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Methane excess production in oxygen-rich polar water and a model of cellular conditions for this paradox

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A B S T R A C T

Summer sea ice cover in the Arctic Ocean has undergone a reduction in the last decade exposing the sea surface to unforeseen environmental changes. Melting sea ice increases water stratification and induces nutrient limitation, which is also known to play a crucial role in methane formation in oxygenated surface water. We report on an excess of methane in the marginal ice zone in the western Fram Strait. Our study is based on measurements of oxygen, methane, DMSP, nitrate and phosphate concentrations as well as on phytoplankton composition and light transmission, conducted along the 79°N oceanographic transect, in the western part of the Fram Strait and in Northeast Water Polynya region off Greenland. Between the eastern Fram Strait, where Atlantic water enters from the south and the western Fram Strait, where Polar water enters from the north, different nutrient limitations occurred and consequently different bloom conditions were established. Ongoing sea ice melting enhances the environmental differences between both water masses and initiates regenerated production in the western Fram Strait. We show that in this region methane is in situ produced while DMSP (dimethylsulfoniopropionate) released from sea ice may serve as a precursor for the methane formation. The methane production occured despite high oxygen concentrations in this water masses. As the metabolic activity (respiration) of unicellular organisms explains the presence of anaerobic conditions in the cellular environment we present a theoretical model which explains the maintenance of anaerobic conditions for methane formation inside bacterial cells, despite enhanced oxygen concentrations in the environment.

1. Introduction

The Arctic Ocean is one of the regions in the world where climate change is most pronounced. Increased summer melting is considered to amplify biological production, due to the shift from an ice-covered to an open water Arctic Ocean (Arrigo et al., 2008). However, increasing water stratification during sea ice melting is likely to limit nutrient availability in near-surface water, which in turn hampers the enhancement of primary production (Sakshaug, 2003). A characteristic feature of the Arctic Ocean is the distinct post-bloom nutrient limitation found in the Atlantic-dominated and Pacific-dominated sectors. The former is nitrate and phosphate co-limited while the latter is mostly nitrate-limited, which results in an excess of phosphate (Yamamoto-Kawai et al., 2006). The role of nutrient limitation as a possible regulator of methane production in surface water has recently been investigated (Karl et al., 2008; Damm et al., 2010) while methane excess in ocean surface water relative to the atmospheric equilibrium has been studied for more than three decades (Scranton and Brewer, 1977). Different nutrient limitations can stimulate the growth of specific members of the bacterioplankton assemblage with consequences not only for the turnover of organic matter, biogeochemical cycling of carbon but also for producing climate relevant traces gases (Thingstad et al., 2008). Methanogenic archaea have been identified to have the ability to metabolize dimethylsulfoniopropionate (DMSP) and its degradation products by producing methane (Kiene et al., 1986; Oremland, 1989). Bacteria may also be methylotrophs, using a series of methylated compounds, including methylated sulphur compounds such as (DMSP) and dimethylsulfide (DMS) (Neufeld et al., 2008). This metabolism is referred as methylotrophic methanogenesis (Sowers and Ferry, 1983). DMSP is produced by marine phytoplankton and when metabolized, is a primary carbon source for heterotrophic bacteria (Kiene et al., 2000). DMSP is the precursor of dimethylsulfide (DMS) or methanethiol. DMS partly escapes to the atmosphere where it is the most important climate-cooling gas, counterbalancing the effect of greenhouse gases (Charlson et al.,

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1987). Methanethiol is a key reactive intermediate utilized as sulphur and carbon sources for biosynthesis or energy generation (Kiene et al., 2000). In anaerobic environments methanethiol acts also as precursor for methane production (Tallant and Krycki, 1997). A switch in the utilization of phosphate and DMSP degradation products in nitrate-limited Pacific-derived water is also considered to produce methane in aerobic environments (Damm et al., 2010). Methane excess in surface water has also been detected under multi-year sea ice and in the marginal ice zone along the North-West Passage, i.e. the region from the southwest edge of Greenland through the Baffin Bay to the Beaufort Sea (Kitidis, 2010).

Here we present data from Fram Strait where Atlantic water and Pacific-derived surface water bodies occur adjacent to each other. We show that ongoing sea ice melting has amplified the environmental differences between both water masses and we postulate that methane production occurs during regenerated production in Pacific-derived water despite an apparent oxygen excess. Methanogenesis in an aerobic environment is called the methane paradox as this process requires strictly anaerobic conditions. However, methane concentrations above the equilibrium concentration with the atmosphere are well known from the ventilated (i.e. oxic) open ocean surface layer (Reeburgh, 2007). Hence we determine the maximum oxygen concentration in seawater, which allows anaerobic processes to take place inside bacterial cells. Since this aspect is fundamentally important we provide a detailed model description to show and explain why and how it can potentially occur.

2. Study area

In Fram Strait, the surface water (<60 m) in general comprises two main water masses, which flow in opposite directions (Rudels et al., 2000). The warm (up to 4 °C) and saline (up to 34.8) Atlantic water (AW) branch flows northward east of about 4°W (Fig. 1). Further west, colder and less saline polar surface water (PSW) occupies the upper water column. In PSW, a portion is Pacific-derived water that varies inter-annually between more than 90% (Jones et al., 2003) to almost zero (Falck et al., 2005). In 2008, this portion had attained just over 60% (Dodd et al., 2012). The salinity of PSW was homogeneous at about 33 indicating unchanged conditions since winter convection, except for some near-surface warming and freshening by melt water (Fig. 2A). This distribution has been described previously for the end of the summer season (Budeus et al., 1997).

The recurrent Northeast Water Polynya (NEWP) is localized in the region of the PSW (Budeus and Schneider, 1995). Polynyas are less light-limited due to early opening of the ice cover compared to adjacent regions, and primary production starts earlier in the year. In the NEWP, nutrient-limited conditions occur at the end of July (Wallace et al., 1995; Kattner and Budeus, 1997). In the summer of 2008, ice fields drifting from the north partly covered the study area (Fig. 1). Hence stations in the middle of transect were located in partly ice-covered AW and PSW and the more eastern and western stations in ice-free AW and PSW, respectively.

3. Sampling and methods

In summer 2008, water sampling for measuring methane, oxygen, nutrients and DMSP was carried out in Fram Strait during the cruise ARK-XXIII/2 with RV "Polarstern", roughly along the 79°N transect and spread on the Greenland sea shelf (Fig. 1). Further oceanographic and biological data were taken in the surface water to 200 m depths. The main sampling sites were along the hydrographic transect and in an opened ice lead on the Greenland shelf where the sampling was repeated twice, first on July 23rd (time 1)

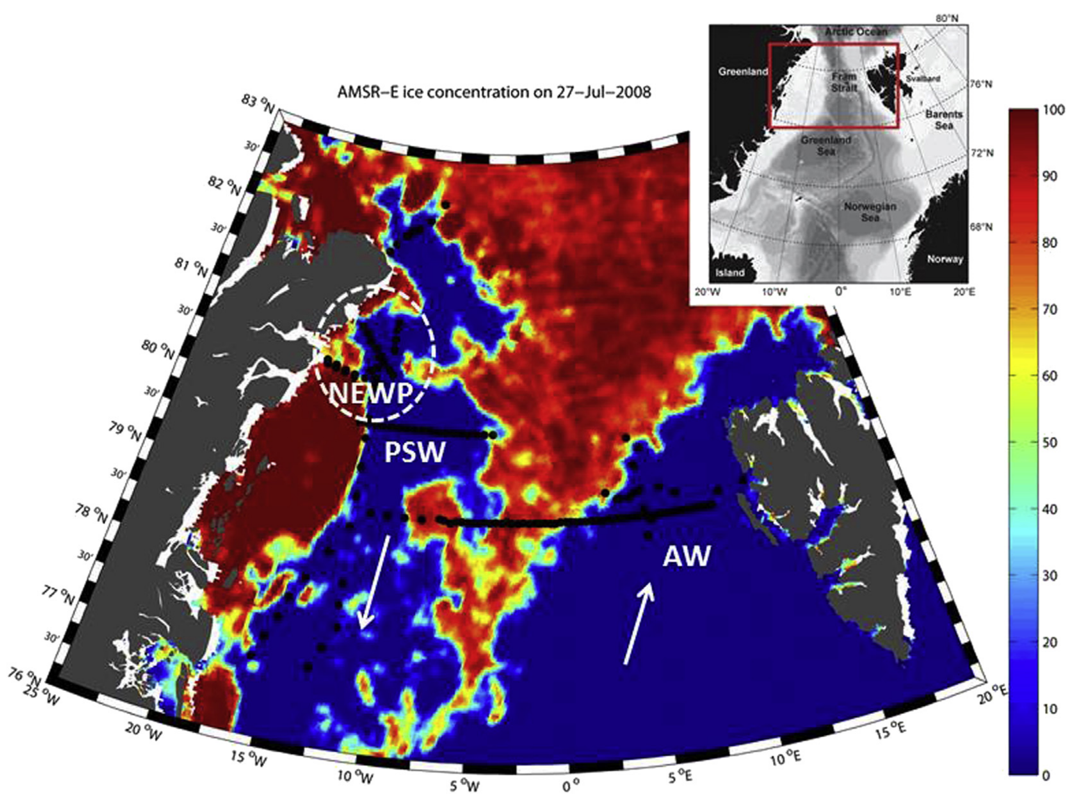

Fig. 1. Map of the Fram Strait with ice coverage (AMSR-E data see Spreen et al., 2008). Ice coverage is shown by colours from red to blue, (100%, 0%) meaning a closed ice cover and open water, respectively. Black circles indicate stations localized in AW (Atlantic water) in PSW (Polar surface water) and NEWP (Northeast Water Polynya).