Diatom vertical migration within land-fast Arctic sea ice

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C.F. Aumack [a,*], A.R. Juhl [a], C. Krembs [b]

[a] Lamont-Doherty Earth Observatory of Columbia University, 61 Route 9W, Palisades, NY 10964, USA
[b] Washington State Department of Ecology, Olympia, WA, 98504, USA

ARTICLE INFO

ABSTRACT

Light levels inside first-year, landfast sea ice were experimentally altered by manipulating overlying snow depths. Irradiance available for ice algae growing near the ice-bottom, and under the ice, was highly dependent on snow depths ranging from 0 to >30 cm. Importantly, algal vertical distributions also changed under different irradiances. Under thick snow (low light), the majority of algae were found several cm above the ice–seawater interface, while progressively more were found nearer the interface at locations with thinner overlying snow (higher light). Short-term field experiments suggested that ice algae were able to reposition themselves within the ice column within 3 days after manipulating snow depths. Laboratory gliding rate measurements of a cultured ice diatom suggested that it is capable of daily cm-scale movement. Vertical migration may help ice diatoms balance opposing light and nutrient resource gradients, similar to strategies used by some benthic and pelagic algae. Moreover, when ice algae congregate near the ice–seawater interface, they may be especially susceptible to loss from the ice environment. Vertical repositioning in response to changing light dynamics may be a mechanism to optimize between vertically-opposing environmental factors and help explain the connection between melting snow cover and export of biomass from sea ice.

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1. Introduction

Arctic sea ice is a porous habitat whose interstitial and undersurface environments support a diverse community ranging from viruses to algae to metazoan heterotrophs (Arrigo et al., 2010; Bluhm et al., 2010; Deming, 2010). Algae production within coastal sea ice, typically dominated in biomass by pennate diatoms (Arrigo et al., 2010; Hsiao, 1980; Smith, 1988), can contribute between 15 and 20% of total primary production in Arctic waters (Arrigo et al., 2010). Environmental conditions that affect sea ice primary productivity, such as light, temperature, salinity, porosity, nutrient fluxes, and loss to the underlying water, vary temporally and along strong horizontal and vertical gradients within the ice.

There is distinct seasonality within the Arctic sea ice community, especially in first-year sea ice that is the focus of this study. Through early spring, algal biomass generally increases through time, especially in the bottom 10 cm of the ice near the ice–water interface (Juhl et al., 2011; Riedel et al., 2008; Smith et al., 1990). Chlorophyll concentrations near the ice-bottom can occasionally exceed $1000 \mu g\,L^{-1}$ (Arrigo, 2003). The high biomass of the spring algal bloom within coastal sea ice contrasts with the pack ice of the central Arctic where algal biomass is typically two orders of magnitude lower (Gradinger, 1999). Later in the season, but before substantial ice thinning or break up, most algal biomass is lost from first-year ice in rapid export pulses that may only last a few days (Fortier et al., 2002; Juhl and Krembs, 2010; Juhl et al., 2011). In addition to living biomass, particulate and dissolved organic carbon (POC, DOC) are found abundantly throughout the entire ice column (Juhl et al., 2011; Thomas et al., 2010). Some of this organic matter is autochthonous, while some may have been incorporated within the ice matrix during freezing. As much as 70% of total POC in sea ice can be extracellular polymeric substances (Meiners et al., 2004; Riedel et al., 2006), mostly produced by ice diatoms (Krembs et al., 2001; Meiners et al., 2003; Riedel et al., 2008). EPS may aid ice diatoms in cryoprotection, anchoring to the ice matrix, and locomotion (Krembs et al., 2002, 2011). While accumulated organic matter is eventually released from seasonal sea ice, the algal biomass appears to be preferentially lost prior to other organic matter pools (Juhl et al., 2011).

Ice algae, as well as associated bacteria and heterotrophs within the ice community, are not uniformly distributed horizontally in first-year sea ice. During the Arctic spring, ice algal growth is primarily limited by low irradiances (Lavoie et al., 2005; Mundy et al., 2005) and algal biomass is often inversely related to the overlying snow depth (Gosselin et al., 1986; Mundy et al., 2005; Welch and Bergmann, 1989), because of the effect of snow cover on light attenuation. Snow depth can vary spatially by tens of centimeters over a few square meters and the annual mean can differ by up to ~20–30 cm during March/April in northern Alaska (Warren et al., 1999), with concomitant effects expected for ice algae biomass. Later in the Arctic spring the pattern often changes, resulting in lower ice algae biomass under thin snow cover than nearby sites with comparatively deeper snow (Mundy et al., 2005; Welch and Bergmann, 1989), even though chlorophyll-

specific production rates remain high under thin snow cover (Smith et al., 1989). This pattern of lower algal biomass under thin snow cover, despite high production rates, suggests that loss of ice algae to the underlying water column is greater under thinner snow cover (Cota et al., 1991; Mundy et al., 2005). In fact, loss of ice algae has been observed following rapid snow melt or experimental snow removals (Apollonio, 1965; Fortier et al., 2002; Juhl and Krembs, 2010).

Once released, algae and other organic materials from the ice are either consumed in the water column (Michel et al., 1996; Tremblay et al., 1989), initiate ice-edge algal blooms (Haecky et al., 1998; Michel et al., 1993), or settle on the benthos where they are either subsequently eaten or buried in the sediments (McMahon et al., 2006; Morata et al., 2011; Renaud et al., 2007). Although specific cues for the rapid export events are undetermined, they occur with such annual regularity that many Arctic marine organisms have adapted life-cycles to take advantage of the seasonal release of organic material from the overlying ice community (Gradinger and Bluhm, 2010; Runge et al., 1991; Søreide et al., 2010). Developing a mechanistic understanding of the accumulation, export, and eventual fate of sea ice organic matter therefore seems imperative to appreciating the full role of sea ice in the greater Arctic ecosystem as well as the ecological consequences of a rapidly changing Arctic environment.

Based on the effects of snow cover on light and heat transmission within the ice (Grenfell and Maykut, 1977), several mechanisms to explain the relationship between thin snow cover and increased algal loss have been proposed. These include local heating and melting of the ice due to light absorption by the algae (Apollonio, 1961; Zeebe et al., 1996), increased brine formation and flushing (Gradinger et al., 1991; Ingram et al., 1989; Mundy et al., 2005), and bottom ablation due to general warming of the ice at air or seawater interfaces (Michel et al., 1988). All these processes have some observational support and none are mutually exclusive. Regardless of the physical processes involved, the vertical position of the algae (or other particles) with respect to the ice–water interface must be relevant. A vertical profile through first-year Arctic sea ice will typically show the greatest algal biomass and POC concentration in the bottom centimeters (Cota et al., 1991; Gradinger et al., 1991; Michel et al., 1996; Mundy et al., 2005), near the ice–water interface where the underlying water column provides a nutrient source. It is reasonable to hypothesize that particles closest to the ice–water interface should be more likely to be lost to the water column than those deeper within the ice.

Strong vertical gradients in environmental conditions within the ice may influence vertical positioning of ice algae. By analogy, many benthic pennate diatoms undergo vertical migration through the upper portion of the sediment in response to light, tides, nutrient availabilities, temperature, and other factors (Consalvey et al., 2004; Happey-Wood and Jones, 1988; Saburova and Polikarpov, 2003; Underwood et al., 2005). This movement is typically a process by which diatoms glide along tracks of secreted EPS adhered to the substratum and connected to transmembrane structures subsequently moved along the raphe (Edgar and Pickett-Heaps, 1983; Edgar and Zavortink, 1983; Underwood and Paterson, 2003), although other modes of locomotion are possible (Apoya Horton et al., 2006). Different species exhibit varying migratory patterns (Underwood et al., 2005) but, in general, there is a tendency for upward migration when irradiance levels are relatively low, presumably to maximize photosynthesis, and a downward migration after exposure to excessive light (Barranguet et al., 1998; Cohn et al., 1999). Downward migration is likely a photophobic response to avoid photoinhibition (Barranguet et al., 1998; Cohn et al., 1999, 2004; McLachlan et al., 2009), but may additionally relocate cells to areas of greater inorganic and organic nutrient availability (Barranguet et al., 1998; Cohn et al., 1999; Happey-Wood and Jones, 1988). Thus, vertical migration facilitates the balance of opposing gradients of light and nutrients found in sediment layers. This same principle is also found in the water column, where the vertical distribution of phytoplankton can be determined by opposing gradients of light

and nutrients (Chorus and Schlag, 1993; Huisman et al., 2006) and optimal cell depth is where both are equally available relative to their needs (Klausmeier and Litchman, 2001).

In this study, we demonstrate that the vertical distribution of ice algae varies with the light field in a manner consistent with the optimization strategies described for many benthic diatoms and phytoplankton. If deep chlorophyll maxima and vertical distributions in sediment can be the products of active motility based on adaptive responses to minimize resource limitation, then ice algae may migrate within the porous sea ice matrix to overcome similar abiotic stresses. Vertical positioning of ice algae in response to light and nutrient gradients within the ice may play an important role in determining their susceptibility to export out of the ice habitat, providing a key flux in polar marine ecosystems.

2. Materials and methods

2.1. Study site

All field observations of ice properties, snow and ice algae in this study were conducted on landfast, first-year sea ice located within 10 km of Point Barrow, Alaska (71.38°, −156.48°) on the near-shore Beaufort and Chukchi Seas (<3 km from shore). Samples were collected April–early June 2005, and April–May 2006. Ice coring used a 10-cm diameter CRELL (in 2005), or an 8-cm diameter Kovacs ice corer (in 2006), driven by an electric hand drill. After field collection, initial sample processing was done in a laboratory of the Barrow Arctic Science Consortium (BASC).

2.2. Ice-bottom layer light and algal biomass under experimental plots

As an overview, field experiments were set up in 2005 and 2006 to quantify snow cover effects on light within and under the sea ice, and on ice algal biomass. In each year, 5 experimental plots of approximately 2×2 m were established along a linear transect. The general location for the plots was selected by finding an area on the near-shore sea ice where snow cover was fairly even and ice was of relatively uniform thickness, and without obvious sediment inclusions (confirmed by drilling exploratory ice cores) to ensure uniform starting conditions. photosynthetically active radiation (PAR) sensors (LICOR underwater quantum sensors) were emplaced within and under the ice near the center of each 2×2 m experimental plot. Snow depth of each plot was then manipulated to generate a snow depth gradient along the transect; from deep snow on the first plot (~30 cm, Plot 1), decreasing from one plot to the next, to thin or no snow cover on the last plot (Plot 5). This gradient in snow cover was maintained for weeks by periodically adjusting the snow cover with loose snow while PAR inside and under the ice was continuously recorded for each plot.

The two PAR sensors in each of the 5 experimental plots measured downwelling irradiance at two depths. The upper sensors at each plot were embedded in the ice 30 cm above the ice–water interface (i.e., above the ice algae biomass maximum) by drilling out partial ice cores (leaving 20–25 cm of ice at the bottom), positioning sensors at the specified depth and orientation using a PVC bracket that extended to the ice surface, and then repositioning the original ice cores above the sensor. During sensor placement, water entered the core holes, freezing the upper sensors in place and securing the ice that had been temporarily removed. The lower PAR sensor was positioned 30 cm below the ice–water interface. A PVC bracket held the sensor directly under a portion of the ice that was at least 10 cm horizontally offset from any of the ice core holes. Ice cores removed to install the lower sensors were replaced and rapidly froze back into place. Thus, there was one PAR sensor above and one below the algal layer within each plot to continuously measure light above and below the bottom ice community under 5 different levels of snow. Average PAR reaching each sensor was recorded every 30 min. The sensor location in each

plot was marked with a pole with centimeter graduations so that snow depth could be determined without having to disturb the snow cover.

In 2005, the experimental plots were maintained from April 20 until June 8. The site was visited 12 times during that interval to measure snow depth. In 2006, experimental plots were maintained from April 27 until May 24, and snow depth was recorded on six dates. In both years, snow had to be periodically adjusted in different plots to maintain experimental snow thickness. The relationship between PAR and snow depth for each year was developed by comparing snow depth at each station with daily integrated PAR measured over the 24 h period preceding each snow depth measurement.

To quantify the long-term effect of snow depth on algal biomass, ice cores were first taken from each plot several weeks after the gradient had been established. In 2005, cores were collected on May 11, 21 days into the observation period. During sampling, an unexpected, apparently isolated patch of sediment was found in some of the cores collected from one plot (Plot 2). We excluded this plot's cores from our analyses due to the unaccounted light attenuation caused by sediment. To supplement the observations, three additional sets of ice cores were collected between plots 1–2, 3–4, and 4–5 (i.e. avoiding the sediment patch) on May 14. During other ice coring (installing and removing sensors, as well as sampling), no further evidence for sediment inclusions was found. In 2006, all five plots were sampled on May 22, 26 days into the experiment.

In both years, ice coring and sample processing were identical. Four replicate cores were collected within each 2 × 2 m plot. A vertical temperature profile of the ice was measured on the first core from each station before collecting the other replicates. Ice temperature was measured by drilling 3 mm diameter holes in the side of the ice core every 10 cm and inserting a digital thermometer probe (±0.1 °C). After retrieval of each core, the bottom 10 cm was sectioned off and sealed into food-grade plastic bags for transport back to the laboratory in an insulated cooler to protect core sections from light and temperature changes. In the laboratory, the 10-cm ice core bottom sections of three cores were further cut into three sub-sections: 0–2, 2–6, and 6–10 cm from the bottom. The sub-sections from each of the three replicate cores per station were combined and gradually melted at 0–4 °C in the dark and processed to measure chlorophyll-*a* concentrations. The bottom 10 cm of the fourth core was melted intact in the same way and was used to measure bulk salinity (using an YSI 30 conductivity meter) and diatom frustules.

Chlorophyll-*a* concentrations (hereafter referred to as "chlorophyll") were determined using a volumetric subsample of meltwater from each ice segment filtered onto a 25 mm Whatman GF/F filter. Sufficient volume was filtered to cause visible discoloration of the filter. Filters were stored frozen (−20 °C) until extraction in 90% acetone (24 h), followed by fluorometric analysis (including acidification) using a Turner Designs fluorometer according to UNESCO (1994). For frustule counts, a meltwater subsample from the fourth core from each plot was preserved in 2.5% formalin. Frustule samples were stained with Rose Bengal before counting, and only frustules that contained stained organic matter (presumably cells that were alive at the time of collection) were quantified. Only total counts, rather than species-level identifications were recorded.

2.3. Short-term changes in vertical chlorophyll distribution

To test how rapidly-increased light could affect the vertical distribution of chlorophyll in the ice, a set of three snow removal experiments was conducted from 13 to 18 May, 2006. These 3 experimental plots were near, though independent of the experiments described in the previous section. In these three experiments, different initial thicknesses of natural snow cover were removed to increase light levels within the ice. At each of three 2 × 2 m plots (A, B, and C, located within 50 m of each other), an ice core was collected to determine the initial chlorophyll concentrations 0–2, 2–6, and 6–10 cm from the ice–water interface, as described in the previous section. Initial overlying snow thicknesses were 9, 5, and 4 cm at Stations A, B, and C, respectively. After the initial ice core was collected, all snow was removed from each plot and the plots were kept essentially snow-free for three days, greatly increasing irradiance to the algal layer. On the third day, each plot was cored again to determine the vertical distribution of chlorophyll within the bottom 10 cm of the ice core.

2.4. Ice diatom motility

Gliding rates of a cultured ice diatom, morphologically identified as *Cylindrotheca closterium* (Ehrenberg) Lewin and Riemann (Hasle and Syvertsen, 1997), were measured in a controlled laboratory environment. The diatom was isolated by A. Juhl from a mixed enrichment of melted sea ice collected in April 2005 near the study location. The isolate was maintained through serial transfer in sterile L1 medium (Guillard and Hargraves, 1993) at 4 °C with continuous illumination provided by cool-white fluorescent lights. The culture was monoalgal but not axenic.

Qualitative observations showed that cell motility was fastest following transfer to fresh medium. Stationary phase cells became effectively non-motile. The subculture eventually used to determine gliding rates was therefore prepared as follows. Five milliliters of an older culture was transferred to a sterile, 80-ml polycarbonate tissue culture flask containing 35 ml of cold (4 °C) L1 medium. When placed on their side, these tissue culture flasks provided a large, flat surface for adhesion and growth of surface associated cells. The subculture was allowed to grow for several weeks in an incubator at ~0 °C with continuous illumination of ~20 μmol photons m² s⁻¹ from cool-white fluorescent bulbs. Culture studies of other ice diatoms indicate that these irradiance levels should be near saturating for growth (Juhl and Krembs, 2010; Smith et al., 1994). The initial growth period produced a relatively high cell number, easing microscopic observation, and also allowed the diatoms to precondition the growth surface of the flask. Such preconditioning seemed appropriate given the potential importance of an EPS layer for diatom attachment and motion.

Following the preconditioning period, 25 ml of the growth medium was replaced with 25 ml of fresh, sterile, and cold (0 °C) L1 medium. Most cells remained adherent during this transfer. Cells were then allowed to acclimate for another 3 days. Afterwards, the culture flask was analyzed in a temperature-controlled room (0 °C) containing an inverted microscope (Nikon Diaphot) equipped with a Pixelink color digital camera. The location of individual cells relative to non-moving particles was recorded at 200× in still photographs every 2 s for 20 s. Timing of the photographs was controlled by the camera software. Glide speed was calculated for 23 cells by tracking the change in their location in successive photographs. A stage micrometer was used to calibrate measured distances.

3. Results

### 3.1. Ice-bottom layer light and algal biomass under experimental plots

An experimental gradient in snow depth was successfully established and maintained across 5 plots in both 2005 and 2006. Mean snow depths for each plot along the gradient, with the error bars indicating the range (min/max) over the entire observation period are shown in Fig. 1. The range in snow depths across plots had a large influence on irradiance near the bottom of the ice column. The relationship between the thickness of the overlying snow layer and daily integrated PAR reaching the upper light sensor, 30 cm above the ice–water interface, for the 24 h preceding each snow depth measurement can be seen in Fig. 2. Between years, there was no significant difference in the slopes or intercepts in the regression models (slopes: ANOVA $F_{1, 88} = 1.33$, $P = 0.25$; intercepts: ANOVA $F_{1, 89} = 2.04$, $P = 0.16$). As such, 2005 and 2006 data from the upper sensors were combined
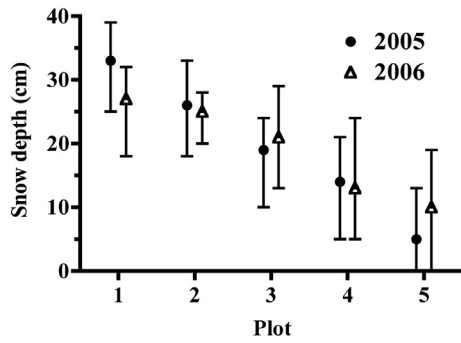
Fig. 1. The mean (symbol) and range (maximum/minimum) of snow depths measured at the experimental plots constructed in 2005 and 2006.

and a single regression line was fit to the pooled data. The combined regression was highly significant (ANOVA $F_{1, 90} = 220$, $P < 0.01$) and explained 71% of the variation in light levels. The residual irradiance variation was the result of changing meteorological (cloud cover, fog, etc.) and seasonal conditions including increased day length and solar angle. For example, the dotted line in Fig. 2 shows the best-fit regression line for five data points collected on April 20, 2005. The slope of this regression was nearly identical to the overall regression, though the intercept was lower. This pattern continued for regressions of data collected at later dates, with slopes remaining nearly equal with intercepts progressively increasing by date (data not shown). Nevertheless, despite pooling data across dates within and between years, the underlying relationship demonstrates the dramatic effect snow cover had on light reaching the top of the algal layer.

Snow cover remained an important factor determining light levels below the ice, and below the algal layers, with significant regressions between snow cover thickness and daily integrated PAR (Fig. 3). However, the regression slopes were significantly different between years (ANOVA $F_{1,88} = 4.88$, $P = 0.03$). This difference between years in the snow depth to PAR relationship below the ice, with correspondingly higher light levels for any snow depth under the ice in 2006, contrasts with the uniform snow depth to PAR relationship found above the algal layer in both years (Fig. 2). The dimmer under-ice light field in 2005 is consistent with higher algal biomass that was observed in 2005 (see next paragraph). In the context of this study, the data in Figs. 2 and 3 demonstrate that light levels, above and passing through the algal layer, were primarily controlled by overlying snow cover. Meanwhile, irradiance differences between experimental plots were not reflected in ice physiochemical properties at the time of sampling. In both 2005 and 2006, mean bulk salinity was fairly consistent in the
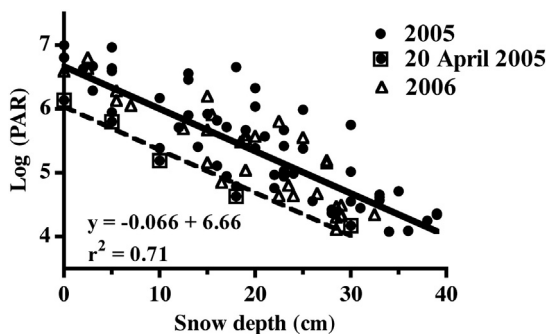
Fig. 2. Relationship between irradiance (log-transformed daily integrated PAR) 30 cm above the ice–water interface, and the thickness of the overlying snow layer in 2005 and 2006. The solid line and equation are from an annual regression for both years combined, since there were no significant differences between the slopes or intercepts in the regression models between years. The dashed line shows the best-fit regression for the five data points collected on April 20, 2005 ($y = -0.067 + 6.03$, $r^2 = 0.95$).
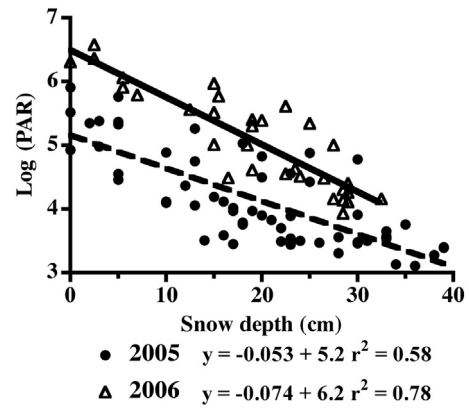

Fig. 3. Relationships between irradiance (log-transformed daily integrated PAR) 30 cm below the ice–water interface, and the thickness of the overlying snow layer in 2005 and 2006. The regressions for 2005 data (dashed line) and 2006 data (solid line) were significantly different from each other.

lower 10 cm sections between 4 and 6 ppt while temperature was consistently ~ -2.0 °C (see Supplemental Table 1).

Algal biomass in the bottom 10 cm of the ice for both years, plotted against mean daily PAR measured above the algal layer at each plot, shows that the greatest biomass was found at intermediate light levels (Fig. 4). Chlorophyll data were combined vertically to estimate the mean value for the bottom 10 cm, so as to highlight the horizontal trend between plots, and for ease of direct comparison to the frustule counts. For the 3 supplemental cores collected in 2005, mean daily PAR was estimated using the regression equation between snow depth and PAR from Fig. 2. In both years, ice algae biomass was unimodally related to light level. There was also a notable decrease in frustule concentrations, compared to chlorophyll concentrations, at stations with increased overlying snow and lower light. This discrepancy indicates elevated chlorophyll per cell in ice algae grown under lower irradiance. Nevertheless, the change in chlorophyll per cell did not obscure the general pattern of peak biomass at intermediate snow depths. Interestingly, although the absolute biomass concentrations differed between years by almost an order of magnitude, the relative pattern of algal biomass as a function of snow depth was qualitatively similar.

While taxonomic identifications were not conducted on the samples used in this study, other observations have shown *Navicula*, *Nitzschia*, *Amphiprora*, *Fragilariopsis*, *Pleurosigma* and *Gomphonema* to be
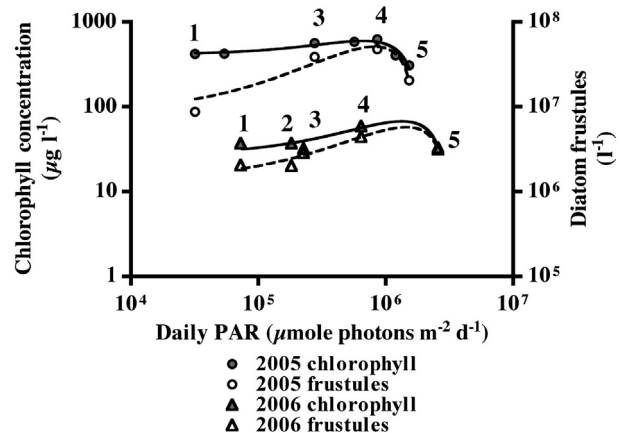
Fig. 4. Mean chlorophyll and diatom frustule concentrations in the bottom 10 cm of ice cores in relation to the mean daily PAR over the observation period preceding sample collection in 2005 and 2006. Second-order polynomial curves were fitted to each set of points. The numbers designate the plots that had embedded PAR sensors and correspond to the plot numbers in Fig. 1 with overlying snow depth decreasing from left to right.

particularly abundant diatom genera in first-year sea ice near Barrow (Horner and Alexander, 1972; Meguro et al., 1966). In addition, Horner and Alexander (1972) described *C. closterium* (identified at the time as *Nitzschia closterium*) as one of the most common species in first-year landfast sea ice near Barrow (see Section 3.3).

In addition to changes in algal biomass under different snow depths, the vertical distribution of the biomass through the lower 10 cm of the ice column also changed consistently from one experimental plot to the next. For example, in 2005 >80% of total chlorophyll measured in the bottom 10 cm of Plot 1, which had the highest overlying snow cover, was found in the 6–10 cm sub-sections (Fig. 5A). Only ~1% of the chlorophyll was measured in the bottom 2 cm of the ice in this plot, consistent with the idea that algae were light limited. In contrast, at Plot 3, with thinner overlying snow, only 6% of the collective chlorophyll was found in the 6–10 cm sub-sections while 86% of the collective chlorophyll was found in the 2–6 cm sub-sections. The downward shift of chlorophyll continued at Plot 4, consistent with the idea that nutrient limitation and/or photoinhibition became more important under thinner snow cover. At Plot 5, with the least overlying snow, only ~2% of chlorophyll was found in the upper 6–10 cm sub-sections. The change in the algal vertical distribution between experimental plots was also visually evident (Supplemental Fig. 1 is a composite photograph of the ice cores where the vertical position of the algal layers can be clearly seen).

Despite much lower overall chlorophyll concentrations, the trends in vertical algal distribution were repeated in 2006 (Fig. 5B), with 40% of the total chlorophyll found in the 6–10 cm sub-sections and only 12% of total chlorophyll residing in the bottom 0–2 cm under the thickest snow at Plot 1. Moving from thicker to thinner snow cover, there was a general decrease in chlorophyll percentage found in the upper 6–10 cm sub-sections, and a corresponding increase in chlorophyll percentage in the bottom 0–2 cm sub-sections. This culminated in Plot 5, where >99% of chlorophyll was located in the bottom 0–2 cm.

3.2. Short-term changes in vertical chlorophyll distribution

Vertical chlorophyll distribution within a location varied within 3 days in response to a change in the light environment (Fig. 6). Vertical chlorophyll profiles at three locations were compared before, and 3 days after snow removal. In each case, there were absolute and relative declines in the 6–10 cm sub-section following snow removal coupled with significant absolute and relative increases (paired *t*-test; $t_2 = 6.9$; $P = 0.02$) in chlorophyll in the 0–2 cm sub-section.

3.3. Ice diatom motility

The gliding speed of 23 individual *C. closterium* cells was measured (Table 1). The majority of the cells (12 of 23) moved in a consistent linear direction during the 20 s observation period. Only two of the observed cells did not move at all. The nine remaining cells reversed direction at least once during the observation. For those nine cells, gliding speed was estimated from the longest period during which they moved in a single direction.

4. Discussion

4.1. Overview

The major novel finding of this study is the relationship between the algal vertical distribution within first-year Arctic sea ice and overlying snow cover. This relationship, based on observations of altered vertical distributions along experimentally-created gradients of snow depth, could be related to differential growth and/or active movement of the algae. However, short-term snow removal experiments indicated rapid changes in the vertical distribution of algal biomass, suggesting active movement in response to environmental change. Additionally, ice diatom gliding rates measured (for one species) were sufficient to explain observed short-term changes in field profiles. Extrapolating from what is known about vertical distributions of algae in the water column and sediments, we hypothesize that ice algae actively position themselves within the ice column to balance the opposing vertical gradients of light and nutrients to optimize growth conditions. Furthermore, we hypothesize that this vertical positioning, in conjunction with physical processes, improves the mechanistic understanding of how snow thinning leads to algae loss via export from sea ice.

4.2. Evidence for different vertical distributions related to snow cover

Data from embedded light sensors provided reproducible relationships between overlying snow depth and PAR levels penetrating the underlying ice that were similar to previously published work (Maykut and Grenfell, 1975; Welch and Bergmann, 1989). The unimodal distribution of algal biomass with snow depth, and subsequent irradiances, resulting in the highest biomasses located under intermediate snow depths, has also been well described previously in field surveys (Mundy et al., 2005; Welch and Bergmann, 1989) and snow manipulation experiments (Smith, 1988). Thus, our observations
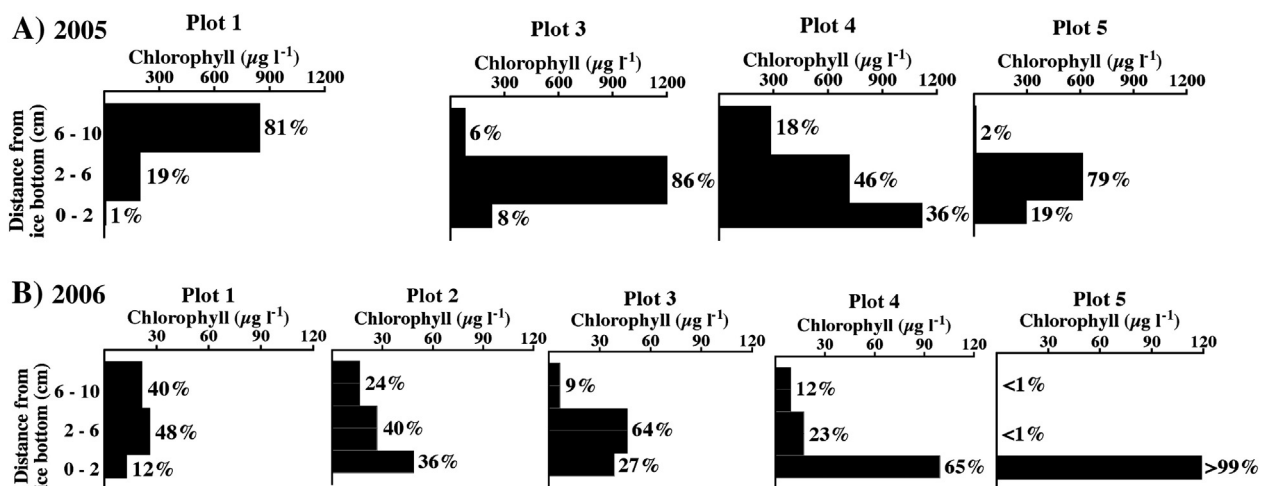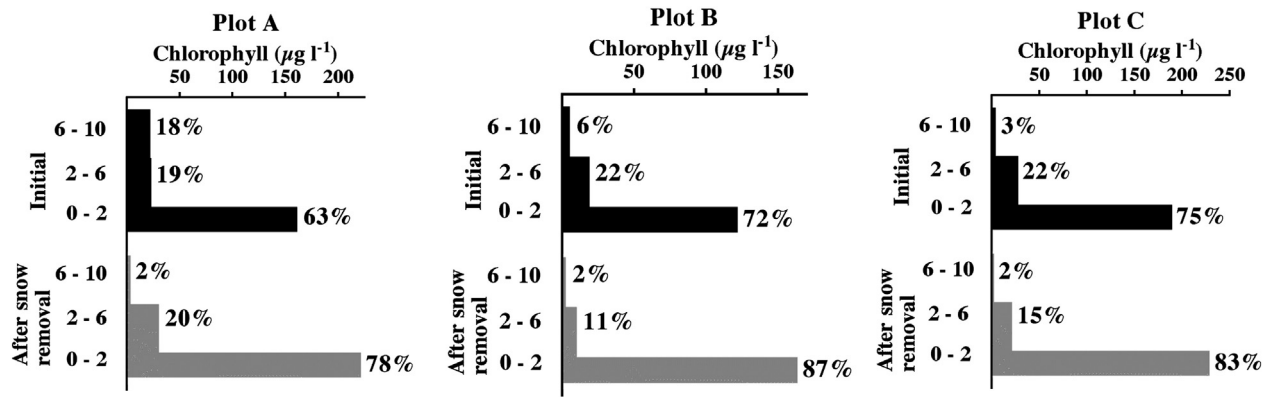

Fig. 5. Vertical distribution of chlorophyll in the bottom 10 cm of sea ice cores collected on A) May 11, 2005 and B) May 22, 2006. Plot numbers correspond to Fig. 1 and snow depths decrease from left to right. For each station, the horizontal bars show the absolute chlorophyll concentration, while the percentages show the relative fraction of the total chlorophyll (of the entire bottom 10 cm) in each subsection. Data from Plot 2 in Fig. 5a were excluded because of a patch of sediment found in some ice cores.

Fig. 6. Vertical distribution of ice algae chlorophyll in the bottom 10 cm of sea ice cores collected before and after complete removal of the overlying snow layer. The upper portion of the graph for each experimental plot shows the vertical chlorophyll distribution before snow removal; the lower portion of the graph shows the corresponding vertical chlorophyll distribution 3 days after snow removal. In each case, the horizontal bars show the absolute chlorophyll concentration, while the percentages show the relative fraction of the total chlorophyll in each subsection. Initial snow depths were 9, 5, and 4 cm at plots A, B, and C, respectively.

of horizontal variability in algal biomass related to snow cover are consistent with prior research. However, though occasional reports have described layers of ice algae vertically elevated from the ice–water interface (Gradinger et al., 1991; Grossi and Sullivan, 1985; Smith et al., 1990) this is the first experimental demonstration that algal vertical distribution in first-year sea ice can change in response to overlying snow cover.

In both 2005 and 2006, peak pigment chlorophyll concentrations under the thickest snow cover were found higher in the ice column, separated further from the ice–seawater interface. Under increasingly thinner snow, the chlorophyll biomass shifted downwards; this culminated under the thinnest snow cover with the bulk of chlorophyll residing at the ice–water interface. It should be pointed out that our cores were truncated at 10 cm because this segment captured all visible pigment layers (see Supplemental Fig. 1), even though Smith et al. (1990) reported peak pigment concentrations as much as 20 cm from the ice–water interface. Undoubtedly there were active algae higher in the cores (Eddie et al., 2010; Juhl et al., 2011), but the bottom 10 cm was sufficient to capture peak abundances.

The trend of algae increasingly concentrating near the ice–water interface was observed in both years with one exception. In 2005, under the thinnest snow cover (Plot 5), chlorophyll concentrations at the interface (0–2 cm) were lower than higher up in the core (2–6 cm). We attribute this pattern to active export of material from the bottom of the ice. Several sources have proposed increased export from the interface under thin snow cover to explain decreased chlorophyll near the ice-bottom (Lund-Hansen et al., 2014; Mundy et al., 2005; Smith, 1988). Export from the bottom of the sea ice was likely occurring in 2006 as well, though the quantity of material was less.

It is important to note that the strength of these observations of algal vertical distribution may be exaggerated because of the artificial snow gradients created in 2005 and 2006. The experimental plots were created in a single ice sheet after the majority of ice growth had occurred. Ice thickness and conditions at the ice–water interface, including nutrient supply, were therefore initially very similar. Under more natural conditions, differences in snow cover could affect ice

thickness (Ledley, 1991; Maykut and Untersteiner, 1971; Rothrock et al., 1999; Warren et al., 1999) and bulk salinity with implications for nutrient flux and algal growth. Also, large differences in nutrient flux, species composition, and EPS concentration/composition could occur from location to location on small scales. The kind of visually obvious differences in vertical distributions that we observed may only develop if nutrient supply and other factors were similar across locations and independent of snow cover.

The snow gradient experiments discussed above showed that algal vertical distributions responded to overlying snow depth over the course of many weeks. On those time scales, it is unclear whether biomass differences were related to differential growth or active migration. Three short-term snow removals were therefore conducted to investigate potential algal redistribution on shorter time scales. The initial natural snow depths were similar to overlying snow found at the thinner end of the snow depth gradient experiments and thus, the concentrations and vertical distributions of chlorophyll were most comparable to Plot 4 in 2006. Snow removal changed the algal distribution within 3 days. Enhanced growth following snow removal could be partly responsible for chlorophyll increasing in the 0–2 cm sub-sections. However, the loss of chlorophyll from the 6–10 cm sub-sections was particularly consistent with active downward migration.

4.3. Quantifying ice algae motility

The ability of many sea ice algae to attach and glide within the interconnected pore spaces of sea ice has previously been mentioned qualitatively (Agatha et al., 1990; Carey, 1985; Ikävalko and Gradinger, 1997; Krembs et al., 2000; Spindler and Dieckmann, 1986; Welch and Bergmann, 1989). Welch and Bergmann (1989) demonstrated a collective ice algal movement equal to a few centimeters per day, but we are unaware of other more quantitative observations of ice diatom gliding speeds within the sea ice. Lab based tests showed average gliding speeds of the sea ice diatom *C. closterium* to be ~0.1 mm min^{-1}, or ~14.4 cm d^{-1}, assuming consistent unidirectional travel. Despite the low temperature, these recorded speeds are comparable to many

Table 1
Gliding speed of cultured *Cylindrotheca closterium*. Observations were made on 23 individual cells. The majority (21 of 23) moved either in a consistent linear direction or started on one course but reversed direction during the 20 s observation period. Calculations of mean velocities included the two cells that did not move.

	Cell length (μm)	Glide velocity (μm s^{-1})	Glide velocity (mm min^{-1})	Glide velocity (body lengths s^{-1})	Glide velocity (body lengths min^{-1})
Mean	104.8	1.7	0.1	0.017	0.99
SD	5.9	1.1	0.6	0.011	0.63
SE	1.2	0.2	0.01	0.002	0.13

reports of benthic diatom gliding (Cohn and Weitzell, 1996; Cohn et al., 2004; Edgar and Pickett-Heaps, 1983). Thus, although based only on a single species, these observations may be representative for other ice diatoms. The main caveat is that these measurements were not carried out in the confines of a brine channel, which likely affect gliding speeds. Though the elongated morphology of *C. closterium* may actually be advantageous for moving within the interstitial sea ice environment, mobility of other diatom species through brine channels may vary depending on their respective morphologies and chaining structure. Further research on this subject would be warranted. Still, calculated gliding speeds are well within the velocities required to relocate vertically within the time and space scales measured in our snow removal experiments.

4.4. Diatom vertical migration and algal distributions within sea ice

Many diatom species, both pelagic and benthic, vertically orient themselves to optimize available resources, thereby increasing their overall productivity. In most circumstances, this entails moving upward through their respective medium for increased irradiance and downward to prevent photoinhibition and/or relocate to areas of greater nutrient availability (Barranguet et al., 1998; Happey-Wood and Jones, 1988; Villareal et al., 1996). These same adaptive processes could also occur with sea-ice algae. Light attenuates while passing through the ice and many studies have indicated that irradiance levels near the ice–water interface limit ice algae growth (Gosselin et al., 1986; Grossi and Sullivan, 1985; Lavoie et al., 2005; Smith, 1988; Welch and Bergmann, 1989). Previous research has also shown that the bottom of coastal sea ice is generally more replete with nutrients (Cota and Horne, 1989) and regularly re-accumulates nutrients from tidal inundation (Cota et al., 1987, 1990). With opposing resource gradients, modeling and laboratory studies suggest that motile algae will form a biomass maximum layer where light and nutrient limitation is balanced (Klausmeier and Litchman, 2001; Mellard et al., 2011, 2012). Those studies make three further predictions about the algal layer that are consistent with our observations. 1) When light levels increase, up to a certain threshold, overall biomass will be higher and the layer will move down. 2) If light levels decrease, overall biomass will be lower and the layer will move up. 3) The fraction of total biomass found within the layer will rise as total biomass increases because of self-shading effects. This last prediction is explained as follows. If algal biomass increases at some optimal depth in the ice column, light attenuation by that algal layer also rises. The decrease in light availability below the layer stimulates upward-directed movement or energetically prohibits further growth below, thereby increasing the fraction of total biomass found at the optimal depth (Klausmeier and Litchman, 2001).

All these predictions are consistent with our observations of sea ice algae. Under thinner snow, biomass was higher and there was shift in chlorophyll biomass toward the ice–water interface. This downward movement may be a directed response to greater nutrient availability lower in the ice column, once saturating irradiances are readily available. Alternately, downward movement may also be a photophobic response. Neither strategy is necessarily exclusive. The predicted effects of higher biomass and self shading (prediction 3 in prior paragraph) could also explain the notable difference in vertical algal profiles between 2005 and 2006 under thicker snow covers (i.e., comparing plots 1–3 in Fig. 5a and b). In 2005, the algal layering was very distinct and little chlorophyll was found below the respective chlorophyll maximum layer. In 2006, under similar snow cover, chlorophyll was vertically more evenly distributed than in 2005. The difference in algal biomass between years clearly impacted light levels below the ice (Fig. 3), and as described above, the shading effect of higher biomass would be expected to result in a more exaggerated vertical chlorophyll profile. In this context, it is worth pointing out that the dramatic shading caused by algae in 2005 was probably unusual, as the chlorophyll concentrations measured at the 2005 experimental plots were the

highest we have seen in eight years of sampling near Point Barrow, while the 2006 data were more characteristic of this region (Juhl and Krembs, 2010; Juhl et al., 2011). The explanation for this order of magnitude difference in chlorophyll concentrations between years is unknown.

4.5. Implications

Field experiments conducted in this study either maintained consistent overlying snow depths for many weeks or changed them very rapidly. The natural progression in the surrounding ice sheet was a more gradual decline in snow depth as air temperature increased through time. Based on our results we predict, when overlying snow decreases gradually, algae will progressively congregate toward the ice–seawater interface. At that location, they would be most susceptible to export, either through directed motion into the water column, involuntary physical melting processes, or grazing. Thus, vertical positioning in the ice as related to overlying snow depth may help explain the connection between algal export events and snow loss (Apollonio, 1965; Fortier et al., 2002; Juhl and Krembs, 2010). Lund-Hansen et al. (2014), in a recent study, showed that complete snow removal caused an exponential decrease in chlorophyll accompanied by undetectable levels of fluorescing biomass. They hypothesized that the loss of algae biomass resulted from diatom emigration from the ice in response to ice temperatures and brine volume. Our results concur, clearly demonstrating vertical repositioning and active diatom migration downward through the ice column in response to higher irradiances. Such downward directed movement of motile algae, concentrating them near the interface, may also help explain the preferential loss of chlorophyll relative to other pools of organic matter that occur prior to significant spring ice melt (Juhl et al., 2011; Riedel et al., 2008).

Recent modeling of ice algae growth both underestimated the peak algal biomass achieved and the rapidity of algal loss following snow melt (Pogson et al., 2011). A more realistic parameterization of algal vertical positioning within the ice column may improve model performance. In particular, the pace of algal biomass loss in Pogson et al. (2011) was improved (relative to observations) by increasing loss rates due to brine drainage beyond the best estimate of realistic levels. If ice algae moved closer to the ice–water interface as snow cover melted, then brine drainage, or any other physical loss process present in the model, would be more effective in removing algae from the ice. Adding algal behavior to such models might therefore obviate the need to assume unrealistic parameterizations for physical processes within the models.

Apparent increases in annual precipitation in the Arctic nearshore environment (Christensen et al., 2007) can yield more or less snow cover depending on local air temperatures relative to the freezing point of water. Understanding the sea ice community's response to such changes is imperative to predict any future contributions sea ice can have on underlying marine ecosystems in a rapidly changing Arctic environment.

Acknowledgements

References

Agatha, S., Wilbert, N., Spindler, M., Elbrächter, M., 1990. Euplotide ciliates in sea ice of the Weddell Sea (Antarctica). Acta Protozool. 29, 221–228.

Apollonio, S., 1961. The chlorophyll content of Arctic sea-ice. Arctic 14, 197–200.

Apollonio, S., 1965. Chlorophyll in Arctic sea ice. Arctic 18, 118–122.

Apoya Horton, M.D., Yin, L., Underwood, G.J., Gretz, M.R., 2006. Movement modalities and responses to environmental changes of the mudflat diatom *Cylindrotheca closterium* (Bacillariophyceae). J. Phycol. 42, 379–390.

Arrigo, K.R., 2003. Primary production in sea ice. In: Thomas, D., Dieckmann, G. (Eds.), Sea Ice. An Introduction to Its Physics, Chemistry, Biology, and Geology. Wiley-Blackwell, Oxford, pp. 143–183.

Arrigo, K.R., Mock, T., Lizotte, M.P., 2010. Primary producers and sea ice. In: Thomas, D., Dieckmann, G. (Eds.), Sea Ice. Wiley-Blackwell, Oxford, pp. 283–326.

Barranguet, C., Kromkamp, J., Peene, J., 1998. Factors controlling primary production and photosynthetic characteristics of intertidal microphytobenthos. Mar. Ecol. Prog. Ser. 173, 117–126.

Bluhm, B.A., Gradinger, R.R., Schnack-Schiel, S.B., 2010. Sea ice meio- and macrofauna. In: Thomas, D., Dieckmann, G. (Eds.), Sea Ice. Wiley-Blackwell, Oxford, pp. 357–394.

Carey Jr., A.G., 1985. Marine ice fauna: arctic. In: Horner, R.A. (Ed.), Sea Ice Biota. CRC Press, Boca Raton, pp. 173–190.

Chorus, I., Schlag, G., 1993. Importance of intermediate disturbances for the species composition and diversity of phytoplankton in two very different Berlin lakes. Intermediate Disturbance Hypothesis in Phytoplankton Ecology. Springer, pp. 67–92.

Christensen, J.H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, R., Jones, R., Kolli, R.K., Kwon, W., Laprise, R., 2007. Regional climate projections. In: Christensen, J.H. (Ed.), Climate Change, 2007: The Physical Science Basis. Contribution of Working group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. University Press, Cambridge, pp. 847–940.

Cohn, S.A., Weitzell, R.E., 1996. Ecological considerations of diatom cell motility I. Characterization of motility and adhesion in four diatom species. J. Phycol. 32, 928–939.

Cohn, S.A., Spurck, T.P., Pickett-Heaps, J.D., 1999. High energy irradiation at the leading tip of moving diatoms causes a rapid change of cell direction. Diatom Res. 14, 193–206.

Cohn, S.A., Bahena, M., Davis, J.T., Ragland, R.L., Rauschenberg, C.D., Smith, B.J., 2004. Characterisation of the diatom photophobic response to high irradiance. Diatom Res. 19, 167–179.

Consalvey, M., Paterson, D.M., Underwood, G.J., 2004. The ups and downs of life in a benthic biofilm: migration of benthic diatoms. Diatom Res. 19, 181–202.

Cota, G.F., Horne, E.P., 1989. Physical control of Arctic ice algal production. Mar. Ecol. Prog. Ser. 52, 111–121.

Cota, G., Prinsenberg, S., Bennett, E., Loder, J., Lewis, M., Anning, J., Watson, N., Harris, L., 1987. Nutrient fluxes during extended blooms of Arctic ice algae. J. Geophys. Res. Oceans 92, 1951–1962.

Cota, G.F., Anning, J.L., Harris, L.R., Harrison, W.G., Smith, R.E., 1990. Impact of ice algae on inorganic nutrients in seawater and sea ice in Barrow Strait, NWT, Canada, during spring. Can. J. Fish. Aquat. Sci. 47, 1402–1415.

Cota, G., Legendre, L., Gosselin, M., Ingram, R., 1991. Ecology of bottom ice algae: I Environmental controls and variability. J. Mar. Syst. 2, 257–277.

Deming, J.W., 2010. Sea Ice bacteria and viruses. In: Thomas, D., Dieckmann, G. (Eds.), Sea Ice. Wiley-Blackwell, Oxford, pp. 247–282.

Eddie, B., Juhl, A., Krembs, C., Baysinger, C., Neuer, S., 2010. Effect of environmental variables on eukaryotic microbial community structure of land-fast Arctic sea ice. Environ. Microbiol. 12, 797–809.

Edgar, L.A., Pickett-Heaps, J., 1983. The mechanism of diatom locomotion. I. An ultrastructural study of the motility apparatus. Proc. R. Soc. Lond. Ser. B Biol. Sci. 331–343.

Edgar, L.A., Zavortink, M., 1983. The mechanism of diatom locomotion. II: identification of actin. Proc. R. Soc. Lond. Ser. B Biol. Sci. 218, 345–348.

Fortier, M., Fortier, L., Michel, C., Legendre, L., 2002. Climatic and biological forcing of the vertical flux of biogenic particles under seasonal Arctic sea ice. Mar. Ecol. Prog. Ser. 225, 1–16.

Gosselin, M., Legendre, L., Therriault, J.-C., Demers, S., Rochet, M., 1986. Physical control of the horizontal patchiness of sea-ice microalgae. Mar. Ecol. Prog. Ser. 29, 289–298.

Gradinger, R., 1999. Vertical fine structure of the biomass and composition of algal communities in Arctic pack ice. Mar. Biol. 133, 745–754.

Gradinger, R., Bluhm, B., 2010. Timing of ice algal grazing by the Arctic nearshore benthic amphipod *Onisimus litoralis*. Arctic 355–358.

Gradinger, R., Spindler, M., Henschel, D., 1991. Development of Arctic sea-ice organisms under graded snow cover. Polar Res. 10, 295–308.

Grenfell, T.C., Maykut, G.A., 1977. The optical properties of ice and snow in the Arctic Basin. J. Glaciol. 18, 445–463.

Grossi, S.M., Sullivan, C., 1985. Sea ice microbial communities V. The vertical zonation of diatoms in an Antarctic fast ice community. J. Phycol. 21, 401–409.

Guillard, R., Hargraves, P., 1993. *Stichochrysis immobilis* is a diatom, not a chrysophyte. Phycologia 32, 234–236.

Haecky, P., Jonsson, S., Andersson, A., 1998. Influence of sea ice on the composition of the spring phytoplankton bloom in the northern Baltic Sea. Polar Biol. 20, 1–8.

Happey-Wood, C.M., Jones, P., 1988. Rhythms of vertical migration and motility in intertidal benthic diatoms with particular reference to *Pleurosigma angulatum*. Diatom Res. 3, 83–93.

Hasle, G.R., Syvertsen, E.E., 1997. Marine diatoms. In: Tomas, C.R. (Ed.), Identifying Marine Phytoplankton. Academic Press, San Diego, CA, pp. 290–294.

Horner, R., Alexander, V., 1972. Algal populations in Arctic sea ice: an investigation of heterotrophy. Limnology and Oceanography. 17, pp. 454–458.

Hsiao, S.I., 1980. Quantitative composition, distribution, community structure and standing stock of sea ice microalgae in the Canadian Arctic. Arctic 33, 768–793.

Huisman, J., Thi, N.N.P., Karl, D.M., Sommeijer, B., 2006. Reduced mixing generates oscillations and chaos in the oceanic deep chlorophyll maximum. Nature 439, 322–325.

Ikävalko, J., Gradinger, R., 1997. Flagellates and heliozoans in the Greenland Sea ice studied alive using light microscopy. Polar Biol. 17, 473–481.

Ingram, W., Wilson, C., Mitchell, J., 1989. Modeling climate change: an assessment of sea ice and surface albedo feedbacks. J. Geophys. Res. Atmos. 94, 8609–8622.

Juhl, A.R., Krembs, C., 2010. Effects of snow removal and algal photoacclimation on growth and export of ice algae. Polar Biol. 33, 1057–1065.

Juhl, A.R., Krembs, C., Meiners, K.M., 2011. Seasonal development and differential retention of ice algae and other organic fractions in first-year Arctic sea ice. Mar. Ecol. Prog. Ser. 436, 1–16.

Klausmeier, C.A., Litchman, E., 2001. Algal games: the vertical distribution of phytoplankton in poorly mixed water columns. Limnol. Oceanogr. 46, 1998–2007.

Krembs, C., Gradinger, R., 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, 55–80.

Krembs, C., Mock, T., Gradinger, R., 2001. A mesocosm study of physical–biological interactions in artificial sea ice: effects of brine channel surface evolution and brine movement on algal biomass. Polar Biol. 24, 356–364.

Krembs, C., Eicken, H., Junge, K., Deming, J., 2002. High concentrations of exopolymeric substances in Arctic winter sea ice: implications for the polar ocean carbon cycle and cryoprotection of diatoms. Deep-Sea Res. I Oceanogr. Res. Pap. 49, 2163–2181.

Krembs, C., Eicken, H., Deming, J.W., 2011. Exopolymer alteration of physical properties of sea ice and implications for ice habitability and biogeochemistry in a warmer Arctic. Proc. Natl. Acad. Sci. 108, 3653–3658.

Lavoie, D., Denman, K., Michel, C., 2005. Modeling ice algal growth and decline in a seasonally ice-covered region of the Arctic (Resolute Passage, Canadian Archipelago). J. Geophys. Res. 110, C11009.

Ledley, T.S., 1991. Snow on sea ice: competing effects in shaping climate. J. Geophys. Res. Atmos. 96, 17195–17208.

Lund-Hansen, L.C., Hawes, I., Sorrell, B.K., Nielsen, M.H., 2014. Removal of snow cover inhibits spring growth of Arctic ice algae through physiological and behavioral effects. Polar Biol. 37, 471–481.

Maykut, G.A., Grenfell, T.C., 1975. The spectral distribution of light beneath first-year sea ice in the Arctic Ocean. Limnol. Oceanogr. 20, 554–563.

Maykut, G.A., Untersteiner, N., 1971. Some results from a time-dependent thermodynamic model of sea ice. J. Geophys. Res. 76, 1550–1575.

McLachlan, D.H., Brownlee, C., Taylor, A.R., Geider, R.J., Underwood, G.J., 2009. Light-induced motile responses of the estuarine benthic diatoms *Navicula perminuta* and *Cylidrotheca closterium* (Bacillariophyceae). J. Phycol. 45, 592–599.

McMahon, K.W., Ambrose Jr., W.G., Johnson, B.J., Sun, M.-Y., Lopez, G.R., Clough, L.M., Carroll, M.L., 2006. Benthic community response to ice algae and phytoplankton in Ny Ålesund, Svalbard. Mar. Ecol. Prog. Ser. 310, 1–14.

Meguro, H., Ito, K., Fukushima, H., 1966. Diatoms and the ecological conditions of their growth in sea ice in the Arctic Ocean. Science. 152, pp. 1089–1090.

Meiners, K., Gradinger, R., Fehling, J., Civitarese, G., Spindler, M., 2003. Vertical distribution of exopolymer particles in sea ice of the Fram Strait (Arctic) during autumn. Mar. Ecol. Prog. Ser. 248, 1–13.

Meiners, K., Brinkmeyer, R., Granskog, M.A., Lindfors, A., 2004. Abundance, size distribution and bacterial colonization of exopolymer particles in Antarctic sea ice (Bellingshausen Sea). Aquat. Microb. Ecol. 35, 283–296.

Mellard, J.P., Yoshiyama, K., Litchman, E., Klausmeier, C.A., 2011. The vertical distribution of phytoplankton in stratified water columns. J. Theor. Biol. 269, 16–30.

Mellard, J.P., Yoshiyama, K., Klausmeier, C.A., Litchman, E., 2012. Experimental test of phytoplankton competition for nutrients and light in poorly mixed water columns. Ecol. Monogr. 82, 239–256.

Michel, C., Legendre, L., Demers, S., Therriault, J.-C., 1988. Photoadaptation of sea-ice microalgae in springtime: photosynthesis and carboxylating enzymes. Mar. Ecol. Prog. Ser. 50, 177–185.

Michel, C., Legendre, L., Therriault, J.-C., Demers, S., Vandevelde, T., 1993. Springtime coupling between ice algal and phytoplankton assemblages in southeastern Hudson Bay, Canadian Arctic. Polar Biol. 13, 441–449.

Michel, C., Legendre, L., Ingram, R., Gosselin, M., Levasseur, M., 1996. Carbon budget of sea-ice algae in spring: evidence of a significant transfer to zooplankton grazers. J. Geophys. Res. 101, 18345–18360.

Morata, N., Poulin, M., Renaud, P.E., 2011. A multiple biomarker approach to tracking the fate of an ice algal bloom to the sea floor. Polar Biol. 34, 101–112.

Mundy, C., Barber, D., Michel, C., 2005. Variability of snow and ice thermal, physical and optical properties pertinent to sea ice algae biomass during spring. J. Mar. Syst. 58, 107–120.

Pogson, C., Tremblay, B., Lavoie, D., Michel, C., Vancoppenolle, M., 2011. Development and validation of a one dimensional snow ice algae model against observations in Resolute Passage Canadian Arctic Archipelago. J. Geophys. Res. Oceans 116.

Renaud, P.E., Riedel, A., Michel, C., Morata, N., Gosselin, M., Juul-Pedersen, T., Chiuchiolo, A., 2007. Seasonal variation in benthic community oxygen demand: a response to an ice algal bloom in the Beaufort Sea, Canadian Arctic? J. Mar. Syst. 67, 1–12.

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, 195–206.

Riedel, A., Michel, C., Gosselin, M., LeBlanc, B., 2008. Winter–spring dynamics in sea-ice carbon cycling in the coastal Arctic Ocean. J. Mar. Syst. 74, 918–932.

Rothrock, D.A., Yu, Y., Maykut, G.A., 1999. Thinning of the Arctic sea-ice cover. Geophys. Res. Lett. 26, 3469–3472.

Runge, J.A., Therriault, J.C., Legendre, L., Ingram, R.G., Demers, S., 1991. Coupling between ice microalgal productivity and the pelagic, metazoan food web in southeastern Hudson Bay: a synthesis of results. Polar Res. 10, 325–338.

Saburova, M.A., Polikarpov, I.G., 2003. Diatom activity within soft sediments: behavioural and physiological processes. Mar. Ecol. Prog. Ser. 251, 15–126.

Smith, R.E.H., 1988. Abundance and production of ice algae in Resolute Passage, Canadian Arctic. Mar. Ecol. Prog. Ser. 48, 251.

Smith, R.E., Clement, P., Head, E., 1989. Biosynthesis and photosynthate allocation patterns of Arctic ice algae. Limnol. Oceanogr. 34, 591–605.

Smith, R.E., Harrison, W.G., Harris, L.R., Herman, A.W., 1990. Vertical fine structure of particulate matter and nutrients in sea ice of the high Arctic. Can. J. Fish. Aquat. Sci. 47, 1348–1355.

Smith, R.E., Stapleford, L.C., Ridings, R.S., 1994. The acclimated response of growth, photosynthesis, composition, and carbon balance to temperature in the psychrophilic ice diatom *Nitzschia seriata*. J. Phycol. 30, 8–16.

Søreide, J.E., 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. Chang. Biol. 16, 3154–3163.

Spindler, M., Dieckmann, G.S., 1986. Distribution and abundance of the planktic foraminifer *Neogloboquadrina pachyderma* in sea ice of the Weddell Sea (Antarctica). Polar Biol. 5, 185–191.

Thomas, D., Papadimitriou, S., Michel, C., 2010. Biogeochemistry of sea ice. In: Thomas, D., Dieckmann, G. (Eds.), Sea Ice. Wiley-Blackwell, Oxford, pp. 425–468.

Tremblay, C., Runge, J., Legendre, L., 1989. Grazing and sedimentation of ice algae during and immediately after a bloom at the ice–water interface. Mar. Ecol. Prog. Ser. 56, 291–300.

Underwood, G.J., Paterson, D.M., 2003. The importance of extracellular carbohydrate production by marine epipelic diatoms. Adv. Bot. Res. 40, 183–240.

Underwood, G., Perkins, R.G., Consalvey, M., Hanlon, A., Oxborough, K., Baker, N., Paterson, D., 2005. Patterns in microphytobenthic primary productivity: species-specific variation in migratory rhythms and photosynthetic efficiency in mixed-species biofilms. Limnol. Oceanogr. 50, 755–767.

UNESCO, 1994. Protocols for the Joint Global Ocean Flux Study (JGOFS) core measurements. In: Knap, A., Michaels, A., Close, A., Ducklow, H., Dickson, A. (Eds.), JGOFS Report No. 19, pp. 119–122 (vi+170 pp.).

Villareal, T.A., Woods, S., Moore, J.K., Culver Rymsza, K., 1996. Vertical migration of *Rhizosolenia* mats and their significance to NO_3^- fluxes in the central North Pacific gyre. J. Plankton Res. 18, 1103–1121.

Warren, S.G., Rigor, I.G., Untersteiner, N., Radionov, V.F., Bryazgin, N.N., Aleksandrov, Y.I., Colony, R., 1999. Snow depth on Arctic sea ice. J. Clim. 12, 1814–1829.

Welch, H.E., Bergmann, M.A., 1989. Seasonal development of ice algae and its prediction from environmental factors near Resolute, NWT, Canada. Can. J. Fish. Aquat. Sci. 46, 1793–1804.

Zeebe, R.E., Eicken, H., Robinson, D.H., Wolf Gladrow, D., Dieckmann, G.S., 1996. Modeling the heating and melting of sea ice through light absorption by microalgae. J. Geophys. Res. Oceans 101, 1163–1181.

Overlying snow depth

Plot 5 Plot 4 Plot 3 Plot 1

Graphical abstract/Supplemental figure 1