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Draft: Sea ice microbiology summary for MOSAiC science planners

This document is motivated by the excellent discussion generated during the MOSAiC science planning workshop held in Boulder from June 27-29 to help guide future planning efforts. The document describes in broad terms the state of understanding of sea ice microbial ecology as it pertains to MOSAiC and identifies several questions of high relevance to the overarching objectives of MOSAiC. A brief discussion of methods is included to serve as a rough guide for future science planning only. This document does not attempt to be all-inclusive, and many processes of relevance to MOSAiC are not covered here. In particular the microbiology of melt ponds is not covered. Ideally these will be added by other authors in later versions. Similarly citations have been added to suggest background reading on key concepts, but many relevant works have not been included.

Introduction

A central theme of the MOSAiC concept is the changing Arctic, best illustrated by the shift from a multiyear to a seasonal ice regime. Marine biological communities in the Arctic are structured around the presence of sea ice, whether seasonal or continuous, and major shifts to the composition, structure, and dynamics of these communities are expected in response to changing ice conditions. The biological, chemical, and physical elements of the Arctic ecosystem are tightly coupled through feedbacks, thus changes to the biological community will drive further change in the regional and global climate systems. Anticipating these changes requires a concerted modeling effort based on a comprehensive understanding of these feedbacks. Currently this effort is limited by the lack of knowledge regarding the structure, function, and dynamics of biological – and particularly microbial – processes in the marine high Arctic. MOSAiC represents a unique opportunity to fill this knowledge gap through interdisciplinary research across at least one annual cycle, covering seasons and geographic regions that are particularly understudied from a biological standpoint.

Sea ice, derived from seawater containing Bacteria, Archaea, and phytoplankton, always contains some number of these microorganisms as a result of scavenging by frazil ice (Riedel et al. 2007; Gradinger and Ikävalko 1998; Garrison et al. 1983) and the circulation of seawater through consolidated ice (Weissenberger and Grossmann 1998). Low biomass Arctic sea ice might contain 10⁴ bacteria (here meaning members of the domains Bacteria and Archaea) per milliliter of bulk melt, and a concentration of chlorophyll A below the level of detection using standard methods (personal observation). High biomass Arctic sea ice can contain in excess of 10⁷ bacteria per milliliter (Maranger et al. 1994; Smith et al. 1989), and over a milligram of chlorophyll A per liter (Smith et al. 1989). This huge range in biomass is a result of the high heterogeneity in sea ice, between seasons and across large and small geographic areas. The availability of nutrients (C, N, P, Si, Fe) and light are the main drivers of primary production, and the availability of organic carbon and physical transport are the main drivers of bacterial abundance.

In general the biomass of Arctic sea ice follows predictable temporal patterns. Fall blooms can occur in the water column and the chlorophyll concentration of young ice is significantly higher than in older ice

present during feeze up (Meiners et al. 2003). Primary production however, is low in young fall sea ice relative to spring ice due to the relatively low biomass in the starting waters and the fast growth of young ice under a cold atmosphere. Studies on the microbiology of young sea ice and winter first year ice are sparse. There is some evidence for a burst of microbial activity during ice formation (Grossmann and Dieckmann 1994)and viral counts, which must be sustained by active microbes, are high in young ice (Collins and Deming 2012). Despite this initial activity bacterial abundance is known to decrease throughout the winter. A time series of microbial community composition through winter suggests that this decrease is non-selective, affecting the major clades of marine bacteria approximately equally (Collins et al. 2010). Exopolymers (EPS), a hydrated gel of varying composition produced by ice algae and bacteria entrained within forming ice, is thought to play a key role by imparting a general survival mechanism on the gross microbial community (Collins et al. 2010).

Ice algal growth occurs very soon after light returns in late winter, while the ice is still growing (Mikkelsen et al. 2008; Maranger et al. 1994). At the ice-water interface temperatures are constant throughout the growth season and do not limit ice algal production in late winter. Bacterial production responds quickly to late winter primary production with a rapid increase in the number of bacterial cells (Maranger et al. 1994). This new bacterial community is phylogenetically and ecologically distinct from that present during ice formation. In general it is more psychrophilic and copiotrophic than the seawater bacterial community, and its members may have unique adaptations specific to the sea ice environment. These include the production of ice-affine EPS, ice binding proteins, and compatible solutes which help in the resistance to osmotic stress (Ewert and Deming 2011; Deming 2010; Marx et al. 2009; Methe et al. 2005). The ice algal bloom ceases when the sea ice melts or nutrients are depleted. The replenishment of nutrients into warm, porous first year ice can drive a second ice algal bloom late in the season.

Connections to MOSAiC

The close coupling of the biological, chemical, and physical elements of the Arctic ecosystem as well as the water column, sea ice, and the atmosphere, requires that key biological questions be addressed in order to fully investigate processes of interest to the MOSAiC campaign. The overarching question that must be addressed is how will microbial communities change in response to a changing climate? The implications of this can be summarized with the subordinate question: what is the impact of the observed or anticipated change on chemical and physical processes in the climate system? This question can be subdivided into three broad, overlapping areas of investigation; the carbon cycle, aerosol production, and biological controls on ice physics.

Carbon cycle

Although ice algal production is a smaller CO_2 sink in the Arctic Ocean than in the Southern Ocean it can nonetheless account for a significant fraction of CO_2 uptake there (Horner and Schrader 1982) [but see Mikkelsen et al. (2008)]. Organic carbon that is not remineralized by sea ice bacteria is exported to the water column at a rate determined by its composition (Juhl et al. 2011) and the dynamics of the melt. In Arctic sea ice algal primary production is though the greatly exceed bacterial consumption (Smith et al. 1989), and particle export in Arctic waters is generally higher than in the lower latitudes (Buesseler 1998). Once in the water column this carbon can be remineralized, exported to the benthos, or exported to the deep ocean depending on location, particle size, and microbial community composition in the water column and on the particle itself (Kellogg et al. 2011; Kellogg and Deming 2009; Moran et al. 1997). On the continental shelf sea ice derived organic carbon supports the growth of a rich and diverse benthos (McMahon et al. 2006). Over the deep Arctic basins sea ice derived POC can be sequestered below the mixed layer. In either location sea ice derived POC consumed in the water column fuels bacterial production in a process known as the microbial loop (Azam et al. 1983). The microbial loop counters sequestration, by expanding the pool of organic carbon contained within the water column and transferring it to higher trophic levels. At each stage in this transfer some of the carbon is remineralized. Numerous factors, most of which are poorly constrained, determine the rate of primary production and the fate of sea ice derived organic material. These factors include the abundance and renewal of nutrients by transport and *in-situ* regeneration, the availability of light, the size, composition, and density of sea ice derived POC, the rate of bacterial production and respiration in sea ice and the water column, and grazing rates at the ice-water interface and in the water column.

An additional element of the polar carbon cycle is the inorganic carbon pump (Rysgaard et al. 2007). When temperatures in sea ice are sufficiently cold the calcium carbonate mineral ikaite may precipitate. It has been suggested that brine rejection can transport this precipitate to the water column. As in the case of POC, carbon contained in ikaite crystals transported below the mixed layer is effectively sequestered away from short term exchange with the atmosphere. Although not explicitly a biological process the inorganic pump may be mediated by biological factors including the presence of EPS. In other environments EPS has been shown to influence the precipitation of calcium carbonate (Knowles and Castenholz 2008). EPS also has the potential to diminish the inorganic pump by reducing the amount of salt that is rejected during ice formation (Krembs et al. 2011).

Aerosol production

The source of cloud condensating nuclei (CCN) for the expansive stratus deck clouds observed in the Arctic is unknown. Ice algae and the sea ice microbial community may be the source of some of these aerosols (Andreae and Crutzen 1997), although no direct investigations into this have been made so far. The most obvious potential biogenic CCN from sea ice may be DMS (Levasseur et al. 1994). DMS is produced by algae and bacteria in an enzymatic process that cleaves the common algal osmolyte DMSP (Moran et al. 2012). Although DMSP and DMS have been measured in sea ice (Turner et al. 1995; Levasseur et al. 1994; Trevena and Jones 2006; Trevena et al. 2000; Tison et al. 2010; Delille et al. 2007), these investigations have been limited to spring and summertime sea ice and no investigation has attempted to identify the microbial community responsible for DMS production.

Similarly other biogenic aerosol sources in sea ice have not been targeted for detailed study. Leck and Bigg (2005) identified similar particles (EPS, salt, and diatom frustules) in the sea surface microlayer of open leads and the lower boundary layer. Given the high productivity of the surrounding ice relative to the lead waters it is likely that some of this material originated from the ice algal community. In addition the unique environmental stresses of sea ice, including high salinity, high UV light, and a high

level of oxygen stress suggest a physiological stress response in ice algae and bacteria that may include aerosol production, including DMS (Hefu and Kirst 1997). Low molecular weight products produced by the reaction of algal derived HIO with DOC are another example of stress-induced aerosol nucleators that may be significant in sea ice (Hill and Manley 2009). Although there is not an explicit relationship to aerosol production, ice algae are additionally known to produce organohalides, including bromoform (Sturges et al. 1992) which may play a role in Arctic tropospheric ozone depletion.

Biological controls on ice physics

It is tempting to think of sea ice biology as a separate system superimposed on the physical structure of sea ice. Biology can be more accurately viewed as an inherent part of sea ice, imparting specific properties to the ice. This is particularly significant as many laboratory studies are conducted on ices that contain only trace levels of organics. Parameterizations derived from such studies may not accurately represent natural processes.

There are four known mechanisms by which biology can influence sea ice physics. As stated earlier many sea ice microorganisms produce EPS as part of a general defense against environmental stress, particularly high salinity and low temperature (Krembs et al. 2002). A hydrated gel, EPS discourages the interaction of water molecules and thus the formation of ice crystals, depressing the freezing point of sea ice brines. Through mechanisms that are not yet clear, EPS also appears to dramatically alter the morphology of brine channels and pore spaces, enhancing their connectivity at low temperatures (Krembs et al. 2011). This physical alteration has important implications for gas flux, brine and nutrient transport, and shear strength.

A strategy for investigation

Biological communities and processes show extreme variation across an annual cycle and can change quickly, within days or even hours. MOSAiC represents a unique opportunity to investigate these processes at fine temporal resolution across the annual cycle. Since only a few biological parameters can be measured by remote sensing this kind of coverage is not usually available for Arctic investigations. By serving as an interdisciplinary research platform MOSAiC also represents an opportunity to develop more integrated biological, chemical, and physical studies. For example measurements by a chemistry group of a key, putatively biological compound in the atmosphere can be closely coordinated with a biology team monitoring sea ice community composition and metabolic function, and with a physics team evaluating sea ice microstructure and large-scale sea ice coverage. This sort of investigation could identify not only the source of the compound but the reason for its production, allowing a prediction of its spatial and temporal distribution in the future.

Given the sparsity of even basic biological information for sea ice in the high Arctic an emphasis should be placed on establishing basic biological parameters including nutrients, chlorophyll A, primary productivity, EPS concentration, ice algal counts, bacterial cell counts, and microbial (algal and bacterial) community composition. The techniques for these measurements are well vetted, inexpensive, and not time intensive. There is a limit to these methods however, and the opportunity should not be lost to more deeply probe specific questions of direct relevance to the MOSAiC science objectives. For the most part these investigations seek to tie the composition of the microbial community to specific physical or biogeochemical processes, a combination that allows for predication if sufficient data can be collected to anticipate how the microbial community will change in response to changing conditions. The impact of biology on a chemical or physical process is a result of metabolic activity, which can be measured through the application of various molecular techniques (transcriptomics and proteomics) and tracer experiments (radioactive or stable isotopes, fluorescent labels, etc.). The science objectives of MOSAiC are in part predictive, thus an additional biological parameter if interest is metabolic potential reflects the ability of a community or organism to undertake a metabolism in response to changing conditions (e.g. increasing salinity during ice formation). Metabolic potential can be assessed using metagenomics or inferred from community composition.

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