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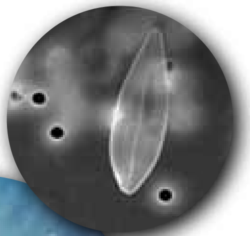

Holes in Progressively Thinning Arctic Sea Ice Lead to New Ice Algae Habitat

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ABSTRACT. The retreat and thinning of Arctic sea ice associated with climate warming is resulting in ever-changing ecological processes and patterns. One example is our discovery of myriad new "marine aquaria" formed by melt holes in the perennial sea ice. In previous years, these features were closed, freshwater melt ponds on the surface of sea ice. Decreased ice thickness now allows these ponds to melt through to the underlying ocean, thus creating a new marine habitat and concentrating a food source for the ecosystem through accumulation of algae attached to refreezing ice in late summer. This article describes the formation of these late-season algal masses and comments on their overall contribution to Arctic ecosystems and the consequences of a continued decline in sea ice.

INTRODUCTION

As a result of climate warming, the surface of the perennial Arctic sea ice pack in summer is now being transformed from a network of closed, surface melt pools into one of holes that completely penetrate the ice. It has long been known that sea ice algae growth in early spring provides a crucial food source for microfauna (Apollonio, 1965; Alexander, 1980; Legendre et al., 1981; Horner and Schrader, 1982; Michel et al., 1996; Gosselin et al., 1997; Lizotte, 2001; Lee et al., 2008). In previous years, with a colder Arctic and thicker perennial sea ice, summer surface melting formed only shallow, freshwater ponds on the sea ice surface without connection to the seawater below. However, higher temperatures over the past several decades have decreased sea ice extent and thickness and reduced the area of perennial sea ice (Vinnikov et al., 1999; Rothrock et al., 2003; Perovich and Richter-Menge, 2009; Perovich, 2011, in this issue) so that now the largely freshwater melt ponds are being transformed into holes. While melt ponds have recognized impacts on the physical environment, such as surface albedo (Lüthje et al., 2006) and heat transmission (Inoue et al., 2008; Skyllingstad et al., 2009), their role in the Arctic ecosystem is rarely studied (Gradinger, 2002). As such, the 3rd Chinese National Arctic Research Expedition (CHINARE), conducted in the Chukchi Sea and Canadian Basin of the Arctic Ocean from late July to September 2008, provided an opportunity to investigate biological processes associated with closed and open melt ponds. We discovered that large ice algal masses formed in melt ponds north of 80°N as temperatures dropped in late summer and holes refroze.

The resulting new marine habitat contains abundant algal species known to be important zooplankton food. The refreezing of these holes in late summer creates a new and previously undescribed habitat for sea ice algae that provides a food source just before the onset of the long, dark Arctic winter, and thus introduces new temporal and spatial dimensions to the Arctic ecosystem. We speculate that this new food resource and habitat type will transit north and perhaps disappear with continued warming and sea ice decline.

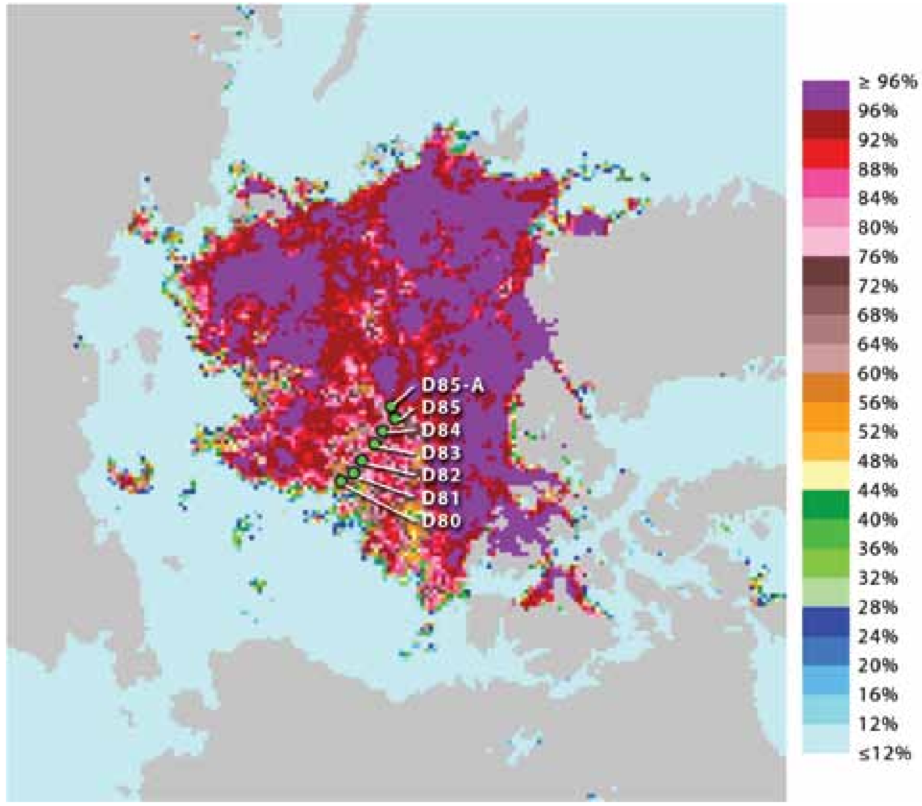

Figure 1. Stations from the 3rd Chinese National Arctic Research Expedition (CHINARE) and sea ice concentrations in August 2008. Sea ice data from Advanced Microwave Scanning Radiometer-Earth Observing System (AMSR-E) instrument on the NASA Earth Observing System (EOS) Aqua satellite. The sea ice image is a daily (averaged) Level-3 gridded product (AE_SI25) for concentrations at 25-km spatial resolution. *Data were obtained from the National Snow and Ice Data Center (http://nsidc.org)*

MATERIALS AND METHODS

Carbon uptake rates were measured using a ^{13}C–^{15}N dual isotope tracer technique (Lee and Whitledge, 2005). Surface seawater and pond water samples were transferred to clean 1 L polycarbonate incubation bottles and inoculated with labeled carbon ($H^{13}CO_3$) and nitrogen ($K^{15}NO_3$ or $^{15}NH_4Cl$) tracers. Bottles for surface seawater were incubated in a shipboard deck incubator cooled with surface seawater; bottles for pond waters were incubated in their original ponds for three to four hours. For ice algal incubations, about 2 cm thickness of sea ice cubes containing ice algal mass were obtained from one of the melt ponds at station D83 (Figure 1) and melted in filtered surface seawater (0.9 L) in a dark container on deck overnight. Then, the melted water was well mixed and each 0.1 L volume of the water was distributed into two polycarbonate incubation bottles (1 L) filled with 0.9 L filtered seawater for a three to four hour incubation on deck. Incubations were terminated by filtration through pre-combusted (450°C) GF/F glass fiber filters (24 mm). Filters were immediately frozen and preserved for mass spectrometer analysis at the Alaska Stable Isotope Facility of the University of Alaska Fairbanks. Particulate organic carbon and abundance of ^{13}C were determined in a Finnigan Delta+XL mass spectrometer after HCl fuming overnight to remove carbonate.

For identification of algal species, water samples (125 mL) were preserved with glutaraldehyde (final concentration 1%). Sample volumes of 50–100 mL

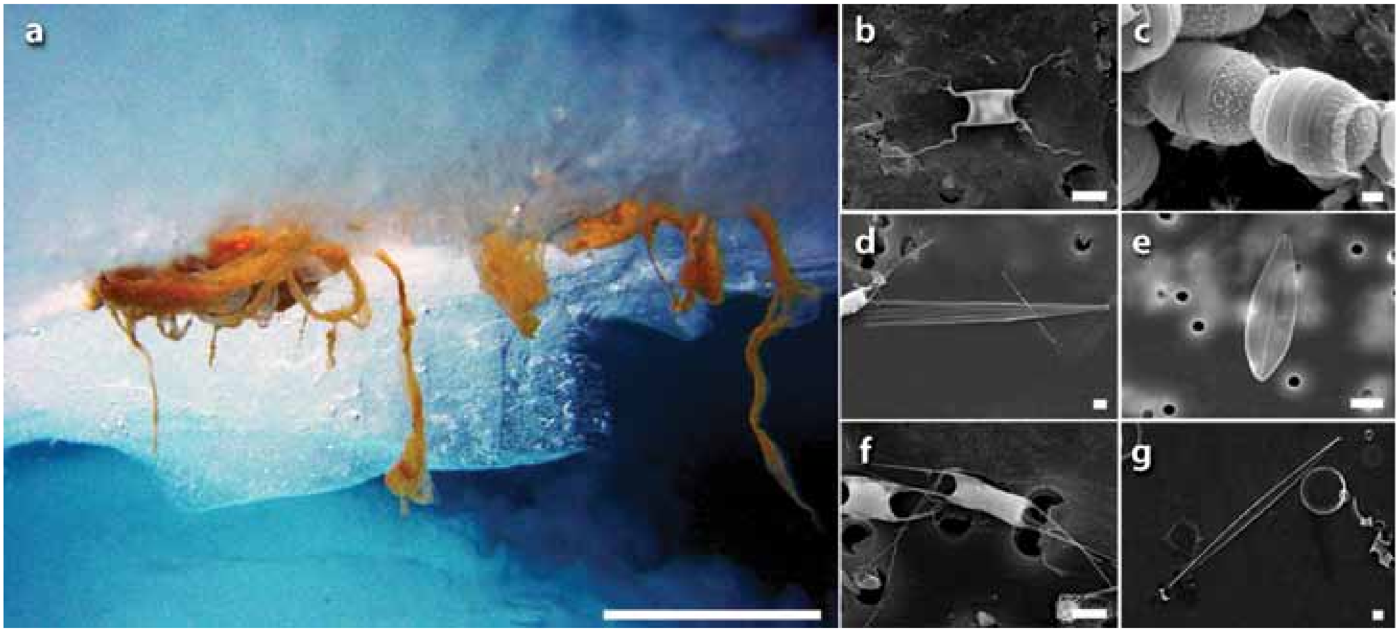

Figure 2. (a) Masses of algae in refrozen surface sea ice of open ponds. (b) *Attheya septentrionalis*. (c) *Melosira arctica*. (d) *Thalassionema sp*. (e) *Navicula sp*. (f) *Chaetoceros sp*. (g) *Nitzschia sp*. Scale bars: (a) 10 cm; (b–g) 5 mm.

were filtered through Gelman GN-6 Metricel filters (0.45 μm pore size, 25 mm diameter; Gelman Sciences Inc., NY). The filters were mounted on microscope slides in a water-soluble embedding medium (HPMA, 2-hydroxypropyl methacrylate) on board. The HPMA slides were used for identification and estimation of cell concentration (Crumpton, 1987). At least 300 cells were identified from each sample using a microscope (BX51, Olympus Inc., Tokyo), with a combination of light and epifluorescence microscopy at 400x for microplankton, and at 1,000x for autotrophic pico- and nanoplankton (Booth, 1993). A JEOL JSM-5600LV scanning electron microscope (JEOL Inc., Tokyo) was used for species that could not be identified with light microscopy.

RESULTS AND DISCUSSION

Melt ponds form in summer from melting snow and surface ice and can cover up to 80% of the Arctic sea ice surface (Lüthje et al., 2006). Two types of pond features can be distinguished by color (Gradinger, 2002). Closed ponds are light blue with depths of ~ 0.5 m and bottoms closed to the surrounding sea. In these, salinities range from ~ 0 to 22, depending on stage and physical structure and connections to seawater. In contrast, open ponds are deep blue with depths of 1–2 m and are freely connected to the sea below. An open pond is a marine environment similar to the surrounding ocean but without wave disturbance.

Small (nano- and pico-sized) flagellates mostly dominate the phytoplankton communities in open pond habitats. We identified nanoflagellates in the closed ponds as *Chlamydomonas nivalis*, a species common on ice floes and in melt ponds in the central Arctic (Gradinger and Nürnberg, 1996). *Dinobryon belgica* was the second dominant in surface waters and open ponds where salinities were 28.1 to 28.6, equivalent to surrounding waters. In two closed ponds, *Pyramimonas* sp. was the second dominant species. Phytoplankton diversity based on the Shannon-Wiener diversity index was significantly higher in the surface ocean than in closed ponds (t-test, $p < 0.05$).

At the northernmost station (D85-A, 85°25.4'N, 147°28.6'W; see Figure 1) on August 29, 2008, in heavy perennial ice, there was no visible algal layer, but as we traveled south through thinner ice, we saw large masses of algae on ice overturned by the ship (stations D84 at 84°N, 148°45.9'W to D81 at 81°N, 155°17.6'W). After station D81 on September 1, algae were not observed again due to the absence of ice floes. During this transit, we had several opportunities to work on ice floes where we found large masses of algae (Figure 2a; diameter > 10 cm) in the refrozen surface ice of open ponds (stations D83, 83°N, 151°W, and D82, 81°56.0'N, 154°10.4'W). No algae were visible in surface ice of closed ponds.

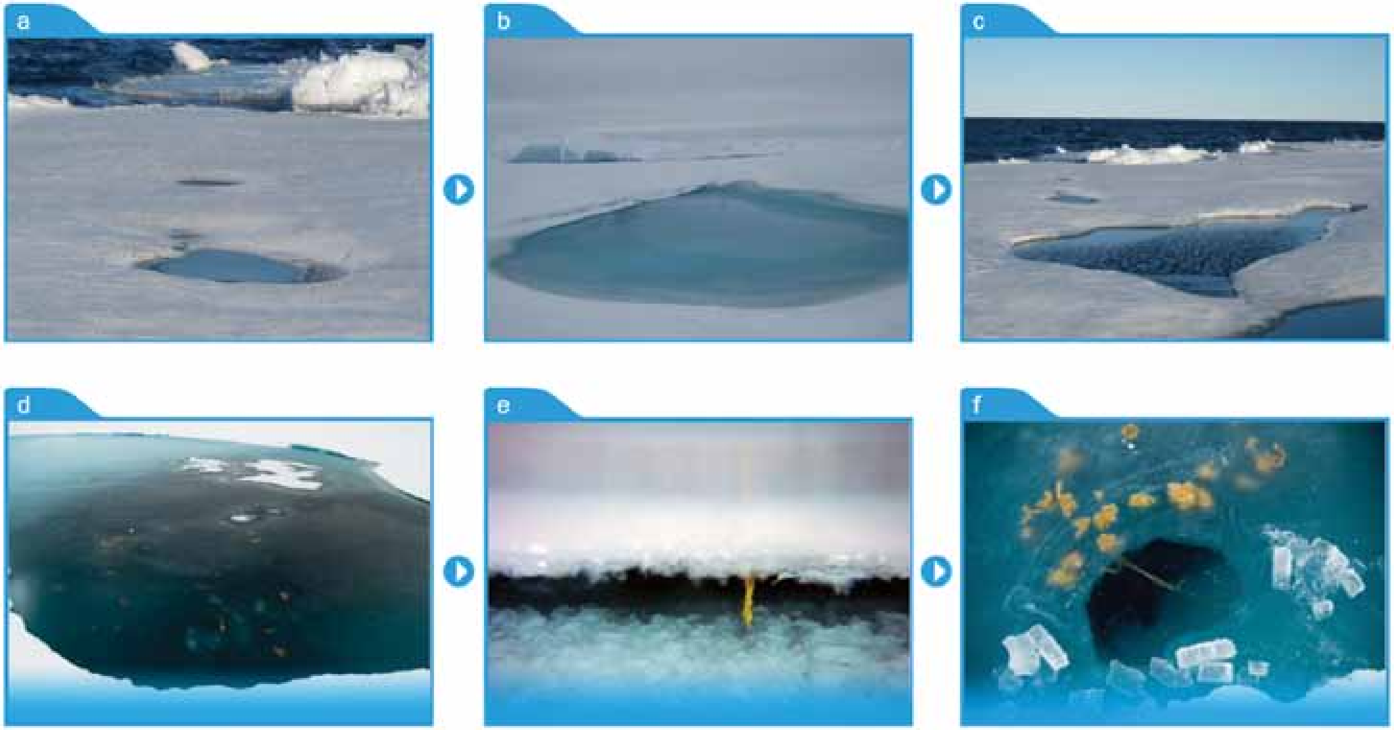

Figure 3. A schematic proposed for the sequence of ice algal development in open ponds based on observations during the cruise: (a) melt pond, (b) deeper melt pond, (c) melt hole, (d) early refreezing with ice algae, (e) under ice detail with ice algae, and (f) frozen surface with large algal colony.

Based on our observations of the different stages of algae in pond ice, we propose the following scenario for algal development in open ponds (Figure 3). As air temperatures decrease in late summer, the surfaces of open ponds refreeze faster than in the open sea due to lower salinity and lack of disturbance from waves. In the early stages of freezing, the surface ice of open ponds (thickness < 1 cm) remains soft (sherbet-like) because of its higher salinity, whereas the surface ice of closed ponds, with much lower salinities, is solid. In this early stage, small yellowish masses (diameter < 1 cm) of ice algae are incorporated in the soft ice of open ponds (Figure 3d). As open pond freezing progresses, the ice becomes harder and thicker (1–2 cm) and the small ice algal masses become larger (diameter = 3–5 cm). The bulk of the ice algae is incorporated in the sea ice with strands (< 5 cm) stretching into the water below (Figure 3e).

A unique characteristic of open ponds is that a second layer of ice forms a partial shelf around the bottom of the pond (Figure 3e,f). This shelf suppresses mixing within the pond, thus promoting further growth of algal mass. As the ice on the pond surface becomes harder and thicker (2–3 cm), algal colonies grow

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Figure 4. Young Arctic cod (*Boreogadus saida*) thrown onto ice by ship transit from stations D84 to D81.

larger (diameter = 8–10 cm) (Figure 3f). At this stage, some strands from the colonies reach lengths of more than 1 m.

Complex mechanisms govern the attachment and formation of algae in sea ice (Melinkov, 1997). Ice layers in contact with the ocean have brine-filled drainage channels containing a diverse diatom flora initially growing in the water below the ice (Melinkov, 1997). The algae grow downward, constrained by the shapes of the drainage channels. Dense accumulations of algal masses form within the ice, with long strands extending into the water under the ice. However, Garrison et al. (1983) found that the algal populations in young sea ice are accreted by a physical mechanism other than growth. They proposed that the harvesting of algal cells by frazil ice crystals rising to the surface to form new sea ice is the most important mechanism during ice formation.

Ice algal accumulations in open ponds were composed of several diatom taxa. Among them, *Melosira arctica* (Figure 2c) was the most abundant, constituting more than 95% of the biomass. *Nitzschia* sp. (Figure 2g) was the second highest, followed by *Navicula* sp. (Figure 2e). *Attheya septentrionalis* (Figure 2b) was second highest in abundance but fourth in biomass due to its small size (< 10 mm).

Primary production in melt ponds, determined by a ^{13}C–^{15}N dual isotope tracer method (Lee and Whitledge, 2005), ranged from 0.01–0.34 mg C m^{-3} h^{-1} (mean ± SD = 0.09 ± 0.11 mg C m^{-3} h^{-1}, n = 11), while that of phytoplankton in the surface waters north of 80°N ranged from 0.02–0.20 mg C m^{-3} h^{-1} (mean ± SD = 0.07 ± 0.06 mg C m^{-3} h^{-1}, n = 6). The values are not statistically different and are within the range for phytoplankton for open waters of the central Arctic (Lee and Whitledge, 2005), which might be evidence for the accumulation theory of Garrison et al. (1983). However, due to accumulated biomass of ice algae, the total photosynthetic carbon uptake rate was up to 20 mg C m^{-3} h^{-1}, a value two to three orders of magnitude higher than those in surrounding surface waters. Based on incubations in different light conditions (from 100% to 1% of surrounding light), the carbon uptake rate of the melt pond ice algae was highest at 100% light and then decreased as the light decreased, indicating light intensity at the pond surface favored, rather than inhibited, carbon uptake rate at that time.

Many small (< 80 mm) fish (see Figure 4), identified as one-year-old Arctic cod (*Boreogadus saida*) (Lowry and Frost, 1981; Craig et al., 1982), were thrown onto the ice by the ship's passage. Arctic cod is a key trophic link from primary producers/zooplankton to higher trophic levels including fish, birds, and mammals (Bradstreet et al., 1986; Gradinger and Bluhm, 2004). It is the most widespread, abundant fish species in the Chukchi and Beaufort Seas (Lowry and Frost, 1981), with reported occurrences to 88°N (Bradstreet et al., 1986). Arctic cod associate with sea ice to avoid predators and to seek food (Bradstreet et al., 1986; Gradinger and Bluhm, 2004). The algal masses and strands under ice in ponds provide a known food source for copepods and amphipods (Bradstreet and Cross, 1982; Werner, 1997; Poltermann, 2001; Budge et al., 2008), which are the main prey of Arctic cod (Lowry and Frost, 1981; Gradinger and Bluhm, 2004).

Climate change has decreased sea ice thickness up to 40%, and further thinning of ice is expected (Vinnikov et al., 1999; Laxon et al., 2003; Rothrock et al., 2003; Perovich and Richter-Menge, 2009). We propose two possible scenarios for melt pond evolution (Figure 5).

During a cold phase, increased perennial ice, thicker than 3–4 m, favors more closed ponds than open ponds because thick ice restricts melting through to the sea during summer. In early fall, due to low salinity and freezing temperatures, these ponds form hard surface ice, which does not support algae. During warm periods, with less than 2 m of ice, ponds melt through to the underlying ocean (Fetterer, 1998) and develop a soft ice cover that hosts algae upon refreezing.

The ecological impact of ice algae in the Arctic has previously been thought to be its early appearance in spring, prior to a pelagic phytoplankton bloom, which serves as a first food source for zooplankton grazers (Michel et al., 1996; Lizotte, 2001; Lee et al., 2008). We show here that ice algal masses accumulating in refrozen open ponds provide an important food supplement for higher trophic animals as the ecosystem enters winter. The open ponds, with typical dimensions on the order of a few meters, also introduce a new length scale to the predator/prey landscape, with unknown consequences (Holling, 1992). Ongoing climate warming and decreasing extent and thickness of sea ice will result in loss of the open pond habitat in lower Arctic regions but may extend this habitat to remaining perennial sea ice in the higher Arctic.

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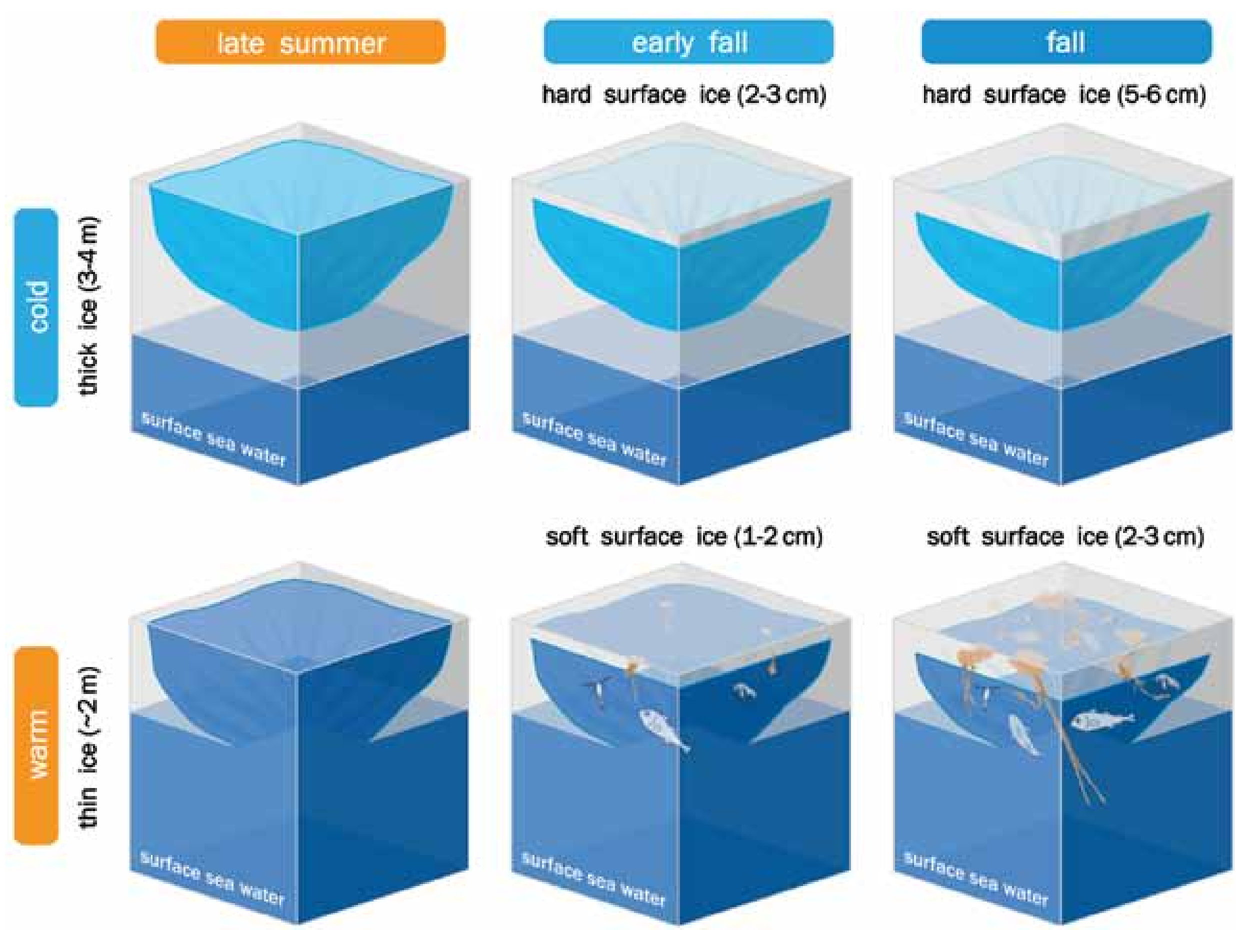

Figure 5. Alternative scenarios for response of pond algae to climate changes in the Arctic.

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