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Response of under-ice prokaryotes to experimental sea-ice DOM enrichment

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ABSTRACT: Marine dissolved organic matter (DOM) plays a key role in the global carbon cycle. In this study we show experimentally that Arctic sea-ice DOM can stimulate prokaryotic activity when added to surface waters. Time-series and dose-response enrichment microcosm experiments were conducted, in which first-year, sea-ice DOM was added to surface waters from Resolute Passage, Canadian Arctic Archipelago. Sea-ice DOM concentrations in this productive region averaged nearly 2000 µmol l^{-1} in May 2011 and 2012. The abundance, activity (high [HNA] versus low [LNA] nucleic acid cells) and apparent size of surface water prokaryotes were quantified along with dissolved organic carbon (DOC) and dissolved nitrogen (DN) concentrations during the experiments. Following a 4 d lag, prokaryotic abundance increased more than 30× in the time-series enrichment experiment and the proportion of HNA cells increased from 60 to >99% of total prokaryote abundance. DOM dose-response experiments conducted in 2011 and 2012 yielded prokaryotic growth rate estimates between 0.35 and 0.67 d^{-1} in response to the addition of sea-ice DOM. On average, 20% of the sea-ice DOC pool was utilized by the surface water prokaryotes and the observed increase in cell abundance and individual cell size indicated a release from carbon limitation of initial *in situ* conditions. Prokaryotic growth yields ranged from 0.02 to 0.07 cell µmol l^{-1} DOC and 0.01 to 0.06 cell µmol l^{-1} DN and experimental conditions shifted from net autotrophic to net heterotrophic. Heterotrophic activity at the ice–water boundary layer upon the release of labile first-year ice DOM is likely to impact current and future carbon flux estimates as seasonal ice becomes the predominant ice type in the Arctic.

KEY WORDS: Dissolved organic carbon · Prokaryotes · Sea ice · Melt · Heterotrophy · Arctic

INTRODUCTION

Dissolved organic carbon (DOC) represents the largest organic carbon pool in the ocean, thereby having a key role in the global carbon cycle. Increasing global temperatures and CO_2 levels are expected to impact microbial control of DOC fluxes and composition in the ocean, particularly in the Arctic where such changes are rapidly occurring (Kirchman et al. 2009, Boras et al. 2010, Sala et al. 2010, de Kluijver et al. 2013). It is estimated that heterotrophic prokaryotes can process between 10% and 50% of the carbon fixed by photosynthesis in marine systems (Azam et al. 1983, Anderson & Ducklow 2001, Robinson 2008) through ectoenzymatic hydrolysis, respiration, and production of new bacterial biomass (Grossart & Ploug 2001, Grossart et al. 2007). In the Arctic Ocean, phytoplankton is estimated to supply approximately 66 Tg C yr^{-1} of dissolved organic matter with Arctic rivers being a key additional source of labile and refractory DOC (Amon 2004, Raymond et al. 2007). These major sources of DOC differ in their composition and reactivity with respect to microbial communities.

Arctic bacterial groups are selective with respect to the use of DOC substrates. Variations in assimilation occur between locations and seasons (Nikrad et al. 2012), largely explained by differences in the abun-

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dance of different bacterial groups (Elifantz et al. 2007). In general, winter pelagic (i.e. under-ice) bacterial communities are characterized by low abundances (e.g. 10^4 cells ml^{-1}) and activity, whereas maximum bacterial biomass and growth occur during the summer when chlorophyll *a* (chl *a*) concentrations also increase in the Arctic (Garneau et al. 2008, Nguyen et al. 2012). In sea ice, bacterial communities exist in newly formed sea ice and persist throughout the winter (Riedel et al. 2007a, Collins et al. 2010, Nguyen & Maranger 2011). In first-year ice, total bacterial abundances and individual cell size can increase in spring, together with bottom-ice DOC concentrations and ice algal biomass (Riedel et al. 2007b).

Temperature may be expected to exert strong control over bacterial growth in the cold Arctic waters. However, the growth response of Arctic bacteria to temperature shifts is similar to bacterial responses at lower latitudes (Kirchman et al. 2005) and low temperatures within the sea ice do not inhibit bacterial activity or growth (Junge et al. 2004, Riedel et al. 2007a, Collins et al. 2008). DOC, in combination with inorganic nutrients to support primary production, has been identified as the key driver of prokaryote growth in the Arctic Ocean (Thingstad et al. 2008, Kirchman et al. 2009). DOC fluxes associated with the spring/summer phytoplankton bloom and the subsequent microbial respiration and biomass production are thus important to consider for Arctic carbon budgets. Another input of DOC to Arctic surface waters occurs during ice melt. Sea-ice DOC concentrations can be orders of magnitude higher than in the surface waters (Riedel et al. 2008, Song et al. 2011), yet the fate of this DOC flux to surface waters during melt and its impact on surface water prokaryote communities are not known.

The transitional ice melt period could potentially enhance surface water microbial activity due to the release of the large sea-ice dissolved organic matter (DOM) pool, especially since sea-ice DOM could be initially retained within a thin surface layer near the ice–water interface at the time of ice melt (Eicken et al. 2002, Hop et al. 2011). This study investigated the impact of sea-ice DOM on natural communities of surface water prokaryotes (i.e. bacteria and Archaea) in the High Arctic. The study area, in the eastern Canadian Arctic archipelago, is a highly productive shelf region (Michel et al. 2006) and supports the highest ice algal biomass reported in the Arctic (Arrigo et al. 2010). Sea-ice DOC concentrations over 3000 $\mu mol\ l^{-1}$ have been recorded for bottom ice communities under low snow cover in this area (Smith et al. 1997). A low salinity melt layer forms around mid-June at a time when peak concentrations of bottom ice DOC have been reported (Michel et al. 2003). Utilizing *in situ* sources of sea-ice DOM, enrichment experiments were conducted to determine the response of surface water prokaryotes to sea-ice DOM additions. We hypothesized that sea-ice DOM would stimulate surface water prokaryotic growth by overcoming *in situ* carbon limiting conditions that prevail during early spring.

MATERIALS AND METHODS

Surface waters and bottom sea ice was collected on 4 May 2011 and 1 May 2012 at a first-year sea-ice station (74.7° N, 95.5° W) located ca. 2 km offshore in Resolute Passage, Canadian Arctic Archipelago. Resolute Passage is covered annually by landfast sea ice over a period which typically extends from late November to the end of June.

Multiple sea-ice cores were collected using a manual ice corer (Mark II coring system, 9 cm internal diameter, Kovacs Enterprises). The cores were cut to collect the bottom 3 cm section that contains most of the sea-ice biomass. Surface water was collected with a submersible pump held at the ice–water interface. Sea-ice and surface-water samples were stored in sterile WhirlPak bags or acid-washed Nalgene containers, respectively. The samples were kept in the dark at near 0°C temperatures until the beginning of the experiments. Experiments began the day following sample collection to allow the ice samples to melt slowly overnight. Experiments and sample processing were conducted at the Polar Continental Shelf Program laboratory facilities, Resolute Bay, Nunavut.

Experimental design

Two different microcosm experiments were conducted to evaluate the response of surface water bacteria and Archaea, hereafter prokaryotes, to conditions of sea-ice melt — specifically the addition of dissolved sea-ice constituents. Sea-ice prokaryotes, ice algae and other protists were excluded from the inoculum via filtration, as described below. In the enrichment experiment, sea-ice DOM was added to achieve estimated saturating DOC concentrations for surface water prokaryote growth. In the dose experiment, DOM target concentrations ranged from known under-ice surface water concentrations in

Resolute Passage and other Arctic locations (Smith et al. 1997, Riedel et al. 2007b, Juhl et al. 2011) to estimated saturating concentrations. The experimental inoculum represents the entire compliment of biologically relevant DOM in bottom sea ice that would be initially released during melt.

Enrichment experiment

Surface waters containing their natural prokaryotic assemblages were spiked once with the sea-ice DOM inoculum (ca. 20% of total volume) at the beginning of the experiment (T_0). Prokaryotic growth response and DOM concentrations were then monitored over a period of 7 d. To prepare the sea-ice DOM inoculum, bottom ice cores were pooled in acid-washed containers and slowly melted in the dark. The melted ice was then filtered through a pre-combusted 47 mm Whatman GF/F filter and the filtrate collected as the sea-ice DOM inoculum. Surface waters were allowed to settle for 24 h and were then decanted and filtered through a 5 µm filter to remove grazers and phytoplankton from the experiment.

The sea-ice DOM inoculum was added to the surface waters to obtain an initial enrichment concentration of ca. 500 µmol l^{-1} DOC. Initial concentrations were estimated to be at or near saturating concentrations for surface water prokaryotic growth. The enrichment experiment was conducted in duplicate with analytical times at 0, 6, 12, 24, 48, 72, 96, 120, 144 and 168 h. A separate experimental microcosm (sterile Whirl-Pak bag, 2.1 l total volume) was analyzed at each time point. Triplicate control microcosms containing surface waters without any sea-ice DOM addition were analyzed at the beginning and end of the experiment. At each experimental and control time point, the samples were analyzed for prokaryotic abundances, nucleic acid content and apparent cell size and DOC, dissolved nitrogen (DN) and inorganic nutrient concentrations.

Dose experiment

The dose experiment involved the addition of 5 different sea-ice DOM concentrations to surface waters. This microcosm experiment was conducted in 2011 and a similar experiment was repeated in 2012. In 2011, the final concentration of the 5 dose treatments corresponded to background (1×, 68.5 µmol l^{-1}), 2× (156 µmol l^{-1}), 3× (223 µmol l^{-1}), 6× (458 µmol l^{-1}) and 12× (840 µmol l^{-1}) surface water DOC concentrations. The sea-ice DOM inoculum and surface waters were prepared as described above for the enrichment experiment. In 2012, the 5 dose treatments corresponded to background (1×, 59.7 µmol l^{-1}), 3× (185 µmol l^{-1}), 4.5× (267 µmol l^{-1}), 8× (490 µmol l^{-1}) and 10× (580 µmol l^{-1}) surface water DOC concentrations. Grazers and phytoplankton were not removed from surface waters in 2012 and the sea-ice DOM inoculum was prepared by filtration of melted sea ice through a 0.2 µm membrane filter. In both years, each dose treatment was prepared in triplicate in individual sterile Whirl-Pak bags which were analyzed at the beginning and end (168 h in 2011, 216 h in 2012) of the experiment. The volume of inoculum added made up 4 to 36% of total experimental volume (600 to 700 ml). Triplicate experimental controls of surface water without sea-ice DOM addition were also analyzed at the beginning and end of the experiments. Each dose and control sample was analyzed for prokaryotic abundance, apparent cell size and nucleic acid content as well as DOC, DN and nutrient (2011 only) concentrations. The enrichment and dose experiments, along with the experimental controls, were incubated in the dark at 0°C (2011) or 4°C (2012). Experimental temperature was monitored with a HOBO temperature sensor in 2011. The bags were manually shaken at each sampling time.

Analyses

Surface water and sea-ice salinity was measured with a salinometer probe (Portsal 8410A, Technel). Samples for inorganic nutrients were pre-filtered (pre-combusted Whatman GF/F) and stored at –80°C for later determination of nitrate (NO_3^-) and phosphate (PO_4^{3-}) concentrations using a SmartChem discrete analyzer (Westco Scientific Instruments). Nutrient chemistries were adapted from Grasshoff et al. (1999).

Duplicate DOC and DN samples were filtered through pre-combusted (450°C for 5 h) Whatman GF/F filters and stored in the dark at 4°C after being acidified with 50% H_3PO_4. DOC and DN were measured on a Shimadzu TOC-VCPH analyzer with an ASI-V auto sampler and TNM-1 Total Nitrogen module, using high-temperature catalytic combustion (Hedges et al. 1993, Knap et al. 1996). The analyses were systematically checked against consensus reference material, i.e. deep seawater reference (DSR), from the Hansell's Certified Reference Materials (CRM) program. Chl *a* was analyzed fluorometrically (10AU Turner Designs) according to Parsons et al.

(1984). Duplicate chl *a* subsamples were filtered on Whatman GF/F filters and extracted for 24 h in 90% acetone at 4°C in the dark.

Prokaryotic abundance, apparent cell size, and nucleic acid content were determined by flow cytometry according to Belzile et al. (2008). Duplicate samples were pre-filtered through a 40 µm cell strainer (BD Falcon), preserved with glutaraldehyde (0.1% final concentration; Sigma) and stored at −80°C. During analyses, subsamples were stained with SYBR-Green I (0.1% final concentration; Molecular Probes) and counted with an Epics Altra flow cytometer (Beckman Coulter). Sea-ice samples were first diluted with Tris-EDTA. Apparent cell size was estimated by calibrating forward scatter with microspheres of known size (0.5 µm diameter, Fluoresbrite plain YG, Polysciences). Cytograms were analyzed using Expo32 v. 1.2b (Becton Coulter) and side scatter versus green fluorescence plots were used to assess low (LNA) and high (HNA) nucleic acid prokaryotes. The abundance of autotrophic protists (i.e. autotrophic eukaryotes, <20 µm in size) in the sea ice and surface waters of the study site were also determined using flow cytometry.

Data analyses and statistics

Non-parametric *t*-tests and ANOVAs were performed using Mann-Whitney and Kruskal-Wallis tests, respectively. Correlations were calculated using Spearman rank-order correlations. The significance of tests was identified at $p \leq 0.05$. Statistical analyses were performed with JMP (SAS) and SigmaPlot v. 11.0 (Systat Software) software packages. Specific growth rates were estimated according to $(\ln N_t - \ln N_0)/t$, where N_t and N_0 are the final and initial prokaryotic abundance, respectively, after t hours. The dose experiment prokaryote growth rate data (μ, h^{-1}) were fitted to a Monod equation:

$$\mu = s \times \mu_{max} / (K_s + s) \quad (1)$$

where s is the DOC concentration (µmol l^{-1}), μ_{max} is the maximum growth rate (h^{-1}) and K_s is the DOC concentration (s, µmol l^{-1}) at which the growth rate is half of μ_{max}. Nonlinear regression analysis was used to calculate estimates of μ_{max} and K_s and the uncertainty of the regression coefficients are expressed by the standard error.

RESULTS

Environmental conditions

At the sea-ice station, ice thickness was 1.1 and 1.4 m and snow thickness was 8.4 and 7.2 cm in 2011 and 2012, respectively. Environmental variables in the surface waters and sea ice (Table 1) were typical for the Resolute Passage area with high ice algal biomass and associated DOC concentrations. NO_3^- concentrations were similar in the ice and water, but PO_4^{3-} was significantly higher in the sea ice than in the surface waters ($p < 0.05$). Sea-ice and surface-water communities and biochemical characteristics were comparable between years with higher sea-ice protist and prokaryotic abundance in 2012 (Table 1) and fewer HNA (21%) cells than in 2011 (36%). HNA prokaryotic cells in the surface waters comprised 64 ± 0.6% of total prokaryotic abundance (years combined).

Kinetics of growth

Enrichment experiment

The sea-ice DOM inoculum increased the experimental DOC concentrations, on average, 7× relative to control concentrations (545 versus 79 µmol l^{-1}, Fig. 1A). The sea-ice inoculum also significantly

Table 1. Average (SD, n = 2) inorganic nutrients, dissolved organic carbon (DOC) and nitrogen (DN) and total chlorophyll *a* (chl *a*) concentrations and total prokaryote and autotrophic protist abundance at the first-year, sea-ice sampling station, Resolute Passage

Year	NO_3^- (µmol l^{-1})	PO_4^{3-} (µmol l^{-1})	DOC (µmol l^{-1})	DN (µmol l^{-1})	Chl *a* (µg l^{-1})	Protists (10^3 ml^{-1})	Prokaryotes (10^3 ml^{-1})
Surface water							
2011	10.4 (0.9)	1.2 (0.01)	66.8 (5)	14.5 (0.2)	0.1 (nd)	0.084 (nd)	164 (nd)
2012	7.1 (0.04)	1.1 (0.004)	59.5 (2.8)	10.4 (0.31)	0.2 (0.05)	0.094 (nd)	231 (nd)
Sea ice							
2011	13.8 (1.3)	9.2 (0.18)	1972 (0.1)	165 (0.1)	2750 (221)	798 (nd)	6473 (nd)
2012	12.5 (0.35)	8.5 (0.09)	2030 (358)	126 (29)	4563 (391)	1977 (nd)	16278 (nd)

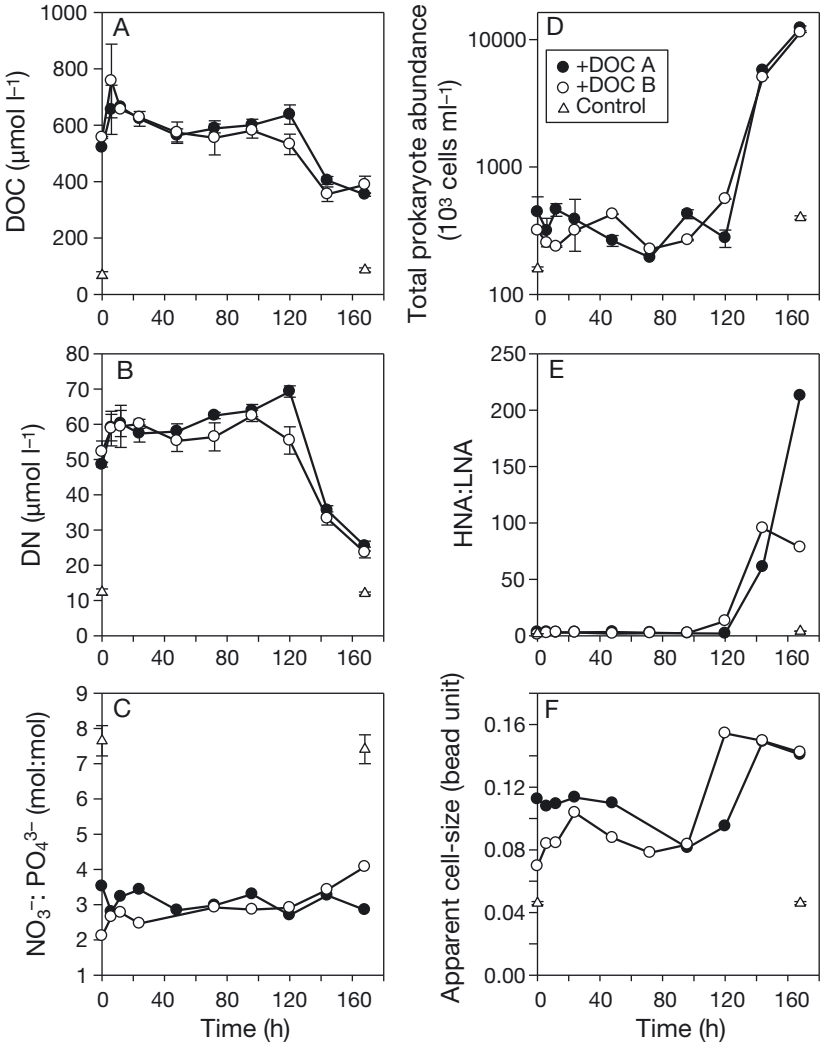

Fig. 1. Trends in organic and inorganic nutrients and surface water prokaryotic abundance: size and activity in replicate (DOC A/B) sea-ice dissolved organic matter (DOM) enrichment experiments in Resolute Passage, spring 2011. Average and standard deviations of controls (n = 3) provided for T_0 and T_{end}

increased experimental DN (average 53 versus 13 µmol l^{-1}, Fig. 1B) and PO_4^{3-} (average 3.8 versus 1.2 µmol l^{-1}) concentrations relative to the control ($p < 0.01$) but did not enrich NO_3^- concentrations (average 10.7 versus 9.6 µmol l^{-1}, data not shown). The addition of PO_4^{3-} from the sea-ice inoculum lowered the experimental N:P ratio from 7.5 to 3 (Fig. 1C). Experimental salinity was 26.4 as compared to 30.5 in the control. Average temperature during the enrichment and 2011 dose experiment was –0.01 ± 0.3°C.

During the first 96 h of the enrichment experiment there was little change in measured variables (Fig. 1). Following 120 h, there was a rapid increase in prokaryotic abundance with an estimated growth rate of 0.11 h^{-1} during exponential growth (120 h to 144 h; Fig. 1D). The increase in prokaryotic abundance was accompanied by an uptake of DOC and DN. Between 120 h and 168 h, average prokaryotic growth yields were 0.02 cells µmol l^{-1} DOC and 0.01 cells µmol l^{-1} DN. There was no clear trend for the uptake or release of inorganic nutrients during the entire experiment, as nutrient concentrations did not change significantly (data not shown). The proportion of HNA prokaryotic cells rapidly increased after 96 h (Fig. 1E) with an average HNA:LNA ratio of 172 at 168 h, when HNA cells accounted for 99.1% of total prokaryotic abundance. Apparent cell size initially decreased and then increased above initial values by 144 h (Fig. 1F).

Experimental control conditions were not significantly different from background environmental concentrations ($p > 0.05$; Table 1). There were small, significant increases in NO_3^- and PO_4^{3-} concentrations in the control at T_{end} versus T_0 ($p < 0.05$; data not shown). However, there were no significant changes in DOC or DN concentrations. In the control, prokaryotic abundance significantly increased (on average, from 159 to 401 × 10^3 cells ml^{-1}) and the HNA:LNA ratio doubled from 2 to 4, from T_0 to T_{end}. However, apparent cell size remained unchanged (0.046 bead units) in the control. The changes in prokaryotic abundance and apparent activity in the control were orders of magnitude lower than under DOM enriched conditions (Fig. 1).

Dose experiment

The DOM dose experiment yielded similar results in 2011 and 2012 despite small changes in methodology and environmental conditions (Table 2). The sea-ice inoculum was the same as for the enrichment experiment. As such DOC, DN and PO_4^{3-} concentrations in Treatments 1 to 4 increased relative to the volume of inoculum added. The salinity of the sea-ice inoculum was, on average, 9.5. Consequently the

Table 2. Initial mean (SD, n = 3) dissolved organic carbon (DOC), dissolved nitrogen (DN), DOC:DN ratio, and salinity in the control (0) and 4 treatments (1–4) of the dose experiment in 2011 (A) and 2012 (B)

DOM dose	DOC (µmol l^{-1})	DN (µmol l^{-1})	DOC:DN (mol:mol)	Salinity
A_0	68.5 (12.1)	12.4 (0.9)	5.5 (0.6)	33 (0.2)
A_1	155.9 (9.9)	17.9 (0.3)	8.7 (0.7)	32.2 (0.4)
A_2	223.3 (31)	26 (1.3)	8.6 (0.5)	31.5 (0.07)
A_3	458.4 (25.2)	44.6 (0.8)	10.3 (0.5)	28.6 (0.07)
A_4	840.2 (113.3)	74.2 (2.7)	11.3 (1.5)	24.9 (0.1)
B_0	59.7 (1.4)	9.4 (0.1)	6.3 (0.2)	32.2 (nd)
B_1	185.1 (18.4)	15.2 (2.2)	12.2 (0.6)	29.5 (nd)
B_2	267.0 (22.6)	20.4 (1.3)	13.1 (0.3)	27.9 (nd)
B_3	489.7 (2.3)	32.4 (0.2)	15.1 (0.04)	23.6 (nd)
B_4	579.6 (7.9)	35.5 (0.3)	16.3 (0.3)	20.7 (nd)

salinity of Treatments 1 to 4 decreased concomitantly with the volume of inoculum added. There was no evidence that the inoculum added any prokaryotes as prokaryotic abundance at T_0 showed no trend across the treatments (Fig. 2A). Initial conditions for the controls (A_0, B_0) and dose treatments (A_{1-4} and B_{1-4}) are summarized in Table 2. Initial prokaryotic abundance (total and HNA) and apparent cell size for the dose experiments were not significantly different between years ($p > 0.6$). In 2011, there was no significant difference in NO_3^- or PO_4^{3-} concentrations between the beginning and end of the experiment.

After the experimental period (168 h in 2011 and 216 h and 2012), prokaryotic abundance, activity and size increased significantly ($p < 0.05$) in each treatment — except for apparent cell size in A_0 and B_0 (Fig. 2). The increase in prokaryotic abundance ($r = 0.74$, $p < 0.05$), HNA:LNA ($r = 0.90$, $p < 0.01$) and apparent cell size ($r = 0.90$, $p < 0.01$) was significantly correlated to the initial concentrations of DOC added to each treatment (years combined). HNA:LNA ratios increased to a maximum of 143 and 100 in 2011 and 2012, respectively. At the end of the dose experiments, HNA cells comprised a minimum of 98% of total prokaryotic abundances in any treatment. Apparent cell size increased by a factor of 3.2 (2011) and 2.1 (2012) in the highest dose relative to the control.

Over the course of the dose experiment, DOC concentrations increased and DN concentrations remained the same in the controls (A_0 and B_0; Fig. 3). The uptake of both DOC and DN significantly increased with increasing dose addition in 2011 and 2012 (A_{1-4} and B_{1-4}, $p < 0.01$; Fig. 3). The average uptake ratio (DOC:DN) was similar between years (5.3 in 2011, 5.7 in 2012). With the addition of sea-ice DOM, prokaryotic growth yields averaged 0.03 and 0.05 cells µmol l^{-1} DOC in 2011 and 2012, respectively, and 0.03 cells µmol l^{-1} DN for both years. Growth yields were significantly negatively correlated to the dose additions ($p < 0.01$). Relative to initial dose concentrations, on average, 19.5 ± 0.9% and 20.5 ± 2.0% of the DOC pool was taken up in 2011 and 2012, respectively. The proportion of DN uptake relative to the initial DN pool was higher in 2012 (50.6 ± 7.7%) compared to 2011 (36.3 ± 5.2%).

In Fig. 4, estimated prokaryotic growth rates for each dose treatment are plotted against the initial DOC doses in 2011 and 2012. Estimated growth relative to the DOM dose additions followed non-linear Monod growth kinetics in both years (Eq. 1). The half saturation constants were 156 ± 59.3 µmol l^{-1} DOC in 2011 and 53 ± 21.2 µmol l^{-1} DOC in 2012. Maximum potential prokaryotic growth rates in this

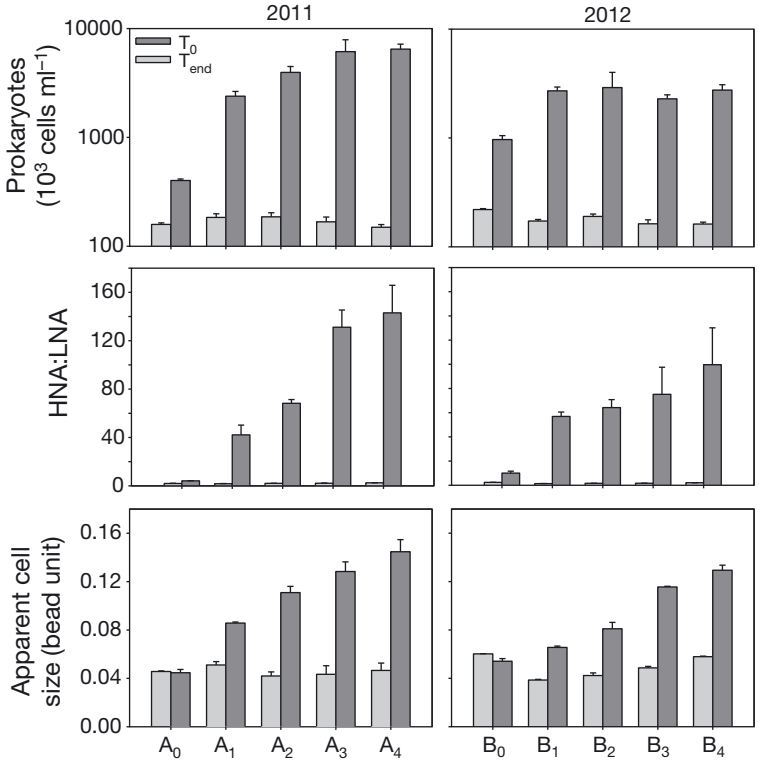

Fig. 2. Prokaryotic abundance, activity (high/low nucleic acid content, HNA:LNA) and size at the beginning (T_0) and end (T_{end}) in the control (0) and 4 (1–4) treatments of the sea-ice dose experiments in 2011 (A) and 2012 (B). Initial sea-ice dissolved organic carbon (DOC) dose concentrations for each treatment are summarized in Table 2

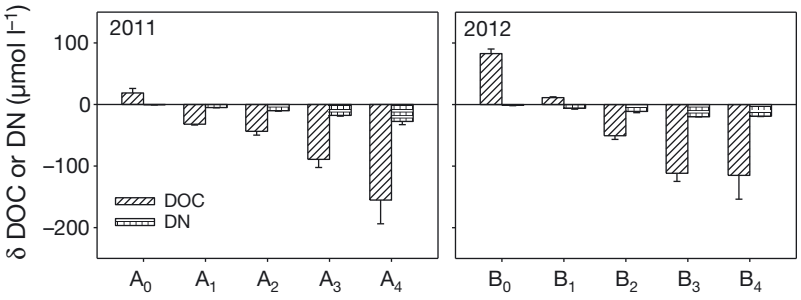

Fig. 3. Production/uptake of dissolved organic carbon (DOC) and dissolved nitrogen (DN) by under-ice surface water prokaryotes in each treatment of the dose experiment in 2011 (A) and 2012 (B)

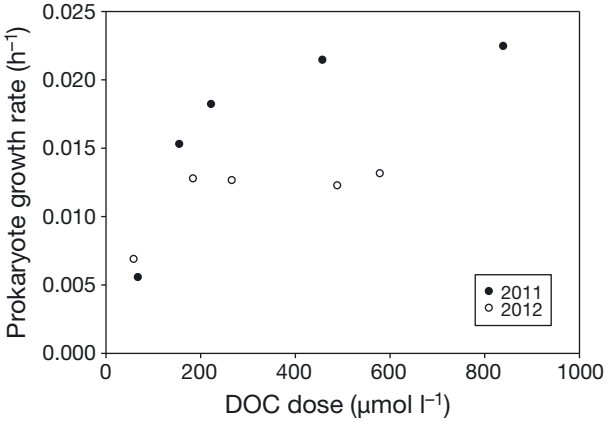

Fig. 4. Prokaryotic growth (h^{-1}) as a function of dissolved organic carbon (DOC) concentrations in the 2011 and 2012 dose experiments

experiment were estimated to be 0.67 ± 0.09 and 0.35 ± 0.02 d^{-1} in 2011 and 2012, respectively. Similar growth curves are observed if prokaryotic growth is plotted against initial DN concentrations or the salinity values of the dose experiment (data not shown). The half saturation constants for DN were 27 ± 17 µmol l^{-1} DN and 8.6 ± 6.3 µmol l^{-1} DN in 2011 and 2012, respectively.

DISCUSSION

In 2011 and 2012, sea ice in Resolute Passage contained high ice algal biomass and associated DOC and DN concentrations (Table 1), as is typical for the region (Michel et al. 2006). The growth and release of ice algae into surface waters during melt has been previously studied in Resolute Passage (Smith et al. 1993, Michel et al. 1996, Fortier et al. 2002). However the fate of sea-ice dissolved constituents during the melt period is not well understood. Microbial communities within the ice actively uptake and remineralize inorganic nutrients, DOC and DN, yet high concentrations of organic and inorganic nutrients can remain in the bottom sea ice at the time of ice melt (Michel et al. 2003, Riedel et al. 2007b, Song et al. 2011).

Contributions of sea-ice melt

During the period of sea-ice melt, multiple changes occur in surface waters including the introduction of the diverse sea-ice community along with particulate and dissolved constituents which can persist in surface waters (Kähler et al. 1997). Surface water salinity decreases during melt altering flow and stratification at scales from decimeters to >20 m (Haas et al. 1997, Falk-Petersen et al. 2000, Hop et al. 2011). Under-ice melt boundary layers, with distinct pycnoclines, and features such as under-ice melt ponds (Eicken et al. 2002, Mundy et al. 2011) are expected to retain dissolved constituents released from the ice within the ice–water interfacial layer. Although fine scale measurements of DOM are lacking for under-ice boundary layers, it is reasonable to assume that the saturating DOM concentrations used in the experiments could occur at the ice–water interface during melt. For example, high under-ice surface water DOC concentrations, not specific to a melt boundary layer, have been previously measured near Barrow, Alaska (300 µmol l^{-1}; Juhl et al. 2011), in Franklin Bay (>250 µmol l^{-1}; Riedel et al. 2007b) and in Resolute Passage (average 365 µmol l^{-1}; Smith et al. 1997).

High DOM concentrations in the under-ice melt boundary layer could be related to the presence of exopolymeric substances (i.e. EPS, a type of colloidal DOM) from bottom sea ice since EPS has been found to be retained within melt water boundary layers (Krembs & Engel 2001). In addition, flocculation of colloidal DOM from the sea ice, induced by low surface salinities, may also enhance the retention time of DOM at the ice–water interface due to the buoyancy of EPS aggregates (Azetsu-Scott & Passow 2004, Riedel et al. 2006) and accumulation of colloids at the pycnocline (Alldredge et al. 2002). The potential retention of EPS and other DOM constituents near the ice–water interface suggests that the experimental growth response observed in this study would likely be closest to natural conditions within the under-ice melt boundary layer.

In this study we characterized the response of surface water prokaryotes to natural sea-ice DOM additions that would be released initially from the bottom of the sea ice. In our study area, the bottom sea ice contains the vast majority of vertically integrated sea-ice DOC concentrations. Characterization of complete core sections show that 98% (2460 ± 5.8 µmol l^{-1}) of the total core sea-ice DOC pool at our site was within the bottom 3 cm section at the ice–water interface. All remaining ice core sections averaged 48 ± 54 µmol l^{-1} DOC (core sampled at the same station, 7 May 2013). Therefore, the experimental sea-ice inoculum represented the bulk of the sea-ice DOC pool, which is also initially released under natural conditions of melt. By inoculating experimental microcosms with natural sea-ice DOM, inorganic nutrients, specifically PO_4^{3-}, and DN were also enriched and salinity decreased in the surface waters (Table 2), as expected under natural conditions of melt. Micronutrients and metals included in the sea-ice DOM inoculum may have also impacted the response of the surface water prokaryotic community to the experimental melt conditions. However, the impact of these inorganic constituents is beyond the scope of this study. The prokaryotic growth observed during the dose experiments was positively correlated to the sea-ice DOM additions and experimental salinities (Table 2). It is possible that the low experimental salinities could have selected for the growth of specific prokaryote species. However, it is unlikely that salinity alone was the driving factor for the high rates of prokaryote growth. In other Arctic studies, salinity has not been identified as the sole or primary factor impacting prokaryote abundance or growth, but rather DOM or temperature have been identified as key regulating factors (Garneau et al. 2008, Sala et al. 2010, Uchimiya et al. 2011, He et al. 2012, Nguyen et al. 2012, Winter et al. 2012).

During the enrichment experiment (Fig. 1) we could not detect prokaryote growth until 120 h. Prior to 120 h, growth of a small group and/or select species of prokaryotes may have occurred but remained undetected. Alternatively, the apparent 4 d lag in prokaryotic growth (Fig. 1d) may have been due to osmotic stress associated with changed experimental salinity (Kaartokallio et al. 2005). During ice melt, very low surface water salinities (e.g. <15) can persist for several weeks (Eicken et al. 2002, Hop et al. 2011, Mundy et al. 2011). The change to low salinity in the experimental microcosms (Table 2) can therefore be considered representative of natural changes in salinity during the melt period, to which surface water prokaryotes would be adapted.

Similar lags (4 to 6 d) in polar marine prokaryotic growth have been observed during organic carbon addition experiments in which salinity was held constant (Dyda et al. 2009, Topper et al. 2010, Ducklow et al. 2011). The lag period may have been necessary for the inactive surface water community to synthesize appropriate enzymes and other metabolic components to utilize the pulse of sea-ice DOM. The addition of sea-ice DOM may have activated a dormant under-ice prokaryotic community, and by doing so could play a key role in priming the surface layer community to take advantage of subsequent increases in DOM supplied by spring/summer phytoplankton blooms (Maranger et al. 1994, Yager et al. 2001).

The delay in growth may have allowed for a shift to different species and/or preparation of metabolic components capable of utilizing sea-ice DOM. Sea-ice DOM is differentiated from surface water DOM at early stages of sea-ice formation and sea-ice DOM is distinct from surface water DOM with respect to concentration, molecular weight and composition, including biologically-relevant labile components (Amon & Benner 2003, Riedel et al. 2006, 2007a, Müller et al. 2011, Aslam et al. 2012). Arctic prokaryotes are phylogenetically distinct based on organic carbon sources available (Sala et al. 2008) and organic carbon preferences vary seasonally and among Arctic bacterial groups (Elifantz et al. 2007, Nikrad et al. 2012). The experimental results demonstrate that at least a portion of the surface water prokaryote community has adaptive capabilities to utilize sea-ice DOM despite exposure to low salinities that would exist under natural conditions of sea-ice melt.

Prokaryotic growth characteristics

Following sea-ice DOM enrichment, nearly the entire prokaryotic community was characterized by cells with high nucleic acid content (average 97% of total prokaryotic abundance). The HNA content indicates that the prokaryotes became metabolically active and shifted into exponential growth phase. The observed increase in prokaryote abundance and shift to HNA cells, in response to sea-ice DOM, was rapid (i.e. days) as observed in other sea-ice DOM enrichment experiments (Eronen-Rasimus et al. 2014). The shift occurs even with an enrichment of only 2 to 3× winter surface water DOC concentrations (Table 1, Fig. 2B,E) similar to summer surface

water DOC concentrations on arctic shelves (e.g. 120 to 250 µmol l^{-1}; Riedel et al. 2007b, Alling et al. 2010, Iversen & Seuthe 2011, Millero et al. 2011).

The enhanced prokaryotic activity and growth observed under DOM-enriched conditions suggest that the under-ice surface water prokaryote community was limited in organic carbon during the study period. There was no preferential usage of DN as uptake occurred within expected elemental ratios for heterotrophic bacteria (e.g. C:N 3.8 to 6.3, Kirchman 2012). NO_3^- and other potential inorganic and organic nitrogen sources (e.g. NH_4^+, amino acids) in the surface water were sufficient to support high rates of exponential growth (2.6 d^{-1}) and the low melt NO_3^-:PO_4^{3-} conditions (Fig. 1C) did not appear to negatively impact increases in prokaryotic abundance. Enhanced individual biomass, as indicated by increases in apparent cell size (Figs. 1F & 2C,D), also supports the release of organic carbon limitation under melt conditions. A decrease in cell size is a well-known carbon starvation response of prokaryotes in oligotrophic environments (Morita 1997). The introduction of organic carbon with concurrent increases in prokaryotic abundance and individual cell size could facilitate carbon transfers to grazers during the melt period (Anderson et al. 2011, Hop et al. 2011).

The dose experiments yielded different growth curves during the 2 years (Fig. 4) and the estimated maximum growth rates (0.35 to 0.67 d^{-1}) were lower than the observed exponential growth rate (2.6 d^{-1}) during the enrichment experiment. Prokaryotic growth in 2012 may have been affected by the presence of grazers, competition for nutrients with phytoplankton and/or by the higher experimental temperature in 2012 than in 2011 (4 versus 0°C). The removal of grazers and phytoplankton from the 2011 microcosms allowed for higher growth rates and a more defined asymptotic growth curve under DOM-enriched conditions (Fig. 4). In 2012, saturating DOC concentrations are likely underestimated due to experimental conditions.

Although experimental growth dynamics were different between years, maximum DOC uptake rates were very similar (average, 0.035 µmol l^{-1} DOC prokaryote^{-1}). The proportion of DOC utilized by the prokaryotes relative to the total DOC enrichment at the beginning of the dose experiments was also consistent in each dose for both years (average 20 ± 1.4%). Even with a longer experimental duration in 2012, no more than 20% of the sea-ice DOC pool was utilized by the surface water prokaryotes. This result is similar to the findings of Amon et al. (2001) where surface water bacteria utilized 30% of ice-algal derived DOC from multi-year ice, with a strong preference for neutral sugar and amino acid components of the DOC. Our results further indicate that DOC usage by prokaryotes during melt is largely dependent on DOC composition rather than concentration. The concentration of DOC in the multi-year sea ice of Amon et al. (2001) (112 µmol l^{-1}) was an order of magnitude lower than this study (i.e. >1900 µmol l^{-1}, Table 1) yet the fraction of DOC utilized is similar. It is possible that only the highly reactive DOC, likely produced by the sea-ice algae, is utilized by the surface water prokaryotes.

The composition of the DOC inoculum varied slightly between years due to the filtration with a nominal pore size of 0.7 µm in 2011 and 0.2 µm in 2012. It is possible that smaller spectrum of sea-ice DOC in 2012 also contributed to a lower maximum growth response (Fig. 4). Sea ice is rich in labile colloidal and exopolymer organic carbon >0.2 µm which enhance bacterial abundance and cell size within the sea ice (Riedel et al. 2007b, Meiners et al. 2008, Underwood et al. 2013). Arctic bacterial communities have been found to actively assimilate diatom-derived extracellular polymers with only a higher preference for free amino acids (Elifantz et al. 2007). This polymer pool of sea-ice carbon can be released in later stages of melt (Riedel et al. 2006, Juhl et al. 2011) potentially supporting additional or prolonged prokaryotic growth in Arctic surface waters at the time of ice melt.

Enhanced heterotrophy

The estimated prokaryote growth rates in this study (Fig. 4) are higher than Arctic estimates based on semi-labile DOC concentrations (0.1 d^{-1}; Kirchman et al. 2009). Higher growth in this study is likely a result of high concentrations of bioavailable DOC from algal-rich sea ice compared to Arctic surface waters impacted by refractory terrestrial DOC. Thus, the enrichment experiments demonstrate that sea-ice melt on Arctic shelves can provide an annual pulse of labile DOC to organic carbon-limited prokaryotic communities near the ice–water interface. The experimental results further support the conclusion that organic carbon enrichment is a major factor driving the increase in bacterial abundance and activity during the winter to summer transition in polar regions (Ducklow et al. 2011). The response to sea-ice DOC released during melt should be considered among several factors (e.g. increasing tempera-

ture and stratification) expected to increase heterotrophic activity and the role of the microbial food web in the Arctic (Kirchman et al. 2009).

DOC concentrations can be very high in the bottom of landfast and pack ice at the onset of ice melt (e.g. ca. 1000 µmol l^{-1}; Michel et al. 2003, Riedel et al. 2007b, Song et al. 2011). In the present study it is likely that a similar or higher DOC concentration would remain at the onset of melt in June, given that DOC concentrations were near 2000 µmol l^{-1} in May (Table 1). Using 1000 µmol l^{-1} as an approximation of bottom ice DOC concentrations at the time of ice melt, we estimate the potential annual flux of DOC from the bottom 5 cm of seasonal Arctic sea ice to be 0.6 g C m^{-2} yr^{-1}. An ice thickness of only 5 cm is used, since the majority of ice algal biomass and associated reactive DOC is located in bottom depth horizon (Song et al. 2011). High ice-algal biomass and production is associated with the extensive Arctic shelves (6.05×10^6 km^2; Jakobsson et al. 2004) such that the release of DOC from melting sea ice on the shelves could contribute a total areal input of 3.6 Tg C yr^{-1}. A high proportion of ice algal production in the central Arctic Ocean can be released as DOC (Gosselin et al. 1997) indicating that seasonal ice throughout the Arctic also contributes to the sea-ice melt DOC flux. In 2012 the area of Arctic seasonal ice increased to just over 11×10^6 km^2 (Snow & Ice Data Centre, Boulder, CO). Extending the estimate of DOC release to total Arctic seasonal ice represents a potential input of 6.6 Tg C yr^{-1} from melting sea ice.

Prokaryotes utilizing the sea-ice DOM would release CO_2 into surface waters that are undersaturated with respect to atmospheric CO_2 concentrations, thereby impacting the air–sea CO_2 flux associated with ice melt (Rysgaard et al. 2011). The continued expansion and thinning of first-year sea ice in the Arctic, as a result of climate change, represents a scenario in which there could be an even greater production and release of sea-ice DOM. Consequently, future seasonal sea-ice melt would support even higher levels of heterotrophic activity with more carbon entering the microbial food web in the surface layer.

Our experimental results demonstrate that enhanced surface water prokaryote growth can be driven by the input of sea-ice DOM. DOM-driven increases in microbial activity can be associated with the melt of first-year sea ice, particularly on Arctic shelves and possibly extending towards the basins in the current context of sea-ice changes, as well as at productive ice margins throughout the Arctic. The processing of sea-ice DOM within the microbial food web at the time of ice melt and/or at marginal ice zones is likely to be impacted by characteristics of the DOM pool, in particular the presence of polymers (i.e. EPS), with potential feedback to microbial community diversity and carbon flux in the changing Arctic.

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