Diatom vertical migration within land-fast Arctic sea ice

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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