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Bioavailability of surface dissolved organic matter to aphotic bacterial communities in the Amundsen Sea Polynya, Antarctica

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Abstract

Antarctic seas, and particularly the Amundsen Sea Polynya, are some of the most productive oceanic regions on Earth. Ice-algal production during austral spring is followed by open-water pelagic production later in the season. Although ice-free growth accounts for a greater percentage of the annual net primary production, ice algae provide an important source of nutrients to organisms throughout the water column and benthos in areas and seasons when open-water production is insignificant. The objectives of this study were to assess the bioavailability of dissolved organic matter (DOM), sourced from ice algae or the chlorophyll maximum (chl max), to marine bacterioplankton and to determine the fate of carbon within these different DOM pools, including loss to respiration, incorporation into bacterial biomass and retention within the DOM pool itself. Nutrient concentrations and bacterial abundance, production, and cell volume were monitored during a 7-day bioassay study involving four treatments conducted shipboard in the Amundsen Sea Polynya, Antarctica. The greatest response in bacterial abundance and activity was observed when ice-algal meltwater was supplied to aphotic zone bacterioplankton collected from 170-m depth. However, bacterial growth efficiency was higher (24%) when chl max water was supplied to the same aphotic zone bacterial community compared to the bacterial growth efficiency of the ice-algal treatment (15%). Approximately 15% of dissolved organic carbon (DOC) from the ice-algal source and 18% from the chl max was consumed by aphotic bacterial communities over the relatively short, one-week incubation. In contrast, 65% of the dissolved organic nitrogen (DON) added as an integral part of the ice-algal DOM was consumed, but none of the DON supplied with chl max water was labile. This study underscores the importance of considering DOM sources when investigating or predicting changes in carbon and nitrogen cycling within the Amundsen Sea.

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Introduction

Antarctic shelves are extremely productive systems that play a crucial role in carbon and nitrogen cycles (Sarmiento et al., 2004; Vancoppenolle et al., 2013). High concentrations of nitrate and increasing inputs of iron from surrounding melting glaciers make the Amundsen Sea a highly productive sink for carbon dioxide (Alderkamp et al., 2012; Yager et al., 2012) and a source of dissolved organic matter (DOM; Williams et al., 2015). In Antarctic seas, phytoplankton and ice algae are the dominant sources of DOM (Knox, 2007) that fuel heterotrophic bacterial growth and respiration. Ice-algal production is made available to planktonic consumers during ice melt, which can release high concentrations of organic matter into the water column (Fischer et al., 1988; Knox, 1990; Thomas and Dieckmann, 2002). Whether DOM from open-water phytoplankton or ice algae affects the activity and growth of bacterioplankton communities differently is not well known. The relative importance of organic matter from these two sources to polar marine food webs and biogeochemical cycles is likely dependent on the timing and location of production, the taxa of algae, and the organisms consuming this production (Daly, 1990; Legendre et al., 1992; Le Fèvre et al., 1998; Lizotte, 2001). Location, timing and intensity of primary production in the Antarctic appear to be intrinsically linked

to climatic conditions, such as ice coverage and the direction and intensity of winds (e.g., Arrigo and Van Dijken, 2004; Saba et al., 2014). Thus, climate-mediated changes in patterns of primary production will likely control heterotrophic microbial activity and biogeochemical cycles in the Southern Ocean.

DOM produced in surface waters or released from sea ice may be made available below the production zone by convective mixing (Carlson et al., 1994), mixing caused by the movement of icebergs (Helly et al., 2011), or sinking of particulate organic matter and its solubilization during transit (Kähler and Bauerfeind, 2001). Generally, bacterial abundance decreases with depth, which is likely related to the quantity and quality of DOM (Church, 2008). In contrast, a recent study reports that a dissolved organic nitrogen (DON) pool that was utilized slowly by euphotic bacterial communities was more quickly used by bacteria from mesopelagic depths (Letscher et al., 2013). This same trend has also been observed for DOC in the Sargasso Sea (Carlson et al., 2004). How bacteria below the production zone respond to DOM from ice algae and how this response compares to that from phytoplankton are not known. Kähler et al. (1997) found that bacterial growth and growth efficiencies were stimulated by the addition of ice-algal meltwater in sub-Antarctic surface waters (56°30′S). Because the ice-algal meltwater included both DOM and bacteria from sea ice, however, the response of bacterioplankton alone could not be evaluated. Studies conducted in the Arctic have also found that surface bacteria are stimulated by the addition of sea-ice DOM (Amon et al., 2001; Niemi et al., 2014).

The objective of this study was to assess the bioavailability of autochthonous dissolved organic matter and inorganic nutrients from different depths to marine bacterioplankton in the Amundsen Sea. To accomplish this objective, water from three locations — the seawater-ice interface (containing ice-algal meltwater), the chlorophyll maximum (chl max), and the aphotic zone — was inoculated with natural bacterial communities. A secondary goal was to compare the growth and nutrient consumption by bacteria collected from the chl max to those from the aphotic zone when exposed to substrates found in the aphotic zone. Changes in nutrient concentrations and bacterial abundance, production, and cell volume were monitored during a 7-day bioassay study conducted shipboard while in the Amundsen Sea Polynya, Antarctica. Results were used to investigate the lability of the DOM in the three water sources for natural microbial communities and to assess the fate of carbon within these different DOM pools (i.e., loss to respiration, incorporation into bacterial biomass or retention within the DOM pool itself).

Methods

Particle-free water from the seawater-ice interface containing ice-algal meltwater, from the chl max, and from the aphotic zone was used as a nutrient source for Amundsen Sea Polynya bacterial communities in a 7-day bioassay experiment. The experiment consisted of four DOM-containing bioassay treatments run in duplicate: ice-algal meltwater inoculated with aphotic zone bacterioplankton (*ice algae*), chl max water inoculated with aphotic zone bacterioplankton (*chl max*), aphotic zone water inoculated with chl max bacterioplankton (*aphotic*), and aphotic zone water (no new DOM) inoculated with aphotic zone bacterioplankton (*control*).

Study area

All samples were collected from the Amundsen Sea, Antarctica, during the NBP 10-05 cruise on the RVIB *Nathanial B. Palmer* in December 2010–January 2011. The Amundsen Sea is located between the Ross Sea and the Western Antarctic Peninsula. It is strongly influenced by glacial melt and the resulting inputs of iron that promote phytoplankton growth within the open-water or polynya region (Thuróczy et al., 2012; Alderkamp et al., 2015). As a result, the Amundsen Sea Polynya supports some of the highest net primary productivity in the Southern Ocean (0.76 g C m^{-2} d^{-1}, Arrigo and Van Dijken, 2003; Arrigo et al., 2012). Approximately 38,000 km^2 of the Amundsen Sea is ice-free during austral summer (Arrigo and Van Dijken, 2003). Although interest in the Amundsen Sea has grown over the past two decades, it remains one of the least studied regions of the Southern Ocean, due in part to its general lack of accessibility.

Collection of source waters and bacteria

Samples representing the seawater-ice interface were taken from a newly formed crack in the ice, where dense patches of brown ice algae were visible, near the northern ice boundary of the polynya at 72° 54.72′S, 114° 56.52′W on 24 December 2010. Although ice-algal samples are typically collected via ice core, movement of the ship exposed the underside of the sea ice, allowing quick and effective sampling from the ship. Water and small pieces of sea ice containing ice algae were collected directly into acid-washed 9-L polycarbonate carboys. Once on ship, ice was melted by incubating the samples in a 4°C walk-in incubation chamber. Salinity was checked frequently (~ hourly) and adjusted to 30–33 continually using small amounts of artificial seawater brine (0.2 μm filtered). The artificial seawater brine was made by adding baked sodium chloride (500°C for 4 h), magnesium sulfate and sodium bicarbonate to Milli-Q water (DOC < 2 μM). Once fully thawed, the meltwater containing the ice algae was filtered in sequence through pre-combusted (450°C for 5 h) GFF filters (nominal pore size 0.7μm) to remove all ice-algal cells, and then through rinsed (300 mL Milli-Q

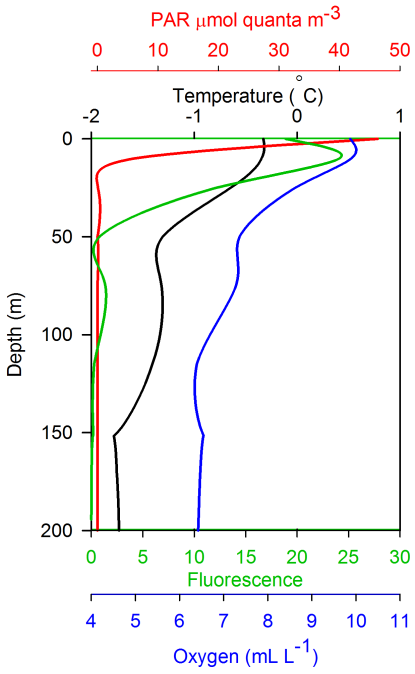

Figure 1

Depth profiles for photosynthetically active radiation (PAR), temperature, oxygen and fluorescence at the study site.

At this station, located at 73°25.01′S, 115°15.103′W in the Amundsen Sea Polynya, Antarctica, volumes of water from the chlorophyll max (10 m) and aphotic zone (170 m) were collected for use in the 7-day incubation experiment.

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water) 0.2 µm Supor filters to remove bacteria. The final filtrate was stored frozen at −20°C in acid-washed HDPE bottles until use in bioassay studies (< 5 days). The goal of this effort was to obtain dissolved ice-algal exudates to use as a nutrient source for aphotic bacterial communities, not to preserve or utilize any live ice algal or bacterial cells. On the day of use, the water was thawed and re-filtered through Milli-Q rinsed 0.2 µm Supor filters to remove any remaining bacteria.

Source waters from the chl max and aphotic zone were collected from 10 m and 170 m depth, respectively, at a nearby open-water site on 29 December 2010 at 73°25.01′S, 115°15.103′W (ASPIRE station 50). Water was collected in Niskin bottles attached to a sampling rosette and CTD. Sample depths were chosen based on data collected during an exploratory CTD cast. Depth profiles for temperature, photosynthetically available radiation (PAR), fluorescence, and oxygen concentrations from this site are shown in Figure 1. The 170-m depth was chosen to ensure that water representing the aphotic zone was collected not only below the euphotic zone (0.1% incident light level) but also below the thermocline, oxycline and evidence (fluorescence) of surface water production (Figure 1). Water from each source was filtered through both GFF and 0.2 µm Supor filters just prior (< 1 h) to use in bioassay treatments. Bacterial assemblages were collected from whole water from the aphotic zone or from the chl max by gravity-filtering each sample through 3-µm polycarbonate filters. The filtrate was collected into acid-washed and combusted (500°C, 5 h) glass flasks and used as the test bacterioplankton in the bioassay treatments.

Bioassays

The four treatments *(ice algae, chl max, aphotic, control)* were established by concentrating 9.5 L of aphotic zone (or chl max) bacterial cells into 1 L via gravity filtration and then adding the concentrated bacterioplankton cells to 16 L of the DOM source. Therefore, the bacterial cells were added to source water in a 0.6:1 ratio, while the ratio of the dissolved nutrient component was 1:16 (vol:vol) aphotic zone to source water. These amended samples were divided into six replicate 2-L polycarbonate bottles, covered with multiple layers of black electrical tape and foil to block all light, and were incubated at ambient water temperatures (approximately −2 to 0°C) in a shipboard flow-through system. Two bottles per treatment were collected at 1, 3, and 7 days for biological parameters (bacterial abundance, production and biovolume) and chemical parameters (ammonium, nitrate, nitrite, phosphate, silicic acid, DOC, and total dissolved nitrogen [TDN]). These same analyses were also done on water from each treatment at the start of the bioassay experiment (T0). Nutrient samples were also collected at discrete depths throughout the water column to evaluate nutrient depth profiles (Supplemental Figure 1).

Analyses

Bacterial abundance and cell size were estimated from three replicate samples taken from each incubation bottle and fixed to a final concentration of 4% formaldehyde. Samples for abundance were stained with SYBER Green and counted on a flow cytometer (FACSCalibur, Becton-Dickinson). At least 10,000 cells

were counted per replicate. Flow rate was measured with fluorescing beads. Cell size was measured from subsamples of formaldehyde-fixed water using digital images obtained by epifluorescence microscopy of DAPI-stained cells. Image analysis was done with the software ImageJ; cell biovolumes (BV) were calculated from at least 200 cells following Massana et al. (1997). Cellular C content (fg C $cell^{-1}$) was calculated using the equation $133.754 \times BV^{0.438}$ (Romanova and Sazhin, 2010). Concentrations of chlorophyll *a* (chl *a*) were measured on bulk water from the ice-algal melt, the chl max, and the aphotic zone samples fluorometrically using a Turner Designs Model 10-AU fluorometer; filters were extracted in 90% acetone overnight at 4°C (Parsons et al., 1984).

Bacterial production was estimated from incorporation of ^{3}H-leucine into protein. Triplicate samples of 1.5 mL of seawater were collected from each treatment bottle and incubated in the dark with 25 nmol L^{-1} of ^{3}H-leucine for 4 h. The incubation was stopped and initially rinsed by adding 0.1 mL of 100% TCA to each sample tube. Samples were then centrifuged and protein was extracted by rinsing the samples again with 1 mL of ice-cold 5% TCA and then by rinsing with 1 mL of 80% ethanol. Samples were centrifuged after each of the three rinses. Radioactivity was measured using a liquid scintillation counter. Parallel incubations for killed controls were done by adding ^{3}H-leucine only after killing the cells with 0.1 mL of 100% TCA.

Ammonium, nitrate, nitrite, phosphate and silicic acid were analyzed in triplicate, shipboard, on a five-channel Lachat Instruments QuikChem FIA+ 8000s series autoanalyzer in conjunction with a Lachat Instruments XYZ AutoSampler (ASX-500 Series). Samples were filtered through pre-rinsed 0.2 µm Supor filters and refrigerated (~ 4°C) until analyzed (< 3 h). Samples collected for DOC and TDN analyses were also filtered through pre-rinsed 0.2 µm Supor filters and stored frozen in glass vials until analyzed at the Virginia Institute of Marine Science. Ammonium concentrations were determined using the indophenol method, EPA-600/4-79-020, Method 350.1 (Colorimetric, Automated Phenate). Nitrate and nitrite concentrations were determined according to Armstrong et al. (1967) modified according to Patton (1983). Phosphate concentrations were measured using a modified molybdenum method (Bernhardt and Wilhelms, 1967). Concentrations of DOC and TDN were measured via high temperature combustion oxidation using a Shimadzu TOCV with TNM analyzer (Sharp et al., 1993; Sharp et al., 2004). Blanks were collected throughout the experiment. All DOC and TDN concentrations in experimental blanks were similar to analytical blanks with concentrations below 2 µM C and 1 µM N, respectively. Concentrations of DON were determined as the difference between the inorganic (ammonium + nitrate + nitrite) and TDN concentration. Standard deviations (SD) were determined through the propagation of error associated with each subsequent analysis.

Results

Sample site and source water characteristics

A 200-m depth profile of the Amundsen Sea Polynya site showed elevated PAR, temperature, fluorescence and oxygen concentrations at the surface that generally decreased with depth (Figure 1). All aphotic water used in the bioassay study was taken from 170 m (and not deeper) to ensure that the bacteria used in the relevant treatments came from below the chl max and euphotic zone, oxycline and thermocline, yet had an opportunity for exposure to sinking, solubilizing surface production. Nutrient and chl *a* concentrations for the three source waters are shown in Table 1. Chl *a* concentrations at the time of collection were similar between the ice-algal meltwater and the chl max. As expected, DOC and DON concentrations were lowest in the aphotic zone and concentrations of inorganic nutrients, with the exception of ammonium, were highest. DON concentrations were 6-fold higher in the ice-algal meltwater and nearly 4-fold higher in the chl max than concentrations observed in the aphotic zone. Phosphate concentrations were lowest in the chl max, while nitrate was lowest in the ice-algal meltwater. These results suggest that the aphotic zone bacterioplankton community was likely carbon-limited at the time of collection.

All three sources appear representative of the greater Amundsen Sea and, in some cases, Ross Sea regions. Another ice-algal sample collected in close proximity to and on the same day (24 December 2010) as our

Table 1. *In situ* chemical characteristics of water used in bioassay experiments[a]

Source water	Depth (m)	Chl *a* (µg L^{-1})	DOC (µM C)	NH_4^+ (µM)	NO_3^- (µM)	DON (µM N)	PO_4^{3-} (µM)
Ice-algal meltwater	Surface	39.8 ± 3.2	123.3 ± 4.3	0.28 ± 0.01	7.62 ± 0.06	12.8 ± 0.9	1.26 ± 0.03
Chlorophyll max	10	33.8 ± 2.2	99.2 ± 8.2	0.65 ± 0.02	11.82 ± 0.02	8.21 ± 1.1	0.98 ± 0.0
Aphotic zone	170	ND	42.3 ± 0.2	0.39 ± 0.0	29.4 ± 0.05	2.2 ± 0.4	1.91 ± 0.01

[a]Bacterial communities were given particle-free water, i.e., filtrates of ice-algal meltwater, chlorophyll max water or aphotic zone water, collected from the Amundsen Sea, Antarctica. ND indicates that chlorophyll *a* was not detected.

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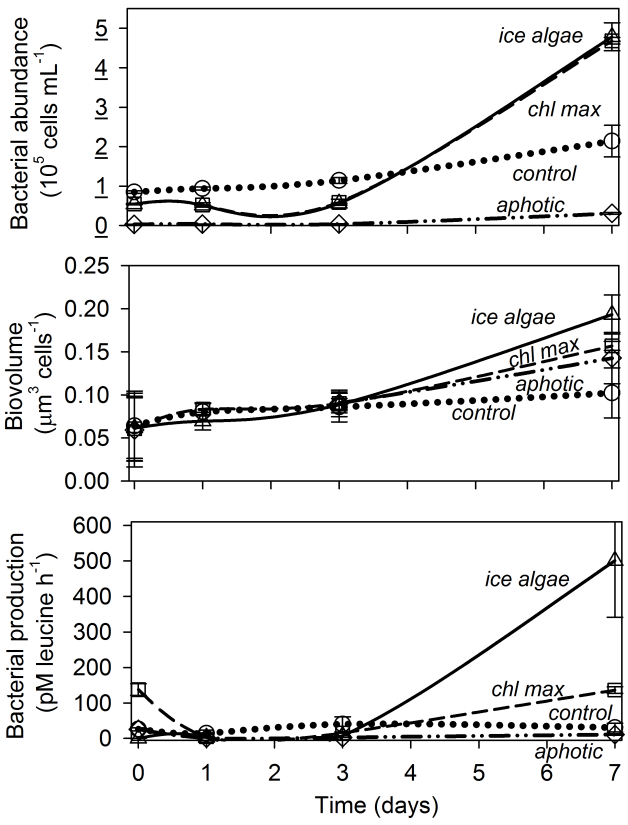

Figure 2

Bacterial responses to DOM treatments over the 7-day incubation experiment.

Bacterial abundance, cell biovolume and heterotrophic production (mean and range of duplicate incubations, n = 2) were measured in particle-free water from ice melt containing ice algae (*ice algae*, solid line), from the chlorophyll maximum (*chl max*, dashed line), or from the aphotic zone (*aphotic*, dotted-dashed line) inoculated with natural bacterial communities. Bacteria for the *ice algae* and *chl max* treatments were collected from the aphotic zone (170 m); bacteria for the *aphotic* treatment were collected from the chlorophyll maximum (10 m). Aphotic zone bacteria receiving no new DOM constituted the control (*control*, dotted line). All water was from the Amundsen Sea Polynya, Antarctica (Figure 1).

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ice-algal sample contained a chl *a* concentration of 38.7 μg chl *a* L^{-1} (station 20 in Arrigo et al., 2014), within one standard deviation of the mean value from our site (39.8 ± 3.2 μg chl *a* L^{-1}, n = 3). High fucoxanthin:chl *a* ratios (0.670) at the site sampled by Arrigo et al. (2014) suggest that the ice-algal mass was dominated by diatoms within the low light interior of the ice in this region. The observed DOC and DON concentrations in the aphotic zone are also similar to concentrations observed in the adjacent Ross Sea. The average DOC concentration in the upper 700 m of the Ross Sea was 41.7 ± 0.3 μM C (Hansell and Carlson, 1998), and DON concentrations ranged between 2.1 and 6.3 μM N (Carlson et al., 2000; Carlson and Hansell, 2003). The average DOC concentration at the aphotic zone depth in this study was 42.4 ± 0.2 μM C (n = 3). The DON concentration at the aphotic zone depth was 2.2 ± 0.4 μM N (n = 3), again well within range of the Ross Sea observations.

Bioassays

Bacterial abundance increased over time in all treatments (Figure 2). As would be expected, the largest increases were observed with the addition of DOM-rich water in both the *ice algae* and *chl max* treatments, amendments that led to increases of 4.24×10^5 cells L^{-1} and 4.14×10^5 cells L^{-1}, respectively, or an approximate 8-fold increase in each case. In the *control,* a modest 2.5-fold (1.29×10^5 cells L^{-1}) increase in bacterial abundance was observed, a result considered reasonable given the dilution of aphotic zone bacterial cells into filtered aphotic zone water. The smallest absolute increase in bacterial abundance was observed in the *aphotic* treatment (2.8×10^4 cells L^{-1}), an amount that corresponded to the greatest relative increase of 11-fold due to low initial abundance.

Like bacterial abundance, cell biovolumes increased the most (2.1-fold) in the *ice algae* treatment. The *chl max* and *aphotic* treatments had lower but similar biovolume increases of 1.6 and 1.4-fold, respectively. As expected, given that no new DOM was introduced, the *control* cell biovolume changed the least (0.6-fold).

Changes in bacterial production throughout the incubation period varied among treatments but reached maximum value at the end of the *ice-algae* treatment. Although bacterial production in the *control* treatments was relatively low and constant throughout the experiment, rates increased in the *ice algae* treatment from < 0.005 pM leucine h^{-1} to ~ 500 pM leucine h^{-1} over the 7-day experiment. This 5-order of magnitude increase held when production rates were normalized to bacterial abundance. Bacterial production rates in both the *chl max* and *aphotic* treatments decreased over the first day, but then increased by day 7. This increase resulted in rates on day 7 being comparable to rates observed on day 0 for *chl max* but lower than rates on day 0 for *aphotic*; on a per cell basis, production rates in both of these treatments were approximately 1 and 2 orders

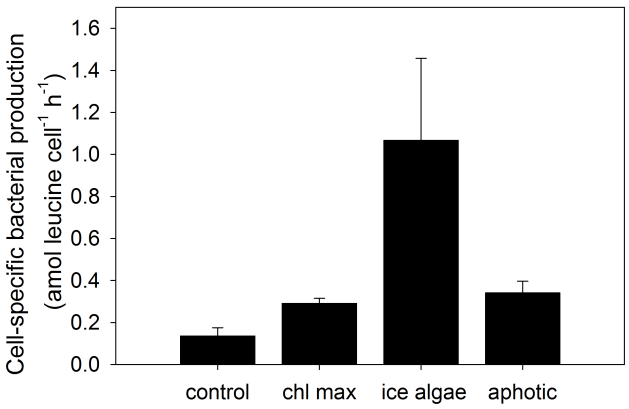

Figure 3

Comparative cell-specific rates of bacterial production at day 7.

The mean and range of duplicate values of cell-specific bacterial production rates are shown for day 7 for all treatments. Bacterial communities were incubated with water from ice melt containing ice algae (*ice algae*), from the chlorophyll maximum (*chl max*), or from aphotic zone water (*aphotic*) for one week. An aphotic zone bacterial control (*control*) containing no new DOM was also included. Bacteria for *ice algae, chl max* and *control* treatments were collected from the aphotic zone (170 m); bacteria for the *aphotic* treatment were collected from the chlorophyll maximum (10 m). All water was from the Amundsen Sea Polynya, Antarctica (Figure 1).

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of magnitude lower, respectively, at day 7 than at day 0. A comparison of cell-specific bacterial production at day 7 (Figure 3) showed that production was greatest for *ice algae,* lowest for *control,* and similar for *chl max* and *aphotic.* These results suggest that the greater response in bacterial production in the *ice algae* treatment was due to both an increase in cell numbers and an increase in the activity of individual cells. The low bulk production rates for the *aphotic* treatment after 7 days (Figure 2) likely resulted from low cell abundance, while the low rates for the *control* treatment reflect low cell-specific activity. Changes in DOC concentration mirrored the bacterial abundance trends (Figure 4, n = 2 in all cases). The greatest decrease in DOC concentration

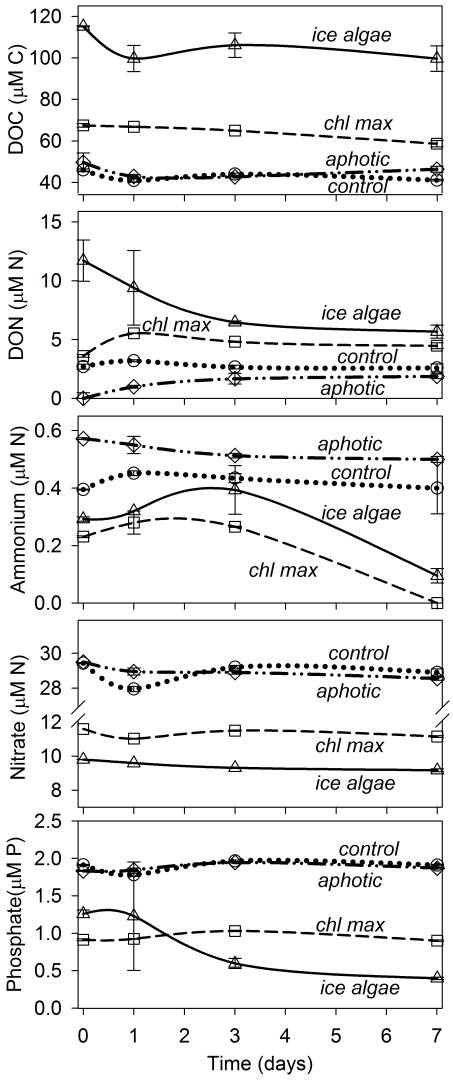

Figure 4

Nutrient dynamics over the 7-day incubation experiment.

Nutrient concentrations (mean and range of duplicate incubations, n = 2) were measured in all treatments over the duration of the experiment, where bacterial communities were amended with particle-free water from ice melt containing ice algae (*ice algae*, solid line), from the chlorophyll maximum (*chl max*, dashed line), or from aphotic zone water (*aphotic*, dotted-dashed line). Bacteria for *ice algae* and *chl max* treatments were collected from the aphotic zone (170 m); bacteria for the *aphotic* treatment were collected from the chlorophyll maximum (10 m). An aphotic zone bacterial control (*control*, dotted line) was also included. All water was from the Amundsen Sea Polynya, Antarctica (Figure 1).

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Table 2. Bacterial carbon demand and growth efficiencies

Treatment[a]	Carbon demand (μM)[b]	Growth (μM C)[c]	Respiration (μM C)[d]	Growth efficiency (%)[e]
ice algae	15.50	2.42	13.08	15.6
chl max	8.85	2.14	6.71	24.2
aphotic	3.25	0.14	3.11	4.2
control	4.91	0.60	4.31	12.1

[a] Bacterial communities were given particle-free water from ice melt containing ice algae *(ice algae),* the chlorophyll maximum (*chl max*), or aphotic zone *(aphotic).* Bacteria for the *ice algae* and *chl max* treatments were collected from the aphotic zone (170 m) and bacteria for *aphotic* were collected from the chlorophyll maximum (10 m). An aphotic bacterial control (*control*) was also tested. All water was from the Amundsen Sea, Antarctic. The bioassay experiments ran for 7 days.
[b] Bacterial carbon demand is the decrease in dissolved organic carbon (DOC) concentration from day 0 to day 7.
[c] Bacterial growth is the increase in bacterial biomass from day 0 and day 7, where biomass was calculated from cell biovolume and abundance using a conversion factor (see text).
[d] Bacterial respiration = Bacterial carbon demand - Bacterial growth
[e] Bacterial growth efficiency = Bacterial growth / (Bacterial carbon demand)
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was observed in the *ice algae* treatment (15.5 ± 9.1 μM C) followed by *chl max* (8.8 ± 0.9 μM C) and *control* (4.9 ± 0.1 μM C). At least 15% of the ice algae DOC and 18% of chl max DOC was bioavailable to aphotic bacterial communities. This percentage was calculated assuming that the bioavailable DOC fraction present in the control was also present and used in the *ice algae* and *chl max* treatments. These proportions of labile DOC are conservative estimates. There was no significant change in DOC concentration in the *aphotic* treatment (3.3 ± 4.5 μM C), which also had the smallest overall increase in bacterial abundance.

Nutrient concentration changes within the four bioassay treatments are shown in Figure 4 (n = 2 in all cases). Phosphate concentrations decreased by 0.86 ± 0.09 μM P or 68% within the *ice algae* treatment but did not decrease in any of the other treatments. The greatest decrease in nitrate was observed in *aphotic* treatment (0.95 ± 0.14 μM NO_3^-) followed by the *ice algae* treatment (0.63 ± 0.12 μM NO_3^-), *control* (0.53 ± 0.24 μM NO_3^-), and then *chl max* treatment (0.45 ± 0.07 μM NO_3^-). Less than 6% of the available nitrate was used per treatment. Similar concentrations of ammonium were used in the *chl max* and *ice algae* treatments over the 7-day incubation: 0.23 ± 0.00 μM NH_4^+ and 0.20 ± 0.02μM NH_4^+, respectively. There was little change (0.07 ± 0.02 μM) in ammonium concentration within the *aphotic* treatment and no change in ammonium concentration within the *control* treatment.

Different nitrogen forms were favored in the different treatments. Although all forms of N investigated decreased within the *ice algae* treatment, DON (6.0 ± 1.7 μM N) was the dominant source of N used. This decrease in DON corresponds to 65% of the total DON added in the *ice algae* treatment. Ammonium was favored in the *chl max* (0.23 ± 0.00 μM NH_4^+) treatment, while nitrate was favored in the *aphotic* (0.95 ± 0.14 μM NO_3^-) and *control* (0.53 ± 0.24 μM NO_3^-) treatments.

Combined, the bacterial response and associated drawdown of nutrients show that DOM produced by ice algae is more bioavailable to aphotic zone bacterioplankton than DOM produced, and likely degraded within, the chl max. Bacteria from the chl max responded to nutrients from the aphotic zone but much less so than bacteria from the aphotic zone. The change in bacterial C content derived from cell biovolume, an estimate of bacterial growth, and the change in DOC, an estimate of bacterial C demand, over the course of the experiment was used to estimate the loss of organic C from bacterial respiration (ΔDOC – Δbacterial C content = bacterial respiration; Table 2). Respiration was greatest in the *ice algae* treatment, resulting in a bacterial C demand (bacterial growth + respiration) for ice-algal meltwater of 15.5 μM C over the 7-day experiment. The lowest bacterial C demand was seen in the *aphotic* treatment (3.25 μM C), which also had both the lowest change in bacterial growth (0.14 μM C) and respiration (3.11 μM C). The range in bacterial growth efficiencies among treatments was 6-fold, being highest for *chl max* (24%) and lowest for *aphotic* (4%) treatments.

Discussion

The full importance of ice-algal production and how reduced sea ice coverage will impact polar ecosystems and global elemental cycles are still not well known. These areas of research are crucial for predicting ecological impacts and obtaining accurate global carbon cycle estimates. The DOM produced at the seawater-ice interface differs in concentration and composition from open-water DOM (discussed in Thomas and Dieckmann, 2002; Arrigo and Thomas, 2004). These differences in the quantity and quality of DOM likely contribute to the large variations in bacterial growth efficiencies observed in the Amundsen Sea (2–28%; Williams et al., 2015).

The overall greatest bacterial response in this study occurred when aphotic bacteria were given ice-algal meltwater (*ice algae*). Bacterial abundance and cell biovolume increased nearly 8.8-fold and 2.1-fold, respectively.

Similarly, Niemi et al. (2014) found that the apparent cell size of Arctic surface water bacteria and archaea increased 2.1- to 3.2-fold when DOC from sea ice was added.

The most dramatic response we observed was in bacterial production rates, which increased five orders of magnitude in the *ice algae* treatment over the 7-day experiment. Higher cell-specific production rates at day 7 for *ice algae* treatment compared to the other three treatments further highlight the dynamic response of bacteria to ice algal DOM (Figure 4). Similar results were reported for experiments using seawater cultures in the sub-polar Antarctic where DOM (and bacteria) from ice melt stimulated growth and activity in pelagic water by at least an order of magnitude compared to DOM available in surface waters (Kähler et al., 1997). In combination, these two studies suggest that greater stimulation of bacterioplankton by DOM from sea ice compared to pelagic DOM may be common across sub-polar and polar regions in Antarctic waters for both surface and aphotic bacteria communities.

The different responses by aphotic bacterial communities to DOM from ice algae (*ice algae*) and the chl max (*chl max*) in our experiments may be due to both the quantity and quality of the DOM. Higher concentrations of DOC and DON were added in the *ice algae* treatment than in the *chl max* treatment (Figure 3). However, the bacteria contained in both treatments were still in exponential growth phase (based on changes in cell abundance) at the end of the experiment and had similar changes in bacterial abundance over the 7-day incubation (Figure 2). These observations suggest that DOC was not limiting bacterial growth in the *chl max* treatment throughout the duration of this study, although C-limitation would likely have occurred if the incubations had been longer.

Sea ice is often characterized by high concentrations of DOM (Herborg et al., 2001; Carlson and Hansell, 2003; Papadimitriou et al., 2007; Niemi et al., 2014), sometimes approaching or exceeding millimolar concentrations in sea ice from the Amundsen Sea (Thomas et al., 1998). A large component of the DOM pool in sea ice is from extracellular polymeric substances (EPS; Underwood et al., 2010) that are released by algae and bacteria (Krembs et al., 2011). EPS in Antarctic sea ice can be rich in carbohydrates (Underwood et al., 2010, 2013), thus contributions from EPS may explain the high DOC:DON (19.0 ± 4.2) ratios previously observed in sea ice (Papadimitriou et al., 2007). However, the DOC:DON ratio that we observed in the ice-algal meltwater (9.6) was lower than the DOC:DON ratio observed in the chl max water (12.1), suggesting that the chl max water may have been more processed by heterotrophs before sampling than the ice-algal meltwater. An alternative explanation takes into account the type of algae in the study region. We observed large blooms of *Phaeocystis antarctica* in the Amundsen Sea at the time of sampling (Alderkamp et al., 2015), which can excrete 11% of their primary production as DOM (Carlson et al., 1998). Colonial *Phaeocystis* blooms generate large amounts of extracellular mucus, rich in carbohydrates (Alderkamp et al., 2007), which could have contributed to the higher DOC:DON ratios in the chl max water.

The accumulation of DOM in sea ice indicates that DOM is produced faster than sympagic (ice-associated) heterotrophs consume it (discussed in Pomeroy and Wiebe, 2001; Carlson and Hansell, 2003). When sea ice melts, this ice DOM becomes available to bacterioplankton, stimulating their growth and activity as seen previously in sub-polar Antarctic waters (< 60°S; Kähler et al., 1997; Giesenhagen et al., 1999), in the Ross Sea (Carlson and Hansell, 2003), near Davis Base (Gibson et al., 1990), in the Arctic (Amon et al., 2001; Niemi et al., 2014) and reported here for the Amundsen Sea (> 70°S). DOM from ice algae may also become available to aphotic bacteria through the solubilization of sinking particulates (Kähler and Bauerfeind, 2001) that include ice algae, or possibly through mixing caused by the movement of icebergs (Helly et al., 2011) that have keels estimated to a depth of 633 m in the Pine Island Bay region of the Amundsen Sea and 316 m in the neighboring Ross Sea (Dowdeswell and Bamber, 2007). The direct release of ice-algal DOM into the water column during ice melt, however, does not occur in isolation, but together with living and dead sympagic algae and bacteria. The concurrent release of cells and DOM leads to enhanced bacterial activity in surface waters compared to release of ice DOM alone (Giesenhagen et al., 1999). This enhanced activity likely influences the concentration and composition of ice-algal DOM that eventually reaches the aphotic zone. Interactions among sympagic microorganisms, microplankton and the composition of DOM sourced from ice algae are not well understood and deserve further attention to determine the fate of ice-algal DOM after its release into the water column. This study is a step towards understanding the interactions between pelagic bacteria and sea-ice DOM.

A substantial, but variable fraction of DOM in ice-algal meltwater and the chl max water is labile. At least 15% of DOC and 65% of DON added with the ice-algal meltwater was consumed by aphotic bacterial communities (*ice algae*) over the relatively short, one-week incubation. The DOC contained within the chl max was at least 18% bioavailable to aphotic bacteria (*chl max*), while none of the DON was labile based on an overall increase in bulk DON concentration within that treatment. It is likely that portions of the DON pool were cycled without an observable change in DON concentration (Sipler and Bronk, 2014); however, this cycling would not support large changes in bacterial growth or cell volume. Because bacteria were still exponentially growing in both DOM-enriched treatments at the end of the week-long experiment, these estimates likely underestimate the labile fraction of DOM. The values observed in the current study are lower than those found in sub-polar Antarctic waters, where 63% and 56% of DOC from sea ice and surface waters, respectively, were consumed by bacterioplankton over two weeks (Kähler et al., 1997). In

the sub-polar experiments, however, the sea-ice DOM treatment included additions of sympagic bacteria, which could have enhanced the bacterial response relative to adding ice DOM alone (Geisenhagen et al., 1999). Surface bacterial communities in the southern Ross Sea consumed a similar fraction of DOC (8–17%; Carlson et al., 1999) to what we observed for aphotic bacterial communities in the Amundsen Sea, although the chlorophyll *a* levels in the Ross Sea study (≤ 6 μg L^{-1}) were much lower than what was observed in the current study. The proportions of labile DOC observed in the current study are also similar to those found in the Arctic, where ~ 20 to 30% of sea-ice DOC was found to be bioavailable to surface water bacteria on time scales of one week and ten days, respectively (Amon et al., 2011; Niemi et al., 2014).

The lability of a DOM pool is determined by its chemical composition and the ability of the receiving community to use it. Polar bacteria appear well adapted to take advantage of algae-derived DOM sources despite low temperatures (Kirchman et al., 2009). For example, a large proportion of Arctic surface bacteria are able to actively assimilate specific phytoplankton byproducts including free amino acids (Elifantz et al., 2007; Nikrad et al., 2012; Baer, 2013) and diatom-derived extracellular polymers (Elifantz et al., 2007). Work by Williams et al. (2013) in Newcomb Bay in the Eastern Antarctic suggests that surface *Flavobacteria* are the group primarily degrading phytoplankton-derived DOM. Additional studies are needed to determine if similar groups are responsible for DOM degradation at aphotic depths.

An interesting result from the current study was that different forms of nitrogen were favored in the different treatments. DON was favored in the *ice algae* treatment, while inorganic forms appeared to be favored in the remaining treatments; specifically ammonium in the *chl max* treatment and nitrate in the *aphotic* and *control* treatments. It is unclear if the form of N used in the various treatments limited growth or C uptake, especially for *aphotic* and *control* treatments, which had the lowest growth and respiration and primarily used nitrate. However, it is more likely that the concentration and composition of the DOC and DON supplied with each treatment played a larger role in determining the N source and amount of N used. For example, a study conducted along the western Antarctic Peninsula showed that additions of glucose with or without added ammonium resulted in a much larger increase in bacterial abundance (2–10 fold) and bacterial production (2–30 fold) than additions of ammonium alone, which were more similar to the control treatments (Ducklow et al., 2011). The lack of DON drawdown in the *control*, *chl max* and *aphotic* treatments suggests that DON added in these treatments was less available to the receiving bacterial community than the DON supplied in the *ice algae* treatment. However, some DON cycling likely occurred without observing significant decreases in concentration (Sipler and Bronk, 2014).

Bacterial community composition was also not likely the determining factor for which N substrate was used per treatment. Although the bacterial communities likely changed over time, the *control*, *ice algae* and *chl max* treatments started with the same initial bacterial community. Therefore, based on the community alone, each of these three different treatments began with the same potential for N use. Future studies are needed to determine if the same bacteria are using the various N sources or if different species within a given population become active under these different biogeochemical conditions, and how the use of different N species relates to C cycling and demand, bacterial growth efficiency and phosphorus cycling.

The drawdown of DOC in this experiment reflects a bacterial demand for DOC in ice-algal meltwater that was almost double that for DOC in the chl max. Yet, aphotic bacteria in both the *ice algae* and *chl max* treatments used a similar quantity of DOC for growth over the 7-day incubation. This results in greater amounts of C being lost to respiration and lower growth efficiencies in the *ice algae* treatment compared with the *chl max*. Growth efficiencies were not related to DOC:DON ratios (cf. Goldman et al., 1987) in the initial source water or at the final time point, which suggests that something other than bulk DOC:DON ratios were responsible for the observed growth efficiencies. Surprisingly, there was no obvious use of DON in the *chl max* treatment, which had the highest growth efficiencies, but substantial DON use in the *ice algae* treatment where 68% of DON was used. Further, the fate of DOC in the aphotic zone varied depending on the origin of the bacterial community, where aphotic bacteria (*control*) had higher carbon demands and growth efficiencies than bacteria from the chlorophyll max (*aphotic*). These results emphasize that the fate of DOC in the Amundsen Sea would vary depending on the source of DOM and the bacterial community.

The range of growth efficiencies among treatments in the current study is similar to the range found in the Ross Sea using seawater cultures (Carlson et al., 1999), in the Amundsen Sea from in situ measurements (Williams et al., 2015) and in the western Arctic (Nguyen and Maranger, 2011; Nguyen et al., 2012). Together, these results suggest that the range reported by Williams et al. (2015) for the Amundsen Sea likely resulted from bacterial taxa active in the uptake of DOM and differing contributions of labile DOM from phytoplankton and ice algae and persistent DOM (such as from the aphotic zone). Future research is needed to investigate how the biochemical composition of DOC and DON from the chl max and sea ice change over time, whether the initial composition can predict the fate of C (either to respiration, biomass synthesis, or remaining as DOM), and if the source of DOM alters community composition.

Similar studies conducted in the North Atlantic compared the availability of surface DOM to surface bacterioplankton and upper mesopelagic bacterioplankton populations (Carlson et al., 2004; Letscher et al., 2013). These studies found that upper mesopelagic bacteria may be better at utilizing surface DOC (Carlson et al., 2004) and DON (Letscher et al., 2013) than surface bacterioplankton communities. Bacterial growth

efficiencies for the surface DOM + mesopelagic bacteria ranged between 3 and 15% (Carlson et al., 2004). Carlson et al., (2004) also investigated the associated bacterial community composition, finding that the diversity of the mesopelagic bacterial community decreased over the 7–10 day incubation when surface DOM was added. This result indicates that only a portion of the community may be able to take advantage of the semi-labile surface DOC pool.

Because the response of surface bacterial communities to DOM from the chl max or ice-algal meltwater was not determined, it is not known if DOM from these sources was more available to the deeper community than to the surface community, as found by Carlson et al. (2004) and Letscher et al. (2013). However, the results of the current study emphasize that aphotic bacteria are able to respond to inputs of DOM produced in the euphotic zone. Further, the low drawdown of DOM from aphotic zone water was similar for the aphotic bacterial community (*control*) and the chl max bacterial community (*aphotic*). If the composition of these two communities differed (e.g., Kim et al., 2014), then this similarity in DOM usage would have suggested that community composition had little influence on the utilization of DOM found in the aphotic zone. The DOC concentration in the aphotic zone (42.3 μM) was similar to the mean concentration of DOC in winter and early spring throughout the water column in the Ross Sea (41.8 μM; Carlson and Hansell, 2003), and in deep Antarctic Polar Front water (Hansell and Carlson, 1998), which Carlson and Hansell (2003) consider a 'background' DOC concentration. Thus, DOC concentrations in the aphotic zone in the Amundsen Sea Polynya likely also represent a more persistent, background pool of DOC.

One aspect that may be important, but was not addressed in this study, is the age of the sea ice from which the DOM sample was taken. Newly formed sea ice has a very different microbial assemblage than older sea ice. As sea ice ages the phytoplankton assemblage changes from large pennate diatoms to smaller centric diatoms and nanoflagellates (Gleitz and Thomas, 1993). The thickness, age and type of sea ice may contribute to observed variability in sea-ice inorganic and organic nutrient concentrations (reviewed in Thomas and Dieckmann, 2002). Therefore, many factors, including irradiance levels, inorganic nutrient concentrations, and age and type of sea ice, will directly impact the DOM concentration and composition and thus utilization and respiration efficiency of sea ice DOM.

We suggest that this work has large implications for elemental cycles in a changing climate. Unlike much of the Southern Ocean, climatic changes that include decreases in sea-ice coverage and acceleration of sea level rise in the Western Antarctic (Steig et al., 2009; Lee et al., 2010) and specifically the Amundsen Sea (Jacobs and Comiso, 1997; Kreutz et al., 2000; Thomas et al., 2004; Pritchard et al., 2012) are occurring at alarming rates. The Amundsen Sea Polynya is currently the most productive region of the Southern Ocean, with chl *a* values 2–3 fold higher than other Antarctic polynyas (Arrigo and Van Dijken, 2003). Ice algae represent a small but important portion of the primary production in the region (Arrigo et al., 2012; Arrigo et al., 2014). Therefore, loss of sea ice, earlier retreats and longer ice-free periods have significant implications for those species that depend on ice algae for survival. Ice-algal production accounts for approximately 25% of total annual primary production in ice-covered seas (Arrigo and Thomas, 2004). The expected loss in sea-ice coverage over the next century is predicted to increase primary production through increased pelagic production in the Southern Ocean. A 25% loss in sea-ice coverage is estimated to increase primary production by approximately 10% (Arrigo and Thomas, 2004). The calculated bacterial growth efficiencies and respiration rates for ice-algae and chl max DOM suggest that changes in the timing and intensity of ice-algal and pelagic production could have consequences for C and N cycling, including both organic and inorganic pools. This study emphasizes that DOM sources, their corresponding lability, and the growth efficiency of bacterial consumers must be considered to predict climate change impacts on elemental cycles within the Amundsen Sea and greater Western Antarctic region.

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Contributions

- RES and TLC contributed to conception and design, acquired, analyzed and interpreted the data, wrote and revised the article, and approved the submitted version for publication.

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Competing interests

The authors declare no competing interests.

Supplemental material

Figure S1. Depth profiles of nutrient concentrations at the study site.
Depth profiles of dissolved organic carbon (DOC), dissolved organic nitrogen (DON), ammonium (NH4+), nitrate (NO3–), and phosphate (PO43–) are presented for the station in the Amundsen Sea, Antarctica (73°25.01′S, 115°15.103′W), where water from the chlorophyll max (10 m) and aphotic zone (170 m) were collected for use in bioassay experiments. doi: 10.12952/journal.elementa.000060.s001

Data accessibility statement

All data are included within this manuscript.