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Bioconditioning of Arctic Waters and Stimulation of Arctic Phytoplankton by Sea Ice Algae: Vulnerability to Increased Light

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ABSTRACT. Arctic sea ice algae produce extracellular organic products, which, as bioconditioners of seawater, may stimulate early summer growth of pelagic, under-sea-ice phytoplankton in low light and low temperature conditions. Sea ice algae are inhibited or decline in numbers if prematurely exposed to high light conditions, thereby reducing their ability to produce bioconditioners. As climate change creates an early reduction or removal of snow and sea ice cover, the result may be a decrease in primary phytoplankton production.

Key words: ice algae; Arctic phytoplankton; bioconditioning; sea ice decline

RÉSUMÉ. Les algues de la glace de mer de l’Arctique produisent des matières organiques extracellulaires. À titre de bioconditionneurs de l’eau de mer, elles peuvent stimuler la croissance estivale précoce de phytoplancton pélagique sous la glace de mer par basse température et faible luminosité. La quantité d’algues de glace de mer est freinée ou diminuée en présence prématurée de forte luminosité, ce qui diminue leur aptitude à produire des bioconditionneurs. Puisque le changement climatique donne lieu à la réduction ou au retrait précoce de la couverture de neige et de glace de mer, cela pourrait entraîner la diminution de la production du phytoplancton primaire.

Mots clés : algues de mer; phytoplancton de l’Arctique; bioconditionnement; diminution de la glace de mer

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INTRODUCTION

As the reduction of Arctic snow and sea ice thickness, extent, and duration accelerates (e.g., Stroeve et al., 2012), scientists have speculated on the consequences for marine parameters, particularly increased light penetration on primary production. A number of papers (e.g., Arrigo, 2013; Codispotti et al., 2013; Lowry et al., 2014) have suggested increased primary production as a result of greater light penetration. But modeling by Tedesco et al. (2012) suggested that seas with less snow and ice cover and increased light penetration would become less productive and shift to oligotrophic conditions. Leu et al. (2011, 2016) suggested sea ice algae might be exposed to detrimentally high irradiance levels with adverse consequences for their physiology and biochemical composition. Kvernvik et al. (2019) found that high radiation caused dysfunctional photophysiology and non-vital cells in ice algae. But Galindo et al. (2017) proposed a “photoprotective” capacity of ice algae in high radiation.

A review of sea ice ecosystems (Arrigo, 2014) considered important linkages between sea ice ecosystems and pelagic habitats, including processes such as trophic interactions and particle export. It does not consider the possibility of bioconditioning (in the sense of Barber and Ryther, 1969, summarized below) by organic excretions of sea ice algae that may stimulate Arctic phytoplankton productivity. The hypothesis that increased light resulting from reduced snow and ice cover may adversely affect bioconditioning and thereby reduce phytoplankton productivity is the focus of this note.

Primary production in Arctic seas is dependent upon both sea ice algae and phytoplankton. While ice algae have been considered a small proportion of total primary production (e.g., Kohlbach et al., 2016), Matrai and Apollonio (2013) found that ice algae may contribute 50% – 90% of total primary production in the central Arctic Ocean and in adjacent seas in the Canadian Arctic archipelago. Consideration of the effects of increased light penetration as a result of snow and ice reduction should therefore include both ice algae and phytoplankton. Leu et al. (2011) and Tremblay et al. (2015) noted the need for more studies on the relationship between ice algae and phytoplankton. Arrigo (2014) suggested that because high ice algal biomasses may absorb a large fraction of light, phytoplankton blooms must wait until the ice algae population has subsided. Based on model analyses, Mortensen et al. (2017) suggested that the timing and magnitude of under-ice phytoplankton is affected by the timing of seeding of ice algae to the plankton population and by the magnitude of nutrient drawdowns from earlier ice algal blooms. Nitrate, reduced by ice algae drawdown in

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Jones Sound in 1962, had been fully restored to maximum annual values by 26 May, a month before the beginning of the phytoplankton increase (Apollonio and Townsend, 2011). Data from Resolute Passage (Lancaster Sound) show a similar pattern of nitrate drawdown and restoration (Matrai and Apollonio, 2013). These data suggest that the initiations of the phytoplankton blooms were not delayed by nitrate deficiency.

Underwood et al. (2019:170) noted, "Melting FYI [first year ice] provides a strong seasonal pulse of dissolved organic matter (DOM) into surface waters; however, the biological impact of this DOM is unknown." It is possible that before bioconditions are right to facilitate an early summer Arctic phytoplankton bloom in sub-zero temperatures and low light, the organic compounds, such as dissolved carbon (DOC) and exopolymeric substances produced and excreted by ice algae must be flushed into underlying sea by melting snow or ice.

DISCUSSION

My hypothesis is that the metabolism and excretions of DOC or DOM controlled and stimulated the timing and magnitude of principal annual phytoplankton blooms that occurred under snow-free but intact sea ice in the 1960s (Apollonio and Matrai, 2011). These blooms happened decades prior to the presently accelerating reductions of snow and ice. I further suggest that the increased light penetration of recent years could be detrimental to the control and stimulation of phytoplankton production.

Summarized here are the observations leading to this suggestion. High levels of chlorophyll (up to 1460 mg m^{-3}) were found in the bottom of intact, snow-covered sea ice (± 2 m thick) in Jones Sound, Arctic Canada, and in very low light levels ($\leq$ 1% of surface values) in the springs and early summers of 1961–63 (Apollonio, 1961, 1965). It bears noting that sea ice chlorophyll has been found in higher light intensities (e.g., Gradinger, 2009), but it is possible that it was the remnants of higher concentrations produced under minimal radiation. The high ratio of chlorophyll *c* to chlorophyll *a* in ice algae (Arrigo, 2014) is an indication and adaptation to blue light (Strickland, 1960; Ehn et al., 2008), which is found under snow and sea ice cover.

Areas of ice in Jones Sound in 1961–63 were artificially cleared of snow (Apollonio, 1961, 1965), with the expectation that increased light intensities would result in increased chlorophyll. In fact, chlorophyll was greatly reduced (by ± 80%–90%) or disappeared, while adjacent snow-covered areas continued to show high levels of chlorophyll (see also Lund-Hansen et al., 2014 for similar results, whether from ice algal emigration or photodamage). Chlorophyll in all Jones Sound ice disappeared when the snow cover melted. Shortly thereafter, within 30 days from ice algae peaks to phytoplankton chlorophyll peaks and under snow-free but intact sea ice conditions, the phytoplankton bloom began and reached its highest annual values each year (Apollonio and Matrai, 2011). This is in contrast to the 45–90 days between peaks of sympagic and pelagic production for the years 1998–2007 noted by Rubao et al. (2013), which suggests that this delay in recent years might be a result of reduced snow and ice cover and reduced bioconditioning.

Mague et al. (1980) showed that the difference between gross and net microalgae photosynthesis is a source of DOC, and that extracellular leakage or excretion of DOC is a natural function of healthy cells. In 1959, phytoplankton algae in coastal waters off northern Ellesmere Island, in Dumbell Bay in the Arctic Ocean, showed substantial and increasing differences between gross and net photosynthesis under increasing light intensities (Apollonio, 1980). Similar results were found in Jones Sound in 1961–63 (Apollonio and Matrai, 2011). It is reasonable to assume that ice algae would show the same photosynthetic reaction to increasing light as does phytoplankton. Smith et al. (1997:71) found "extremely high values" of DOC (up to 49 mg m^{-3}) under 4–8 cm of snow and concluded that the DOC originated from ice algae. Arrigo (2014) reported that the proportion of excreted photosynthate increases under high light stress, as is implied in Apollonio (1980: Fig. 3c, d). Thus, ice algae exposed to much higher light under newly snow-free ice would be expected to excrete DOC. In addition, Ignatiades and Fogg (1973) proposed that organic materials were excreted from microalgae at a stable growth stage and when nutrients were depleted, as was the case in Dumbell Bay and in Jones Sound (Apollonio, 1980: Fig. 2; Apollonio and Matrai, 2011: Fig. 2). Dominant ice algae in the Arctic Basin produce and release extensive DOC believed to be a consequence of nitrate deficiency of algal physiology (Gosselin et al., 1997; Smith et al., 1997). Extracellular release of DOC by ice algae may thus come from excess light stress and nutrient deficiencies, both of which would be characteristics of the end of the normal ice-algal growing season bloom, which is characterized by increased light penetration as snow cover disappears from sea ice.

Barber and Ryther (1969) discussed the bioconditioning role of natural agents such as DOC in enhancing the photosynthesis of microalgae arising from dark, cold depths into the euphotic zone of temperate upwelling regions. They suggested that an effect of the natural agents may be to act as ligands or chelators affecting the availability of essential trace elements such as iron or to suppress the impact of toxic metals such as copper (Sunda, 1994). Barber and Ryther (1969) noted that given equal amounts of light and inorganic nutrients (e.g., nitrate), two samples of seawater may exhibit vastly different abilities to support the growth of marine organisms, depending on their content of trace elements or bioconditioners.

It was inferred from the report of Barber and Ryther (1969) that an analogous situation might be operative in Arctic waters. Organic matter produced by ice algae and released from melting sea ice could act as a bioconditioner for phytoplankton emerging from dark, cold waters under snow cover and sea ice into spring sunlight. Experiments to test this hypothesis were carried out on 20 occasions in May and June 1986 in Jones Sound (Apollonio et al., 2002), wherein added trace metals and chelators (EDTA) and dissolved organic matter from the bottom of the sea ice stimulated phytoplankton photosynthesis by 119% (sea ice DOC), 166% (EDTA), and 184% (trace metals) above untreated phytoplankton sample controls. Bioconditioning of phytoplankton by ice algae was thus clearly implied.

The implication of all these summarized observations is that ice algae are adapted to and flourish naturally under very low light intensities. Upon exposure to high light intensities and nutrient depletions or both, ice algae produce and excrete DOC. As a bioconditioner in sea water, the DOC then stimulates the early summer growth of phytoplankton even in low temperatures and low light intensities. But if ice algae growth is curtailed by early reduction of snow and ice cover and premature and elevated early spring light intensities, then there will be less ice algae, less bioconditioning, and less primary plankton productivity, at least in those Arctic waters, such as the Canadian Basin that have low spring DOC content. Arctic waters that have higher spring DOC content such as the Chukchi Shelf (Mathis et al., 2007) may not exhibit this stimulation of pelagic phytoplankton by sea ice excretions.

DOC excreted or leaked from ice algae might be expected to accumulate at the halocline just below melting sea ice. The appearance of a halocline flora (Apollonio, 1985), which was found at the halocline about 2 m under the ice at two high Arctic locations, began in Dumbell Bay in 1959 under intact but melting ice and persisted for three weeks (Apollonio, 1980). It began in Jones Sound in 1961 and 1963 within 7–15 days of the beginning of snowmelt (Apollonio and Matrai, 2011). Similar halocline flora found in Frobisher Bay, Baffin Island, preceded the main phytoplankton bloom and persisted for several days (McLaren, 1969). These flora may be examples of pelagic algae stimulated by bioconditioning.

The hypothesis that higher light penetration in early spring may inhibit phytoplankton productivity by reducing bioconditioning has implications for much of the Arctic marine food web. Higher trophic levels, particularly the abundant copepod species grazing on both ice algae and phytoplankton, are likely to be sensitive to the timing of the blooms as well as the time lag between them (Rubao et al., 2013; Leu et al., 2015). Even a small mismatch between phytoplankton blooms and zooplankton reproductive cycles can have consequences for the entire lipid-driven Arctic marine ecosystem (Hill et al., 2018). Further testing of the bioconditioning hypothesis would seem to be of value.

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