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Response of marine bacterioplankton to a massive under-ice phytoplankton bloom in the Chukchi Sea (Western Arctic Ocean)

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ABSTRACT

The activity of heterotrophic bacterioplankton and their response to changes in primary production in the Arctic Ocean is essential to understand biogenic carbon flows in the area. In this study, we explored the patterns of bacterial abundance (BA) and bacterial production (BP) in waters coinciding with a massive under-ice phytoplankton bloom in the Chukchi Sea in summer 2011, where chlorophyll *a* (chl *a*) concentrations were up to 38.9 mg m^{-3}. Contrary to our expectations, BA and BP did not show their highest values coinciding with the bloom. In fact, bacterial biomass was only 3.5% of phytoplankton biomass. Similarly, average DOC values were similar inside (average 57.2 ± 3.1 μM) and outside (average 64.3 ± 4.8 μM) the bloom patch. Regression analyses showed relatively weak couplings, in terms of slope values, between chl *a* or primary production and BA or BP. Multiple regression analyses indicated that both temperature and chl *a* explained BA and BP variability in the Chukchi Sea. This temperature dependence was confirmed experimentally, as higher incubation temperatures (6.6 °C vs. 2.2 °C) enhanced BA and BP, with Q_{10} values of BP up to 20.0. Together, these results indicate that low temperatures in conjunction with low dissolved organic matter release can preclude bacteria to efficiently process a higher proportion of carbon fixed by phytoplankton, with further consequences on the carbon cycling in the area.

1. Introduction

The Arctic Ocean is experiencing significant impacts as a result of global climate change. Among them is a reduction in summer sea ice extent (Serreze et al., 2007) and thickness (Kwok and Rothrock, 2009; Perovich and Richter-Menge, 2009), and shifts in atmospheric circulation patterns (Overland et al., 2012). Phytoplankton blooms in the Arctic Ocean are thought to be restricted to ice-free waters. Hence, sea-ice dynamics such as the extent of summer ice minimum and the prevalence of first-year ice over multiyear ice are especially important to the primary production regime of the Arctic Ocean ecosystem (Arrigo and van Dijken, 2011).

In aquatic ecosystems, bacterioplankton are known to be tightly dependent on organic matter derived from phytoplankton (Cole et al., 1988). A substantial part of carbon fixed during primary production is channeled through the microbial loop, and is either converted into bacterial biomass (bacterial production) or respired to carbon dioxide (Carlson et al., 2007; Kirchman, 2008). The balance between bacterial production and respiration gives us information about the fate of the newly produced organic carbon in the system (exported vs. mineralized). Studying how bacterioplankton respond to phytoplankton blooms can thus have important ramifications for the fate of newly produced organic carbon.

The bacterioplankton dependence on organic matter derived from phytoplanktonic source has traditionally led to co-variations (i.e. linear relationships) between primary production and bacterial production, or between chlorophyll *a* and bacterial biomass (Cole et al., 1988; Gasol and Duarte, 2000). These relationships, however, are variable among aquatic ecosystems, being generally

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weaker in open ocean systems, and particularly weak in high-latitude ecosystems (Bird and Karl, 1999; Duarte et al., 2005). This may be due to the low temperatures that decrease the ability of bacteria to assimilate substrates (Pomeroy and Wiebe, 2001; Stewart and Fritsen, 2004) that frequently leads to a lagged response of bacterioplankton to organic matter inputs (Billen and Becquevort, 1991). Other studies explain this weak coupling by high grazing pressure on bacteria (Duarte et al., 2005).

In early summer (June–July) 2011, a massive phytoplankton bloom was encountered beneath fully consolidated pack ice in the Chukchi Sea (Western Arctic Ocean). That bloom showed peaks of particulate organic carbon biomass of 32 g C m^{-2}, with carbon fixation rates of 1.2–2.0 mg C mg^{-1}chlorophyll *a* (Arrigo et al., 2012). The existence of this bloom allowed us to look at patterns of bacterial abundance (BA) and bacterial production (BP) in an effort to explore phytoplankton–bacterioplankton coupling under these particular conditions.

We also compared the phytoplankton–bacterioplankton coupling in the under-ice bloom with that observed in other areas of the Chukchi Sea and in high latitude marine ecosystems. Finally, we experimentally investigated the bacterial response to organic matter additions coming from the phytoplankton bloom versus dissolved organic matter coming from terrestrially influenced waters under different temperature regimes.

2. Materials and methods

2.1. Study site and sampling strategy

The phytoplankton bloom was observed beneath the annual sea ice on the Chukchi continental shelf. This area was sampled during the 2011 Impacts of Climate on EcoSystems and Chemistry of the Arctic Pacific Environment (ICESCAPE) cruise to the Pacific sector of the Arctic Ocean in late spring and early summer. Under-ice bloom waters were sampled from the 4 to the 8 July 2011. Two transects were performed from open water into the ice pack and covered station numbers 41–73 (stations with bacteria measurements are shown in Fig. 1). In this study, we report BA and BP variations in these two transects, differentiating between stations outside the bloom patch (ice-free waters, stations 41–48 and 64–73) and stations inside the bloom patch (ice-covered stations from 54 to 64). Further information about the bloom characteristics can be found in Arrigo et al. (2014). Water samples were collected from surface to bottom waters (40–150 m deep) using 30-L Niskin bottles mounted on a rosette with a conductivity–temperature–depth (CTD) sensor (Sea-Bird Electronics). Fixed sampled depths were 5, 10, 25, 50, 75, 100, 200 m or 5 m above the bottom if shallower waters. If there were deep chlorophyll maxima, they were also sampled.

2.2. Chemical and biological analyses

2.2.1. Bacterial abundance (BA)

Heterotrophic prokaryotes, including bacteria and archaea, are abbreviated throughout the manuscript as “bacteria”. Bacterial cells were counted on board by flow cytometry using an Accuri C6 (Becton Dickinson, San Jose, CA) equipped with a 488-nm laser. Samples were fixed with glutaraldehyde (0.25% final concentration) and stored at −80 °C until processing (within few days after collection). Samples were then thawed and SYBR Green-I was added at a final dilution of 1:10,000. Samples were incubated in the dark for 15 min before analysis. Bacterial cells were identified on a plot of green fluorescence (515–545 nm) versus right-angle light scatter (SSC), using the green fluorescence as threshold parameter. High Nucleic Acid (HNA) and low Nucleic Acid (LNA) bacteria were discriminated according to their green fluorescence and counted separately (Marie et al., 1997). Bacterial abundance (BA) was converted into biomass (mg m^{-3}) using a standard conversion factor of 15.2 fg C $cell^{-1}$ (Ortega-Retuerta et al., 2012b).

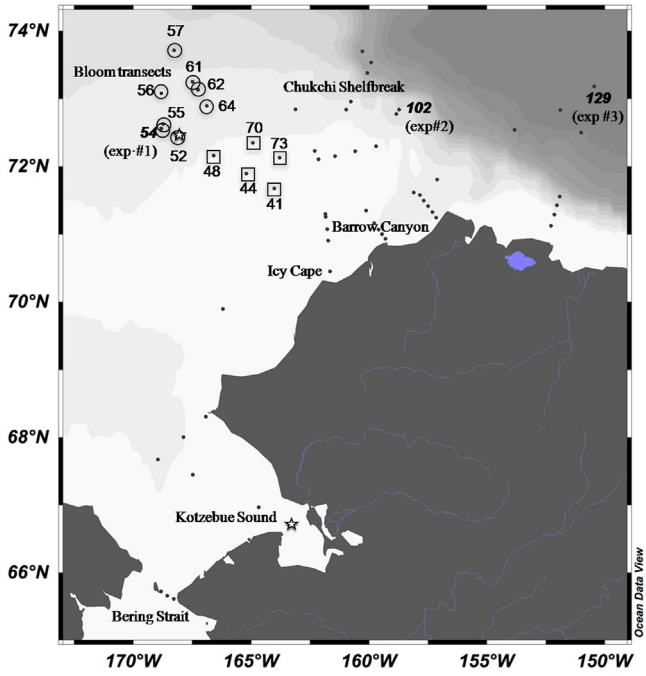

Fig. 1. Map of sampling stations during ICESCAPE 2011. Stations belonging to the bloom transects are marked by either squares (ice-free stations outside the bloom patch) or circles (ice-covered stations inside the bloom patch). Stations where the bioassays were performed are also numbered in bold. Stations where the organic matter sources were taken are marked with a star. The rest of the stations sampled during ICESCAPE 2011 (single black dots), used for the multiple regression analysis, are also shown.

2.2.2. Bacterial production (BP)

Bacterial production (BP) was measured by ^{3}H-leucine incorporation (Smith and Azam, 1992). Samples (1.5 mL in triplicate plus one killed control) were added to sterile microcentrifuge tubes, containing 20–30 nM [4,5-^{3}H]-leucine. This concentration was sufficient to saturate bacterial leucine uptake (data not shown). Incorporation rates were measured after 2-h incubations at in situ temperature, and incubations were stopped by the addition of trichloroacetic acid (5% final concentration). Mean dpm in samples were on average 4.4 of mean dpm's in blanks. We did not detect any contamination in the leucine batches. However, the BP data will only be discussed in terms of variability rather than absolute numbers because blanks showed relatively high values (sometimes above 1000 dpm). Leucine incorporation rates were converted to carbon production using the conversion factor of 1.5 kg C produced per mole of leucine incorporated (Kirchman, 1993), considering no isotope dilution.

2.2.3. Chlorophyll a (chl a)

Samples for chl *a* analysis were filtered onto 25-mm Whatman GF/F filters (nominal pore size 0.7 μm) placed in 5 mL of 90% acetone, and extracted in the dark at 3 °C for 24 h. Chl *a* was measured fluorometrically using a Turner Fluorometer 10-AU (Turner Designs, Inc.). Phytoplankton biomass (mg C m^{-3}) was calculated using the carbon to chl *a* ratio of 88.5 g:g (Arrigo et al., 2008).

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