stages (Mundy et al., 2011); however, Campbell et al. (2016) documented a shift in dominance from pennate to centric diatoms over the spring with a shift from more light to nitrogen limitation in the study region. Under greater nutrient stress and higher light conditions, smaller centric diatoms, with their greater cell surface area to volume ratio and thus lower nutrient requirement for growth, tend to become more dominant in the community, as documented by Różanska et al. (2009) and Campbell et al. (2016). Despite the apparent advantage of nutrient uptake potential for the smaller centric diatom, *Attheya* spp., a sustained dominance of larger pennate diatoms at the majority of sites was documented in this study. Additionally, snow depths were thinner than those sampled in Campbell et al. (2016), where centric diatoms were especially dominant, suggesting that irradiance may not be the primary factor driving ice algal speciation in Dease Strait. Due to the dominance of pennate diatoms at the majority of sites and the increase in relative abundance of pennate diatoms at high-turbulence sites 2 and 3, we concluded that species composition in the present study was largely a result of nutrient stress in relation to cell size (Pogorzelec et al., 2017). The unique dominance of centric diatoms at site 1 relative to all other sites on the transect and the apparent lack of differences between site 1 and others located outside of the tidal strait indicate that other factors not monitored in this study (e.g., time of ice formation and sea ice colonization; Niemi et al. (2011)) could have played a role in the community taxonomic composition.

Conclusions: Enhanced ocean-ice exchange

Indirect evidence based on under-ice turbulence, ice algal standing stocks and nutrient demand support the strong likelihood of a greater nutrient supply to ice algae within the tidal strait. Ice algae are attached to a substrate (the ice bottom) such that increased advection of surface water across the ice bottom increases exposure to a greater nutrient supply, similar to that occurring in a benthic setting (Davies and Bothwell, 2012). The increased water motion enhances exposure of the algae to a greater nutrient concentration than that available via molecular diffusion in a relatively still water column (e.g., the case for phytoplankton). Decreased POC:chl a ratios and a greater relative abundance of pennate diatoms also support the hypothesis of enhanced nutrient replenishment within the tidal strait environment. Accounting for the algae documented higher up in the ice at site 2, observed chl a concentrations were nearly seven times greater where current velocities were stronger and more variable at the center of the tidal strait than in surrounding bottom-ice communities.

Three additional mechanisms of nutrient supply beyond a greater advective supply have been proposed to explain the increased biomass (Cota et al., 1987; Vancoppenolle et al., 2013): i) water column mixing, ii) ocean-ice molecular diffusion, and iii) within-ice forced convection. For the first mechanism, increases in tidal energy or topographical features cause increases in turbulence and lead to vertical mixing of stratified water columns under seasonal ice cover (Cota et al., 1987). For the second mechanism, the increase in turbulence associated with increasing currents can affect the viscose sublayer thickness by reducing it and thus enhancing exchange of nutrients across the ocean-ice boundary layer (Cota et al., 1987; Shirasawa and Ingram, 1997). For the final mechanism, within-ice forced convection is associated with sub-ice turbulence and an enhanced ocean-ice heat flux (Widell et al., 2006) where low temperature brine is physically exchanged with warmer interface waters. This exchange allows more nutrients to penetrate across and further up the brine channels in the bottom ice (Feltham and Worster, 1999; Vancoppenolle et al., 2013), helping to explain the considerable amount of biomass found higher up in the ice matrix.
Open water polynyas have long been identified as biological hotspots (Stirling, 1997; Barber and Massom, 2007). However, the contribution of similar hotspots with strong current velocities but stable ice-covers, i.e., invisible polynyas (Melling et al., 2015), has not previously been considered. In this case study, observations were made that supported, for the first time, an increase in ice algal biomass associated with an enhanced sub-ice turbulence regime across a tidal strait. The algal response provided indirect evidence of a greater nutrient supply to the bottom ice habitat along the more dynamic water column of the tidal strait. Given that tidal straits are a ubiquitous feature throughout the coastal Arctic, we stress that similar biological hotspots need to be identified and assessed. Furthermore, the influence of sub-ice turbulence on nutrient supply to bottom-ice algal communities can be expanded to different environments such as nearshore tidal flow around headlands as well as pack-ice environments where movement of the ice pack relative to the underlying water column can also develop enhanced ocean-ice exchange (Fernández-Méndez et al., 2018). Identification of potential hotspot locations and their incorporation into regional assessments are likely to increase our estimates of ice algal contributions to marine productivity, similar to the recently observed ice algal concentrations under hummocked multi-year sea ice (Lange et al., 2017). Such an addition to our baseline knowledge of the system is critical to better understand how the ecosystem will respond to the rapidly changing Arctic icescape. Of particular importance towards this end are invisible polynyas, such as the one observed in this study. Williams et al. (2007) suggest that invisible polynyas are very sensitive to the warming climate and will become open water polynyas as air and water temperatures increase. With the loss of sea ice, there will be a loss of the ice algal habitat which will greatly influence current ice pelagic-benthic coupling in the system.

Data Accessibility Statement
The following datasets were generated and will be archived at the following:


Supplemental files
The supplemental files for this article can be found as follows:

- Figure S1. Images of ice algal bottom cores collected during field campaign. Photographs of bottom ice cores illustrating visible banding (VB) coloration by ice algae, observed further up in the ice at site 2 in comparison to other sites. The site numbers are indicated in the top left corner of each panel, and the bottom of the cores are oriented in the same way with top indicated by the star symbol. The visible coloration of the algae in the bottom ice core extended to approximately 8 cm up into the ice at site 2, versus being restricted to the bottommost 1 cm at other sites. Site 2 encompassed the greatest observed current velocities and ice algal chl a biomass during the study. (tiff) DOI: https://doi.org/10.1525/elementa.361.s1

- Figure S2. Tidal model and vertical profiles of current speed. Tidal model showing elevation of tides (a) from 2 May to 17 May 2016, spanning two full spring-neap tidal cycles, for the region. Profiles of vertical current speed (b) in the top 10 m of the water column over a 48-h deployment at each site. Lines connecting the tidal model (a) to the current speed panels (b) depict when measurements were made at the corresponding sites in relation to the tidal cycle. The current speed panels are stacked in their deployed pairings. The vertical dashed lines on the tidal model (a) illustrate the approximate time the separate pairs of ADCPs were set. (tiff) DOI: https://doi.org/10.1525/elementa.361.s1

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Competing interests
The authors have no competing interests to declare.

Author contributions
- Contributed to conception and design: LAD, EC, WJJW, CJM
- Contributed to acquisition of data: LAD, BE, PJD
- Contributed to analysis and interpretation of data: LAD, EC, KC, SK, CJM
- Drafted and/or revised the article: LAD, BE, DB, EC, WJJW, KC, PJD, CJM
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