Short-term processing of ice algal- and phytoplankton-derived carbon by Arctic benthic communities revealed through isotope labelling experiments

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ABSTRACT: Benthic ecosystems play a significant role in the carbon (C) cycle through remineralization of organic matter reaching the seafloor. Ice algae and phytoplankton are major C sources for Arctic benthic consumers, but climate change-mediated loss of summer sea ice is predicted to change Arctic marine primary production by increasing phytoplankton and reducing ice algal contributions. To investigate the impact of changing algal C sources on benthic C processing, 2 isotope tracing experiments on ^{13}C-labelled ice algae and phytoplankton were conducted in the North Water Polynya (NOW; 709 m depth) and Lancaster Sound (LS; 794 m) in the Canadian Arctic, during which the fate of ice algal (C_{IA}) and phytoplankton (C_{PP}) C added to sediment cores was traced over 4 d. No difference in sediment community oxygen consumption (SCOC, indicative of total C turnover) between the background measurements and ice algal or phytoplankton cores was found at either site. Most of the processed algal C was respired, with significantly more C_{PP} than C_{IA} being released as dissolved inorganic C at both sites. Macroinfaunal uptake of algal C was minor, but bacterial assimilation accounted for 33–44 % of total algal C processing, with no differences in bacterial uptake of C_{PP} and C_{IA} found at either site. Overall, the total processing (i.e. assimilation and respiration) of C_{PP} was 33 and 37 % higher than processing of C_{IA} in NOW and in LS, respectively, suggesting that the future changes in quality of organic matter sinking to the seafloor could impact the C residence time at the seafloor.

KEY WORDS: Arctic · Carbon cycling · Sediment · Respiration · ^{13}C · Bacteria · Benthic–pelagic coupling · Sea ice cover

INTRODUCTION

Benthic communities below the euphotic zone rely on the particulate organic carbon (POC) exported from surface waters as their main C source, which closely links the euphotic zone primary production (PP) to deep sea ecosystem functioning (Ambrose & Renaud 1995, Gooday 2002). In the Arctic Ocean, the bulk of the organic matter flux to the seafloor is made up of the 2 main groups of primary producers: ice algae living in association with sea ice, and phytoplankton living in the water column. Ice algae can contribute up to 40 % to overall annual PP in season-ally ice-covered regions (Gosselin et al. 1997, Hegseth 1998, Forest et al. 2011, Dupont 2012), with their contribution increasing to 90 % in the central Arctic Ocean (Matrai & Apollonio 2013, Fernández-Méndez et al. 2015). Ice algae can take advantage of low light levels and bloom early in the spring when zooplankton grazing is low (Hunt et al. 2002, Caron et al. 2004, Tremblay et al. 2006). This allows for a large proportion of the ice algal biomass to sink to the seafloor after ice break-up, where it provides an important initial C source for benthos after the food-limited winter (McMahon et al. 2006, Boetius et al. 2013, North et al. 2014). However, climate change is

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rapidly reducing the thickness and extent of the multi-year sea ice while delaying the formation of new first-year ice (Frey et al. 2015, Wang & Overland 2015, Wood et al. 2015), changing the patterns of Arctic PP. As ice algae are dependent on sea ice for growth (Leu et al. 2015), the shortening of the ice-covered period is likely to reduce ice algal PP (Søreide et al. 2010, Leu et al. 2011) and consequently, export of ice algal biomass to the seafloor (Carroll & Carroll 2003). On the other hand, the longer open water period benefits pelagic algae as it increases their habitat and lengthens the phytoplankton growth season (Arrigo et al. 2008, Arrigo & van Dijken 2015). As a consequence, the overall annual Arctic marine PP has increased by 1.6–10% yr^{-1} since 1998 (Arrigo et al. 2008, Bélanger et al. 2013, Arrigo & van Dijken 2015). The increasing phytoplankton PP has been proposed to enhance the efficiency of the biological pump that transports POC to the seafloor (Caron et al. 2004, Nishino et al. 2009, Manizza et al. 2013), although warmer conditions can also increase zooplankton grazing, limiting the C export (Piepenburg 2005, Carmack & Wassmann 2006, Grebmeier et al. 2006b).

Benthic communities play a significant role in marine C cycling through assimilation and remineralization of the POC deposited at the seafloor (Moodley et al. 2005). The speed and magnitude of the processing depends on environmental factors such as water temperature (Moodley et al. 2005, Woulds et al. 2009), as well as the quantity (Bühring et al. 2006b, Morata et al. 2015) and quality (Byrén et al. 2006, Morata & Renaud 2008, Mayor et al. 2012a, Hunter et al. 2013) of the organic matter available. High-quality organic matter is often characterized by having a high labile organic carbon content, often measured through the fatty acid composition and pigment and C:N ratios (Morata & Renaud 2008, Mayor et al. 2012a, Hunter et al. 2013). Ice algae have a higher essential fatty acid content than phytoplankton (Falk-Petersen et al. 1998, McMahon et al. 2006, Sun et al. 2009, Wang et al. 2014), which makes them a superior-quality food item for marine consumers that require these fatty acids for growth and reproduction (Jónasdóttir et al. 2009, Søreide et al. 2010, Leu et al. 2011). Although ice algal aggregates can remain buoyant under sea ice due to photosynthetic gas bubble production (Assmy et al. 2013, Fernández-Méndez et al. 2014), ice algae rapidly sink below the euphotic zone once the buoyancy is lost, often reaching the deep seafloor within a day after being released to the water column (Syvertsen 1991, Haecky et al. 1998, Katlein et al. 2015). Phytoplankton, on the other hand, have a

longer residence time in the water column due to the slow sinking rates and resuspension (Rutgers van der Loeff et al. 2002), which can lead to higher bacterial degradation during sinking, decreasing the quality of the algal cells reaching the seafloor (Morata & Renaud 2008, Roy et al. 2015). As C respiration and uptake by benthos often increase with the quality of organic matter available (Morata & Renaud 2008, Mayor et al. 2012a, Hunter et al. 2013), the decrease in high-quality ice algal inputs in favour of phytoplankton can impact sediment C cycling.

To date, only a few studies have investigated the responses of benthos to ice algae and phytoplankton, and the consequent impacts on C cycling processes. While certain bivalves and deposit feeding taxa preferentially consume ice algae over phytoplankton in shallow subtidal sites in Alaska and Svalbard (McMahon et al. 2006, Sun et al. 2009), other faunal communities efficiently assimilate both ice algal and phytoplankton C, with no taxa in the Canadian Arctic deep sea exclusively preferring ice algae (Mäkelä et al. 2017a). Macrofaunal uptake, however, is usually a minor pathway in the total POC processing at the seafloor (Heip et al. 2001, Hunter et al. 2012, Findlay et al. 2015).

The responses of bacteria, which are major contributors to the processing of deposited phytodetritus (Gooday 2002, Moodley et al. 2002) are less understood. Sun et al. (2009) demonstrated rapid assimilation of ice algal C by sediment bacterial communities in Alaska, while both ice algal and phytoplankton inputs have been shown to stimulate bacterial growth during sediment incubation experiments (Sun et al. 2007, Hoffmann et al. 2017). The bacterial growth efficiency, describing the ratio of production of new biomass (bacterial secondary production) to remineralization of the organic C (bacterial respiration) (del Giorgio & Cole 1998), is known to vary depending on the quality of the available C source (Tamburini et al. 2003, Mayor et al. 2012a), but the impacts of ice algae and phytoplankton on bacterial growth efficiency have been reported to be similar (Hoffmann et al. 2017).

Respiration, which refers to the oxidation of organic matter (here, POC) to yield energy, and to release CO_2 (abiotic dissolved inorganic carbon, DIC) as a waste product (Findlay et al. 2015), is often the main pathway for POC processing in Arctic shelf sediments (Graf et al. 1995, Macdonald et al. 1998, Findlay et al. 2015). A commonly used proxy for assessing the benthic C respiration rates is measuring the sediment community oxygen consumption (SCOC), which can be converted into respiration rates using a C conver-

sion factor (Rowe et al. 1997). Several studies have demonstrated that deposition of phytodetritus to the seafloor, often after spring algal blooms, triggers a measurable increase in SCOC rates (Rysgaard et al. 1998, Renaud et al. 2007b, 2008). Additionally, incubation experiments with added phytodetritus have shown SCOC to be higher after ice algal than phytoplankton deposition (McMahon et al. 2006, Sun et al. 2007), suggesting preferential respiration of ice algal POC by Arctic benthic communities. However, while SCOC provides an indication of the total C turnover, it encompasses both the biological respiration of all organisms in the sediments and the chemical oxidation of reduced compounds, without differentiating the role of different organisms in the measurement (Piepenburg 2005). As information on the role of specific benthic community fractions in the cycling of C in the Arctic Ocean is still limited (Piepenburg 2005, Werner et al. 2016), an isotope tracing approach can be applied to investigate the contributions of specific actors and pathways to POC processing (Witte et al. 2003b, Moodley et al. 2005, Gontikaki et al. 2011a). Addition of a ^{13}C-enriched C source allows for the flow of the added C to be traced into tissues of consumers or through respiration via release of ^{13}C-enriched DIC (to be distinguished from total C respiration calculated from SCOC), allowing for the rates of processing of the added C to be quantified (Peterson 1999). Additionally, the role of microbes in C processing can be shown through incorporation of the isotope tracer into bacterial specific biomarkers, such as certain phospholipid fatty acids (Boschker et al. 1998, Boschker & Middelburg 2002). Following the fate of ice algal (C_{IA}) and phytoplankton (C_{PP}) C through different C processing pathways therefore allows us to estimate the potential impact of changing the C source on benthic ecosystem functioning.

The aim of this study was to compare, through isotope labelling experiments, the short-term processing of C_{IA} and C_{PP} by intact Arctic deep sea benthic communities in 2 Canadian Arctic Archipelago sites, i.e. the North Water Polynya and Lancaster Sound. Detailed macroinfaunal uptake of C_{IA} and C_{PP} during the experiments is reported in Mäkelä et al. (2017a). Here the fate of C_{IA} and C_{PP} is traced through algal-derived respiration (i.e. release of $DI^{13}C$) and assimilation into bacterial biomass during 4 d incubation experiments. Additionally, the impact of ice algae and phytoplankton on bacterial growth efficiency and the total sediment C turnover, calculated from SCOC, were measured. We hypothesize that the rates of C_{IA} processing (release of $DI^{13}C$ and bacterial uptake) are higher than C_{PP} processing rates at both sites.

MATERIALS AND METHODS

Sampling sites

The experiments took place aboard the research icebreaker CCGS 'Amundsen' during the ArcticNet 2013 cruise. The 2 study locations, the North Water Polynya (NOW, Station 124) and Lancaster Sound (LS, Station 323), are located in western Baffin Bay in the Canadian Arctic Archipelago (Fig. 1, Table 1). The sites are known as hotspots for both Arctic marine PP (Klein et al. 2002, Lalande et al. 2009, Roy et al. 2015) and benthic faunal diversity and biomass (Thomson 1982, Link et al. 2013b, Mäkelä et al. 2017b). The annual PP rates in LS (60 g C m^{-2} yr^{-1}) and NOW (254 g C m^{-2} yr^{-1}) (Welch et al. 1992, Klein et al. 2002) are dominated by phytoplankton, with 3 and 10 % of PP attributed to ice algae in NOW and LS, respectively (Welch et al. 1992, Michel et al. 2002, Tremblay et al. 2006). The difference in the type and magnitude of PP creates an interesting contrast between LS and NOW, which contributed to the study site selection. Sampling sites are described in detail in Mäkelä et al. (2017a,b).

Algal cultures

Prior to the experiments, axenic cultures of the pennate ice algal species *Synedropsis hyperborea* (CCMP 1422) and the centric phytoplankton species *Thalassiosira nordenskioeldii* (CCMP 995, both Bigelow Laboratory for Ocean Sciences) were grown in the laboratory at 0°C on a 12:12 h light:dark cycle in f/2 artificial seawater media (Grasshoff et al. 1999), amended with 50 % ^{13}C-bicarbonate and 50 % ^{15}N-nitrate. The seawater was sterilized prior to the addition of filter-sterilized nutrients. Both species are diatoms and are commonly found in the ice algal and phytoplankton communities, respectively, in the Arctic Ocean (Hegseth 1998, Lovejoy et al. 2002, von Quillfeldt et al. 2003, Tamelander et al. 2009). The algae were harvested by centrifugation, freeze dried and stored at −80°C until the research cruise.

Sample collection and experimental design

Sample collection and experimental design are described in detail in Mäkelä et al. (2017a). Briefly, 2 USNEL box cores (0.25 m^2) were taken from the seafloor at each station to allow for the collection of 15 sediment cores (~40 cm tall, 9.4−10 cm diam-
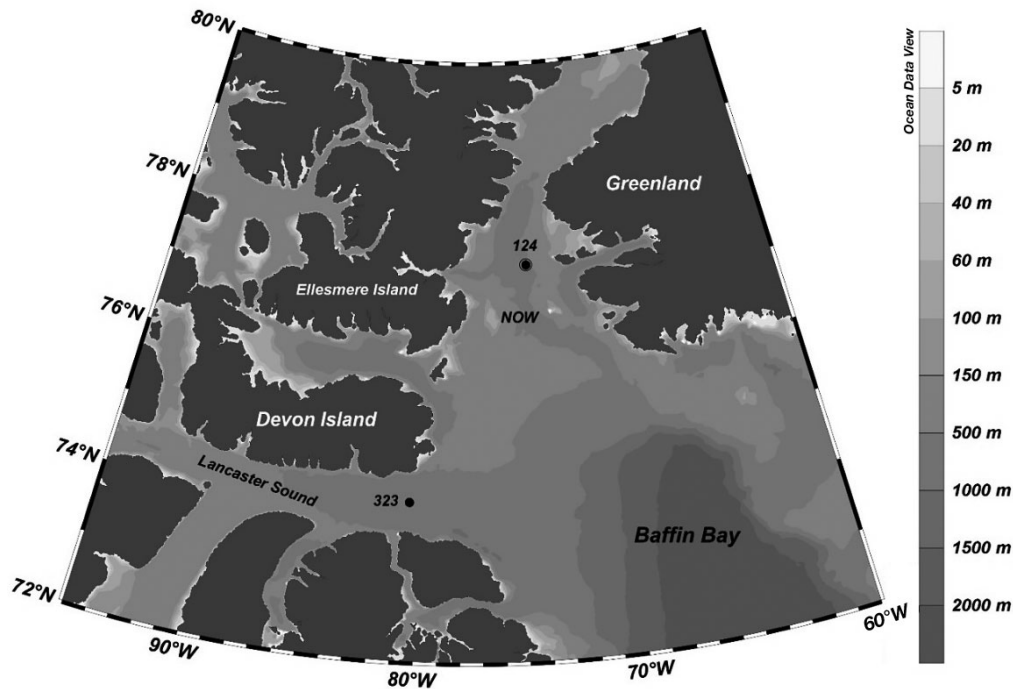
Fig. 1. Locations of the sampling sites in the North Water Polynya (NOW, Stn 124) and Lancaster Sound (LS, Stn 323) in the Canadian Arctic Archipelago

Table 1. Station locations and hydrographic and sediment characteristics during the ArcticNet 2013 cruise

Parameter	Lancaster Sound	North Water Polynya
ArcticNet 2013 station number	323	124
Date sampled	14 August 2013	27 August 2013
Depth (m)	794	709
Latitude	74° 9.41 N	77° 20.79 N
Longitude	80° 28.32 W	74° 17.50 W
Bottom O_2 concentration (ml l^{-1})	4.1	5.6
Bottom temperature (°C)	1.2	−0.1
Bottom salinity	34.5	34.4
Ice free conditions before sampling (d)	59	79

eter). The sub-cores were topped with bottom water, sealed and allowed to settle for 8–15 h before algae were added to the cores to mark the beginning of the experiments. The amount of algae added corresponded to 25% of the estimated annual POC flux at the study sites, but as no POC flux data for LS exist, the POC export estimate for Cape Bathurst Polynya (Lalande et al. 2009) was used as a reference point following the approach of Mäkelä et al. (2017a). The resulting algal additions were 1475 mg C m^{-2} in NOW and 600 mg C m^{-2} in LS, adjusted to C content of ice algae and phytoplankton appropriately. At each site, 3 cores acted as controls (without algal addition) for background SCOC measurements and bacterial phospholipid fatty acid and macrofaunal $\delta^{13}C$ signatures, while 6 experimental cores were amended with ice algae and 6 cores with phytoplankton. The cores were incubated for 4 d in darkness at 4°C. The overlying water column was continuously stirred with magnetic stirrers attached to a motor on the core lid. Oxygen concentration was recorded once a day using an oxygen dipping probe (DP-PSt3 and Fibox 3 LCD-trace v6, PreSens), inserted through a small opening in the core lid. A 10 ml water sample was taken every day for DIC analysis, and the water volume was replaced by previously collected bottom water from the sampling sites. The DIC samples were filtered through a 0.2 µm syringe filter into a gas-tight 3.6 ml glass vial poisoned with saturated $HgCl_2$ to stop bacterial activity, and stored at 4°C until analysis. At the end of the experiments, the cores were halved vertically, with one half used for macrofaunal tissue isotope analysis. For detailed macrofaunal sample preparation, analysis and algal uptake results see Mäkelä et al.

(2017a,b). The other half was sliced at 0–0.5, 0.5–1 and 1–2 cm sediment horizons and stored at −80°C for phospholipid fatty acid analysis to examine bacterial biomass and label uptake. Three control, ice algal and phytoplankton cores each were analysed for phospholipid fatty acids. The sediments were freeze dried prior to lipid extractions.

Respiration of labelled algae

In the laboratory, 100 µl of each poisoned water sample were pipetted into a 12 ml Exetainer® vial and capped. The vials were then flush-filled with N_2 gas using a Gas-bench II (Thermo Finnigan), and 100 µl of 1.3M H_3PO_4 were injected through the septa of the cap into the sample and left overnight. The C isotope ratio of the CO_2 released into the headspace of the Exetainers was analysed using a Gas-bench II connected to a DeltaPlus Advantage isotope ratio mass spectrometer (Thermo Finnigan). Through use of the Valco valve and a sample loop within the gas bench and the instrument Isodat NT software version 2.0, each Exetainer was sampled 9 times, of which the last 5 values were averaged to give a single sample value. The carbon isotope ratios, all expressed relative to Vienna PeeDee belemnite (VPDB), were traceable to International Atomic Energy Agency (IAEA) reference material NBS 19 TS-Limestone. Repeated analysis of a quality control standard gas indicated that the precision of the gas bench for analysing $\delta^{13}C$ of CO_2 at a concentration of 450 ppm in exetainers was −35.03 ± 0.24‰ (mean ± SD, n = 65).

Lipid extraction and separation

The lipids were extracted following the extraction protocol of Bligh & Dyer (1959) as modified by White et al. (1979). Approximately 3 g of freeze-dried sediment were weighed into glass centrifuge tubes and extracted with a single-phase extraction mixture containing chloroform, methanol and citrate buffer (1:2:0.8 v:v:v) over 2 h. The total lipid extract was fractionated on silicic acid columns (6 ml ISOLUTE SI SPE columns, International Sorbent Technologies) by sequential elution with chloroform (neutral lipids), acetone (glycolipids) and methanol (phospholipids). Phospholipids were transmethylated under alkaline methanolysis to obtain fatty acid methyl esters (FAMEs).

FAME quantification and identification and compound-specific $\delta^{13}C$ determination

The quantity and $\delta^{13}C$ signature of individual FAMEs was determined simultaneously on a GC Trace Ultra with combustion column attached via a GC Combustion III to a Delta V Advantage isotope ratio mass spectrometer (all Thermo Finnigan). Running conditions, data processing and peak identification are described by Main et al. (2015). The $\delta^{13}C_{VPDB}$ values (‰) of the FAMEs were calculated with respect to a CO_2 reference gas injected with every sample and traceable to IAEA reference material NBS 19 TS-Limestone. Typical $\delta^{13}C$ FAME analysis precision for natural abundance samples was confirmed by the $\delta^{13}C$ values determined for the C19 internal standard added to all samples, with $\delta^{13}C$ = −32.44 ± 0.67‰ (mean ± SD, n = 23), as reported by Main et al. (2015). Measurement of the Indiana University reference material hexadecanoic acid methyl ester no. 1 (certified $\delta^{13}C_{VPDB}$ = −30.74 ± 0.01‰) gave a value of −30.86 ± 0.17‰ (n = 13). Due to high enrichment of our samples, some carryover from sample enrichment into C19 internal standard was found, with the average $\delta^{13}C$ = −37.70 ± 4.64‰ (n = 41), but the effect of this in comparison to overall enrichment is minimal. The combined area of mass peaks (*m/z* 44, 45 and 46) after background subtraction were collected for each individual FAME peak. These combined areas, relative to those of the internal standard, were used to quantify 43 FAMEs and subsequently the phospholipid fatty acids (PLFAs) from which they were derived as described by Thornton et al. (2011).

Label uptake calculations

Stable isotope values are expressed in the δ notion (‰) relative to the reference material according to the equation:

$$\delta^{13}C \ (‰) = R_{sample} - R_{reference}) - 1 \times 1000 \qquad (1)$$

where R_{sample} is the $^{13}C:^{12}C$ ratio of the sample and $R_{reference}$ is the $^{13}C:^{12}C$ ratio of the VPDB reference material (R_{VPDB} = 0.0112372). The incorporation of ^{13}C (I_{DIC} or I_{PLFA}) was calculated from the excess ^{13}C (E) and the concentration of DIC or bacteria-specific PLFAs using the formula:

$$I = E \times PLFA \ or \ DIC \ concentration$$
$$(in \ µg \ g^{-1} \ or \ µmol \ ml^{-1}) \qquad (2)$$

Excess ^{13}C (E) is calculated as:

$$E = F_{\text{sample}} - F_{\text{background}} \quad (3)$$

where $F = R/(R + 1)$ and $R = (\delta^{13}\text{C}/1000 + 1) \times R_{\text{VPDB}}$. The background DIC δ^{13}C was obtained from Day 0 measurement of each experimental core to account for any introduction of ^{13}C-bicarbonate when adding the labelled algae (Moodley et al. 2005). The bacterial PLFA background δ^{13}C was calculated from the average of the 3 control cores at each site and time point. The incorporation of algal label by bacteria was based on the ^{13}C labelling of the most common bacteria specific PLFAs in the sediment (i14:0, i15:0, a15:0 and i16:0) (Moodley et al. 2002, 2005, Evrard et al. 2010). The total incorporation into bacterial biomass was calculated following Middelburg et al. (2000):

$$I_{\text{bacteria}} = \sum [I_{\text{PLFA}} / (a \times b)] \quad (4)$$

where I_{bacteria} = incorporation into bacterial biomass, a = average PLFA concentration in bacteria (0.056 g PLFA C g^{-1} of C biomass) (Brinch-Iversen & King 1990), and b = fraction of the bacteria-specific PLFAs found in the sediment samples at each station (NOW = 0.085, LS = 0.087). Finally, the total algal C incorporation into bacterial biomass and DIC pool (I_{algae}) was then calculated as a quotient of the algal labelling factor for ice algae and phytoplankton (ice algae: 60.1 atom% ^{13}C and phytoplankton 53.8 atom% ^{13}C) following the equation:

$$I_{\text{algae}} = (I_{\text{bacteria}} \text{ or } I_{\text{DIC}}) / \text{labelling factor} \quad (5)$$

Bacterial biomass was calculated from the concentration of the bacteria-specific PLFAs at each site and the average PLFA concentration in bacteria (0.056).

Bacterial growth efficiencies were estimated following Mayor et al. (2012a), where the partitioning of respiration between macrofaunal and bacterial components was calculated using the equation:

$$R_{\text{B}} = R_{\text{T}} - [I_{\text{M}} / \text{NPE}_{\text{M}} \times (1 - \text{NPE}_{\text{M}})] \quad (6)$$

where R_{B} and R_{T} are the bacterial and total respiration of algal-derived C, respectively, I_{M} is the total macrofaunal algal-derived C uptake from Mäkelä et al. (2017a), and NPE$_{\text{M}}$ is the net production efficiency of macrofauna, which was assumed to be 0.5. Bacterial growth efficiency (BGE) was then estimated using the equation:

$$\text{BGE} = \frac{I_B}{(I_B + R_B)} \quad (7)$$

where I_{B} is the total algal-derived C assimilation into bacterial biomass.

Statistical analysis

The oxygen flux, or SCOC, was calculated from the slope of the linear regression of oxygen concentration over time during the 4 d incubation. The SCOC was converted to benthic C respiration assuming a respiration quotient of 0.85 (Rowe 1983).

Differences in the macrofaunal biomasses between the control (n = 3), ice algae (n = 6) and phytoplankton (n = 6) cores within stations were tested using a Kruskal-Wallis test (as the normality assumption of at least one of the groups was not met), and differences in bacterial biomasses using a 1-way ANOVA, followed by a Bonferroni post hoc test when significant differences were found. Differences in the SCOC between the control cores (n = 3) at NOW and LS were tested using an independent samples t-test, and within-site differences between the control and experimental cores (6 ice algae and 6 phytoplankton) were examined using a 1-way ANOVA followed by a Bonferroni test when appropriate. The treatment effect was tested separately for the 2 study sites, as the absolute amounts of algae added to the experimental cores were different. Differences in the bacterial assimilation of C_{IA} and C_{PP} (n = 3 each), and slopes of ice algae (n = 6) and phytoplankton (n = 6) derived DIC release over time within the sites were tested with an independent samples t-test. The normality of the data residuals was tested using the Shapiro-Wilk test, and the homogeneity of residual variance was tested visually. Deviations from homogeneity of variance assumption were corrected by using the Welch correction when appropriate. All values are presented ±SE of the mean.

RESULTS

Bacterial and macroinfaunal biomass

While in the control cores macroinfaunal biomass was higher than bacterial biomass at both sites, the opposite was found in the ice algae and phytoplankton cores after rapid increase of bacterial biomass following algal addition (Table 2). No statistically significant differences in the macroinfaunal biomass between the 3 control and the 6 ice algal and 6 phytoplankton treatment cores in NOW were observed (χ^2 = 5.025, df = 2, p = 0.081) or LS (χ^2 = 3.525, df = 2, p = 0.172). A 1-way ANOVA showed significant differences in bacterial biomass between control, ice algal and phytoplankton cores in NOW ($F_{2,7}$ = 9.102, p = 0.011), and a Bonferroni post hoc test showed that

Table 2. Bacterial and macroinfaunal biomass (g C m^{-2}) in control, ice algal and phytoplankton cores in the North Water Polynya (NOW) and Lancaster Sound (LS). Values are means ± SE. Bacterial biomass is estimated from the concentration of bacterial specific fatty acids (iC14:0, iC15:0, aiC15:0, iC16:0)

Sediment layer (cm)	NOW			LS		
	Control	Ice algae	Phytoplankton	Control	Ice algae	Phytoplankton
Bacterial biomass (g C m^{-2})						
0–0.5	1.16 ± 0.22	1.42 ± 0.12	1.26 ± 0.19	0.72 ± 0.27	0.96 ± 0.19	1.39 ± 0.10
0.5–1	0.44 ± 0.08	1.04 ± 0.06	1.36 ± 0.36	0.34 ± 0.31	0.73 ± 0.02	0.69 ± 0.11
1–2	0.82 ± 0.11	1.57 ± 0.08	1.31 ± 0.08	0.50 ± 0.02	0.92 ± 0.17	1.10 ± 0.02
Total 0–2	2.42 ± 0.32	4.04 ± 0.20	3.94 ± 0.39	1.56 ± 0.57	2.60 ± 0.36	3.18 ± 0.20
Macroinfaunal biomass (g C m^{-2})						
0–10	3.77 ± 0.25	2.58 ± 0.34	2.77 ± 0.25	2.12 ± 0.96	2.73 ± 0.69	1.53 ± 0.18

the control core biomass was lower than the biomass in ice algae (p = 0.016) and phytoplankton (p = 0.031) cores. No significant differences between ice algae and phytoplankton cores were found (p = 1.000) in NOW. No statistically significant differences in bacterial biomass between the ice algal, phytoplankton and control cores were found in LS ($F_{2,5}$ = 4.645, p = 0.072).

SCOC

No significant difference in the background SCOC (measured from the 3 control cores) between the 2 stations was found (t = 0.948, df = 4, p = 0.397; Fig. 2). A 1-way ANOVA revealed significant differences in the SCOC between the control, ice algal and phytoplankton treatment cores in LS ($F_{2,12}$ = 4.280, p = 0.040), and a Bonferroni test showed that SCOC in phytoplankton cores was significantly higher than in ice algal cores (p = 0.038). No significant differences between the control, ice algal and phytoplankton core SCOC were found in NOW ($F_{2,12}$ = 1.231, p = 0.326).

Respiration of C_{IA} and C_{PP}

At the end of Day 4, 111 and 134 mg C m^{-2} of C_{IA} and C_{PP} were respired in NOW, compared to 31 and 43 mg C m^{-2} in LS (Fig. 3). Respiration of C_{PP} was significantly higher than C_{IA} both in NOW (t = −2.657, df = 8, p = 0.029) and in LS (t = −4.799, df = 7.274, p = 0.002). In LS, 51% (ice algae) and 30% (phytoplankton) and in NOW 60%
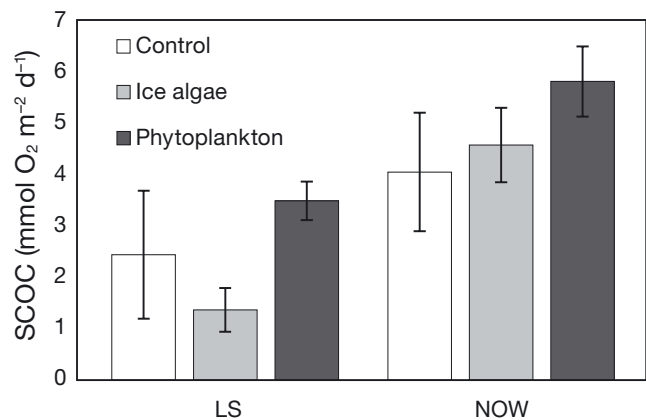

Fig. 2. Mean (± SE) sediment community oxygen consumption (SCOC) in the control (n = 3) and ice algal and phytoplankton treatment cores (n = 6 each) in the North Water Polynya (NOW) and Lancaster Sound (LS)
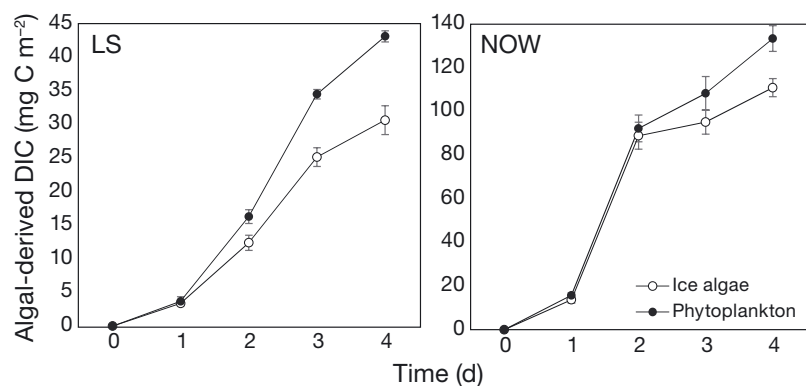

Fig. 3. Ice algal- and phytoplankton-derived C respiration (i.e. release of dissolved inorganic carbon, DIC) over the duration of the incubation experiments in North Water Polynya (NOW) and Lancaster Sound (LS). Data are mean ± SE. Three cores were analysed for time points 1 and 3, and 5 (NOW) and 6 (LS) cores for time points 0, 2 and 4. Note differences in *y*-axes scales
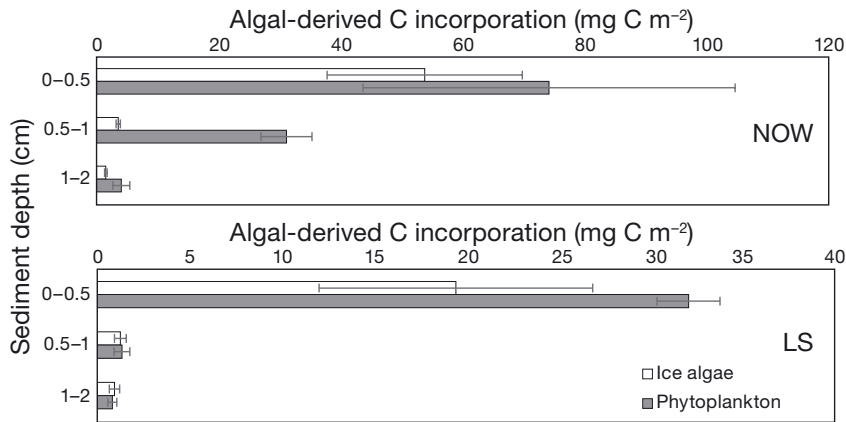
Fig. 4. Mean incorporation (± SE, n = 3 each) of ice algal- and phytoplankton-derived C into pooled bacterial fatty acids in the North Water Polynya (NOW) and Lancaster Sound (LS) during 4 d incubations. Note differences in *x*-axes scales

(both ice algae and phytoplankton) of total benthic respiration (derived from SCOC) was attributed to respiration of added algal C. Total bacterial respiration of C_{PP} was significantly higher than respiration of C_{IA} at both LS (40.2 ± 1.9 vs. 25.9 ± 2.9 mg C m^{-2}, $t = -4.217$, df = 4, p = 0.014) and NOW (128.9 ± 7.4 vs. 105.2 ± 3.8 mg C m^{-2}, $t = -3.113$, df = 5, p = 0.026). However, the difference in biomass-specific respiration of C_{IA} and C_{PP} by bacterial communities in LS (10.3 ± 1.9 mg C_{IA} g^{-1} and 12.8 ± 1.3 mg C_{PP} g^{-1}) was not statistically significant ($t = -1.097$, df = 4, p = 0.344), but in NOW, significantly more C_{PP} ($33.1. \pm 1.7$ mg C g^{-1}) than C_{IA} (26.3 ± 1.8 mg C g^{-1}) was respired by the bacteria ($t = -2.624$, df = 5, p = 0.047).
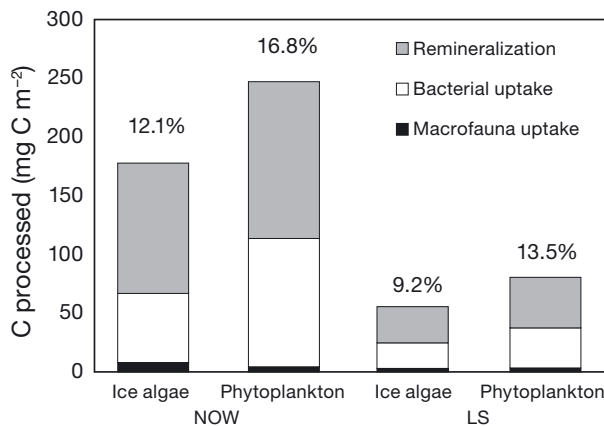

Fig. 5. Mean amount of ice algal- and phytoplankton-derived C taken up by bacteria and macrofauna and released as dissolved inorganic C in the North Water Polynya (NOW) and Lancaster Sound (LS). Data on macrofaunal uptake are from Mäkelä et al. (2017a). The value above the columns refers to the average % of added algae processed by the benthic community by the end of the 4 d incubations

Incorporation of C_{IA} and C_{PP} into bacterial biomass

The total amounts of C_{PP} and C_{IA} incorporated into bacterial biomass in NOW were 109.6 ± 28.9 and 59.0 ± 16.5 mg C m^{-2}, respectively, whereas in LS the corresponding amounts were 34.3 ± 1.4 and 21.7 ± 8.0 mg C m^{-2} (Fig. 4). No significant differences between the ice algae and phytoplankton treatments were found in NOW ($t = -1.519$, df = 4, p = 0.203) or LS ($t = -1.552$, df = 2.117, p = 0.254). When normalized to biomass, the bacteria in NOW incorporated 44.3 ± 12.2 mg C_{IA} g^{-1} and 84.5 ± 23.8 mg C_{PP} g^{-1}, whereas in LS, the uptake was 21.6 ± 5.2 mg C_{IA} g^{-1} and 26.1 ± 1.7 mg C_{PP} g^{-1}. These differences were not significant at NOW ($t = -1.501$, df = 4, p = 0.208) or LS ($t = -0.811$, df = 4, p = 0.463). The bacterial growth efficiency, calculated from the amounts of added C assimilated vs. respired by the bacterial communities, were 0.36 (ice algae) and 0.46 (phytoplankton) in NOW, and 0.44 (ice algae) and 0.46 (phytoplankton) in LS.

Total C_{IA} and C_{PP} processing

After 4 d of incubation, the total amounts of C_{PP} and C_{IA} processed (including algal-derived respiration, assimilation into bacterial biomass and uptake by macrofauna) by the NOW benthic community were 247.2 and 177.9 mg C m^{-2}, respectively, whereas in LS, 80.7 and 55.4 mg C m^{-2} were processed (Fig. 5). The major pathways of C processing at both stations were bacterial respiration and assimilation, whereas the role of macroinfauna was small (Fig. 6).

DISCUSSION

Benthic C respiration

The responses of benthic communities to algal addition were investigated through changes in benthic C respiration rates. The C respiration rates were determined from 2 measurements: SCOC, a common method used for assessing the total benthic C turnover, and release of DI^{13}C, a direct measurement of the respiration of the added C_{IA} and C_{PP}.
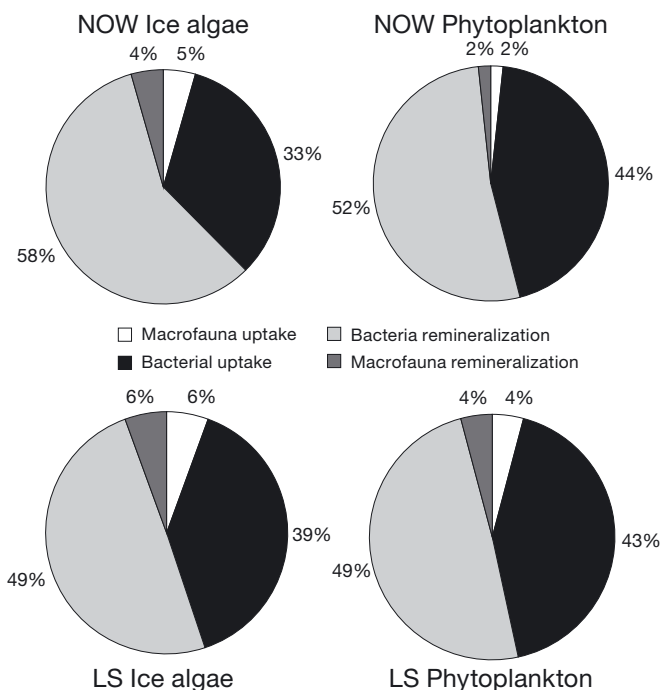
Fig. 6. Contribution of each measured pathway to the overall ice algal- and phytoplankton-derived C processing in the North Water Polynya (NOW) and Lancaster Sound (LS) after 4 d incubations. Data on macrofaunal uptake are from Mäkelä et al. (2017a)

We hypothesized that ice algae would be the preferred C source for the benthos, and therefore the rates of C_{IA} respiration would be higher than rates of C_{PP} respiration. As SCOC is an indiscriminate measurement of the respiration taking place in the sediment cores, only DIC release, which can be specifically associated with ice algae or phytoplankton, was used to investigate the hypothesis. SCOC was higher in phytoplankton than ice algal cores in LS, but neither measurement was significantly different from the control core measurements. Additionally, no difference between the treatments was found in NOW. The DIC release, however, revealed significant differences in respiration of algal-derived C by the benthos, with 18–34% higher respiration of C_{PP} than C_{IA}. The hypothesis was therefore rejected. These results are the first to directly show higher benthic respiration of C_{PP} than C_{IA} in the Arctic Ocean.

The background SCOC measurements in LS (2.4 mmol O_2 m^{-2} d^{-1}) and NOW (4.0 mmol O_2 m^{-2} d^{-1}) are in good agreement with the previously measured rates of 1–4 mmol O_2 m^{-2} d^{-1} (LS) and 1–5+ mmol O_2 m^{-2} d^{-1} (NOW) (Grant et al. 2002, Link et al. 2013b). SCOC is thought to be highest in

the nutrient-rich Arctic inflow and interior shelves with high primary productivity, whereas in outflow shelves like the Canadian Arctic Archipelago, the mean sediment oxygen demand is 3.9 mmol O_2 m^{-2} d^{-1} (Bourgeois et al. 2017). However, the SCOC in NOW and LS exceed the rates that could be expected in the Arctic for depths >500 m (Clough et al. 2005, Grebmeier et al. 2006a, Bourgeois et al. 2017), suggesting that both sites are hotspots for deep-sea respiration in the Canadian Arctic (Link et al. 2011, 2013b). Our measurements were taken during the productive summer period, as the main algal blooms in LS occur in May–June (ice algae) and July–August (phytoplankton) (Michel et al. 2006) and May–June in NOW (Klein et al. 2002, Tremblay et al. 2002). Although maximum POC export in NOW occurs in May–June (Klein et al. 2002, Michel et al. 2002, Sampei et al. 2004), some export of particles to the seafloor also occurs in August (Amiel et al. 2002, Caron et al. 2004, Ardyna et al. 2011). This is then reflected in the SCOC, with highest values recorded in July–September (Grant et al. 2002, Link et al. 2013b). Our measurements therefore represent typical summertime SCOC.

Previous studies have found that a pulse of phytodetritus reaching the seafloor after spring or summer algal blooms can induce a peak in benthic respiration (Rysgaard et al. 1998, Renaud et al. 2007b, Bourgeois et al. 2017), but the phytodetritus addition during our experiments did not appear to significantly impact the SCOC. In NOW, no differences in SCOC were found between control, ice algal and phytoplankton cores, and similarly in LS, the SCOC in neither algal-amended cores was different from the background values. The differences between phytoplankton and ice algal core SCOC cannot therefore be attributed to the algal addition. As our measurements were taken at a time when SCOC rates in NOW and LS are usually at their annual peak, it is possible that the effect of the algal addition was masked by the already high background SCOC. The sediment C:N ratio (6.5 at both sites) and organic matter (10–11%) and chl a (13–21 mg dry weight m^{-2}) contents recorded at NOW and LS during sampling indeed suggest recent deposition of labile organic matter (Mäkelä et al. 2017b). A similar dampening effect has also been suggested by Sun et al. (2007), who observed algal addition to have no marked effect on SCOC in Smeerenburg Fjord, Svalbard, where the sediments had a high initial organic matter loading and surface sediment chl a content of <2.5 μg g^{-1} dry

sediment. Conversely, in the extremely food-limited HAUSGARTEN deep-sea observatory, Hoffmann et al. (2017) found that addition of both ice algae and phytoplankton increased the bacterial community oxygen consumption compared to the background values, but no difference between the algal types was found. Their experiment took place in July–August, at the onset of the settling summer phytoplankton bloom, when the sediment organic carbon content was already sufficient to meet the energetic needs of the bacterial community (Hoffmann et al. 2017).

Our hypothesis on preferential ice algal respiration was derived from 2 experiments, which showed that ice algae significantly stimulate SCOC, whereas phytoplankton deposition did not increase the SCOC compared to background measurements (McMahon et al. 2006, Sun et al. 2007). The experiment by Sun et al. (2007) was carried out in the Storfjord Trench in Barents Sea during May, when the sediments contained a low initial content of labile organic matter (indicating pre-bloom/algal deposition conditions). On the other hand, McMahon et al. (2006) conducted their experiment in Ny Ålesund, Svalbard, in July–August, after the peak sedimentation in April–May (Hodal et al. 2012, Lalande et al. 2016). The diverse results from these experimental studies conducted during different bloom stages suggests that the SCOC after algal deposition is not solely driven by community 'readiness' or 'priming' due to amount or type of pre-existing sediment organic matter.

However, using SCOC to investigate the responses of benthic communities to ice algae and phytoplankton has several limitations. Firstly, although SCOC is commonly used to measure benthic C respiration, it can be a poor representation of nutrient fluxes and DIC release due to high local variability in environmental and community compositions (Bühring et al. 2006b, Link et al. 2013a). Secondly, anaerobic mineralization is often stimulated during periods of high organic matter supply (Ferguson et al. 2003), and as SCOC does not take anaerobic processes into account, measurements derived from SCOC should be considered as minimum values for sediment C respiration (Moran et al. 2005). Most importantly, when the total sediment respiration rates, calculated from the SCOC, were compared to the algal-derived respiration, only 30–60% of the respiration could be explained by the introduction of algae in our experiments. This proportion is notably higher than the 2.4–25% recorded during other isotope labelling in deep-sea sediments

(Moodley et al. 2002, Bühring et al. 2006a, Gontikaki et al. 2012). The changes in SCOC not attributed to the added phytodetritus could be due labile organic matter triggering the priming effect (Guenet et al. 2010), contributing to further respiration of existing refractory organic matter in the sediments, instead of the introduced algae. On the other hand, algal-derived respiration can also exceeded the total sediment respiration (Bühring et al. 2006b), suggesting a disconnect between SCOC and newly deposited organic matter respiration measurements. Clearly elevated respiration of added C can, however, be revealed through isotope labelling even in cases where the SCOC suggested an arrested benthic respiration (Moodley et al. 2005, Mayor et al. 2012a). For example, in the Northeast Atlantic, 300% higher respiration of high-quality diatoms than poor-quality faecal pellets was recorded through DI^{13}C release, but no difference in the SCOC between the treatments was found (Mayor et al. 2012a). We therefore argue that comparing the algal-derived DIC release rates is a more robust method for investigating the impact of specific C sources (here C_{IA} and C_{PP}) on benthic respiration, whereas SCOC gives an insight into the overall sediment community functioning and C demand.

Bacterial responses to C_{PP} and C_{IA} addition

We originally hypothesized that bacterial assimilation of C_{IA} would be higher than assimilation of C_{PP}. The bacterial assimilation of added algae was rapid in all cores, with C_{PP} and C_{IA} uptake of 110 vs. 59 mg C m^{-2} in NOW and 34 vs. 22 mg C m^{-2} in LS, respectively, but no significant differences between the treatments were found at either site, leading us to reject the original hypothesis. However, the total bacterial respiration of C_{PP} was higher than respiration of C_{IA} at both sites. As the sediment bacterial biomass was higher in NOW than LS, probably due to greater food availability supporting a more diverse and abundant bacterial community in NOW (Boetius & Damm 1998, Bienhold et al. 2012), we also calculated the biomass-specific uptake and respiration of C_{PP} and C_{IA} by the bacteria. The biomass-specific uptake in NOW (44–85 mg C g^{-1}) was higher than in LS (22–26 mg C g^{-1}), but no difference between the treatments was observed. Also, the biomass-specific respiration was higher in NOW (26–33 mg C g^{-1}) than LS (10–13 mg C g^{-1}), with significantly more C_{PP} than

C_{IA} being respired in NOW. The differences in the uptake and respiration efficiencies of the bacterial communities between the 2 sites could be due to higher absolute dose of algae added to the cores in NOW than LS, as food quantity is known to enhance benthic community activity and organic matter processing (Morata et al. 2015).

Contrary to our study, Sun et al. (2007) reported no significant assimilation of the ^{13}C-labelled ice algae into bacterial biomass during their incubation experiments in the Barents Sea, whereas in similar experiments in Kotzebue Sound in Alaska, direct bacterial uptake of ice algae was recorded (Sun et al. 2009). These differences were suggested to be due to the depth difference between the sampling sites (10 vs. 260 m, no incorporation was seen at the deeper site), core preparation (in intact cores, no uptake was found, whereas in homogenized sediment cores, uptake was high), differences in microbial communities or incubation temperatures, or age of the algal material (Sun et al. 2009). As rapid assimilation of algal C was seen in both NOW and LS, which are >700 m deep, water depth is unlikely to inhibit bacterial uptake of algal C. Additionally, as uptake was immediate in our cores, which were undisturbed and received relatively fresh algae, these factors are unlikely to limit bacterial uptake of phytodetritus. The enzymatic and uptake capabilities of bacterial communities do, however, seem to impact their processing of different types of organic matter (Arnosti 2004, Hoffmann et al. 2017). Additionally, the organic matter source available can shape bacterial community structure (Boetius & Lochte 1996, Kanzog et al. 2009, Hoffmann et al. 2017), indicating that organic matter quality can be a major driver for deep-sea bacterial diversity and C turnover.

Bacterial growth was stimulated by the algal addition, and in NOW, the bacterial biomass in both ice algal and phytoplankton cores was significantly higher than in the background cores at the end of the experiment. No difference between the 2 algal treatments was found, suggesting that the type of organic matter introduced was not a limiting factor for bacterial growth. It should be noted that bacterial production is often slower than bacterial respiration (Kritzberg et al. 2010) and therefore the effect of algal type on bacterial assimilation and growth could have been underestimated during these 4 d experiments. Nevertheless, our experiments are in agreement with the findings of Hoffmann et al. (2017), who reported that both ice algae and phytoplankton increased the sediment bacterial biomass, calculated from cell densities, compared to background cores. Bacterial growth efficiency is considered an indication of the fate of organic carbon, with higher growth efficiency implying that more C remains in organic form available to higher trophic levels, instead of being respired (Findlay et al. 2015). The calculated bacterial growth efficiency did not greatly vary between the sites or the algal treatments, but the values (0.36–0.46) confirm high investment into bacterial growth. The bacterial growth efficiencies here are in agreement with the typical range reported during incubation experiments with added diatoms in intertidal and deep-sea environments (Mayor et al. 2012a,b), demonstrating that the bacterial growth efficiency is stimulated by the addition of a labile C source (del Giorgio & Cole 1998). Our values are generally higher than those measured at the HAUSGARTEN deep-sea observatory, where addition of ice algal and phytoplankton material resulted in an estimated bacterial growth efficiency of 0.18–0.42 (Hoffmann et al. 2017). The addition of faecal pellets and chitin have been shown to increase the bacterial growth efficiency more than fresh algae (Mayor et al. 2012a, Hoffmann et al. 2017), as POC transformed by the digestive system of zooplankton grazers is more bioavailable for bacteria in the environment (Witte et al. 2003b). This suggests that the quality of organic matter could impact its processing by bacteria, with the more degraded food items being favoured.

Total processing of C_{PP} and C_{IA}

The total C processed, encompassing the algal-derived DIC release, bacterial assimilation and macrofaunal uptake, was higher in phytoplankton than ice algal cores at both sites. As the dose of algae added to the experimental cores can impact the C processing rates, with a higher dose of organic matter triggering a stronger benthic response (Bühring et al. 2006b, Mayor et al. 2012b, Morata et al. 2015), the absolute amounts of C processed at LS and NOW could not be directly compared. However, the percentage of the added algae processed by the benthic communities suggests similar processing efficiency between our 2 study sites: in NOW, the benthic community processed 12.1 and 16.8% of the added C_{IA} and C_{PP}, whereas in LS the community processed 9.2% (C_{IA}) and 13.5% (C_{PP}). The total amounts of added C processed per hour (1.9–2.6 mg C m^{-2} h^{-1} in NOW and 0.6–0.8 mg C m^{-2} h^{-1} in LS) fall within

the 0.24–3.75 mg C m^{-2} h^{-1} range recorded during other isotope tracing experiments at depths >100 m (Woulds et al. 2016 and references therein). The percentage of the added algae processed at both sites is generally higher than what has been reported from other short-term isotope tracing experiments conducted in Atlantic abyssal plains (Gontikaki et al. 2011a, 2012, Mayor et al. 2012a), where the bottom water temperatures are close to, or below, 0°C. The processing rates in NOW and LS are thus comparable to measurements from warmer regions, despite water temperature being a known limiting factor for C processing at the seafloor (Woulds et al. 2016 and references therein).

Respiration was the main pathway for both C_{IA} and C_{PP} processing, contributing 53–62% to the overall C processing in the cores. This is unsurprising, as the majority of the POC that is processed by the benthos in Arctic shelves is respired and released back into the water column (Graf et al. 1995, Macdonald et al. 1998, Findlay et al. 2015). Additionally, previous deep sea isotope labelling experiments have shown that 45–96% of the processed ^{13}C-labelled phytodetritus was respired (Moodley et al. 2002, Witte et al. 2003a, Woulds et al. 2009, Gontikaki et al. 2011b, 2012). Indeed, the C_{IA} and C_{PP} respiration rates in NOW (1.2 and 1.4 mg C m^{-2} h^{-1}) and LS (0.3 and 0.4 mg C m^{-2} h^{-1}) fall within the typical range of 0.1–2.8 mg C m^{-2} h^{-1} recorded during other deep-sea isotope tracing experiments (Woulds et al. 2009 and references therein). In all cores, the vast majority (>90%) of the respiration of C_{IA} and C_{PP} was attributed to the sediment bacteria. Bacterial uptake of C_{IA} and C_{PP} was also significant, with 33–44% of the total C processing directed towards bacterial assimilation and growth, which was also illustrated by the high bacterial growth efficiency and rapid increase in bacterial biomass after algal additions. Interestingly, despite the high macroinfaunal biomass and density at both LS and NOW (Mäkelä et al. 2017b), the role of these fauna, mainly polychaetes and crustaceans in NOW and polychaetes and bivalves in LS, in the processing of C_{IA} and C_{PP} was negligible. However, the overall biological processing in neither LS nor NOW seems to correspond with the categories of labelled C processing patterns identified by Woulds et al. (2009, 2016). These categories include (1) respiration domination, where >75% of C processing is through respiration, (2) active faunal uptake, where <75% of C is respired and macrofauna, foraminifera and bacteria contribute 10–25% to C uptake, (3) metazoan and macrofaunal uptake dominated and (4) bacteria

uptake dominated, where bacterial uptake is the main C processing pathway. As in NOW and LS, C processing was driven by bacteria, but was not dominated by bacterial uptake or characterized by >75% respiration; the processing could thus best be characterized by both active bacterial respiration and uptake.

If we assume that the proportions of added C respired by different benthic actors can also be applied to SCOC (Gontikaki et al. 2011a), the majority of short-term sediment C turnover in LS and NOW was due to bacterial activities. It should be noted that the meio- and megafaunal contributions to the sediment C turnover were not assessed during these experiments, and while the role of meiofauna is likely to be small (Piepenburg et al. 1995, Heip et al. 2001, Gontikaki et al. 2011a), megafaunal respiration can be significant on a local scale (Piepenburg et al. 1995, Piepenburg & Schmid 1996, Ambrose et al. 2001). Still, bacteria can dominate benthic respiration in the Arctic deep sea (Piepenburg et al. 1995, van Oevelen et al. 2011), while macrofauna tend to be more important in shallower depths (Rowe et al. 1997, Clough et al. 2005, Renaud et al. 2007b). Furthermore, macrofauna dominate SCOC in NOW during summer, whereas the meio-microbial component was more significant during the spring (Grant et al. 2002). Our results, however, indicate that bacteria also dominate the benthic C respiration during summer.

It is important to note that the results of this study only provide a snapshot of the immediate community C processing, and as an excessive amount of algae was added to the cores, the results reflect the maximum processing efficiency of the benthic communities. In experiments where an artificial bloom of organic matter has been introduced to the seafloor, the majority of the activity (uptake and respiration) occurred immediately after the food pulse (Aberle & Witte 2003, Gontikaki et al. 2011a), and often within 1–3 wk, the algal consumption and respiration returned to background levels (McMahon et al. 2006, Sun et al. 2007). Therefore, drawing conclusions on long-term C cycling based on these results must be done with caution, as they can easily overestimate the rates of processes (Woulds et al. 2009). Furthermore, the incubation temperature (4°C) was slightly higher than the ambient temperature at the seafloor, which may have affected processing rates (Renaud et al. 2007a, Morata et al. 2015). However, as the temperature was the same for all incubation cores, it does not affect the experimental design and testing

of the hypotheses themselves. It should also be noted that bacteria and macroinfauna have very limited mobility, and as ice algae often sink to the seafloor in patchy aggregations and not in an evenly distributed rain of cells like phytoplankton do, the smaller size classes of benthic consumers may not have similar access to ice algae as highly mobile consumers do (Iken et al. 2001, MacDonald et al. 2010, Mäkelä et al. 2017b). This agrees with the observations by Boetius et al. (2013), who showed that only mobile megafauna and possibly bacteria used ice algal patches as a food source in the central Arctic Ocean. Phytodetritus patchiness could thus impact the benthic C cycle on a large spatial scale, as the access of small benthic consumers to ice algae might be more restricted and localized.

Reconciling benthic C supply and demand

A longer open water period is thought to increase the oceanic drawdown of CO_2 (Bates et al. 2006), and consequently the importance of Arctic sediments as sites of C sequestration (McGuire et al. 2010, Findlay et al. 2015, Harada 2016). To estimate what fraction of the exported POC is respired by the benthic communities and how much is ultimately buried in the sediments, the POC supply and benthic C demand must be compared. As our experiments only reveal the initial responses of benthos to algal deposition, we did not attempt to extrapolate the results to represent the annual benthic C cycle, but rather relate the measurements to the daily rates of PP and C export during peak bloom times.

The rates of phytoplankton POC production during the spring–summer period in NOW are on average 1.1–1.7 g C m^{-2} d^{-1}, but can reach rates of up to 4.4–5.0 g C m^{-2} d^{-1} (Klein et al. 2002, Mei et al. 2003). In LS, rates of C production range between 0.8 and 1.2 g C m^{-2} d^{-1} during peak bloom times (Sameoto et al. 1986) or 0.25 g C m^{-2} d^{-1} during the whole summer period (Ardyna et al. 2011). The benthic C demand, calculated from SCOC, was 39–56 mg C m^{-2} d^{-1} in NOW and 15–36 mg C m^{-2} d^{-1} in LS. This responds to <1 to 5% of the daily PP in NOW (Klein et al. 2002, Mei et al. 2003), and 3–14% in LS (Sameoto et al. 1986, Ardyna et al. 2011). Tremblay et al. (2006) estimated that 7 and 1% of POC in NOW reaches depths of 200 and 500 m, respectively, whereas Hamel et al. (2002) estimated from long-term accumulation of C into sediments that 4–6% of annual PP sinks to the seafloor. In NOW, the benthic C demand thus seems to be in good agreement with the estimated export

flux, suggesting that the benthic C demand and supply are in good balance at peak algal bloom times. Grant et al. (2002) reported, similar to us, the benthic C demand in NOW to be ~50 mg C m^{-2} d^{-1} (Klein et al. 2002). They were, however, able to compare the benthic C demand to the POC flux recorded by Hargrave et al. (2002) during the same time period, concluding that the benthic C demand exceeded the supply by 5–40 times at 2 locations, whereas at 1 site, the rates matched fairly well (Grant et al. 2002). Still, the inter-annual variability in flux estimates is high, as a 2–5 times increase in POC fluxes from 1997–1998 to 1998–1999 in NOW was reported (Hargrave et al. 2002). This high spatial and temporal variability makes it difficult to detect possible long-term changes to benthic C budgets.

If we estimate that similarly to NOW, 1–6% of the daily PP sinks to the seafloor, the POC export in LS does not meet the calculated C turnover of 3–14% of the PP. There is therefore a potential mismatch between the C supply and demand in LS, suggesting the benthos might rely on allochthonous C sources to meet their energetic needs. A similar discrepancy has also been recorded in in the Amundsen Gulf, where the Cape Bathurst Polynya, which is the reference site for POC export for LS, is located. In the Amundsen Gulf, the sinking flux supplies only 60% of the benthic C demand, and other C sources within the benthic boundary layer are needed to fuel the benthic activities (Forest et al. 2011). Current velocities in LS are known to be some of the highest recorded in the Canadian Arctic (Thomson 1982), which could enable lateral supply of organic matter from outside the study site, helping the benthos meet their C demand. In the absence of any POC export data from LS, the discussion on how well the C supply meets the demand is highly speculative, and illustrates a need for particle trap studies in the region.

These experiments show that during summer, the benthic C demand in NOW and LS either closely matches or exceeds the POC supply, and the high respiration rates render the sediments as sources, rather than sinks, of CO_2. Climate change can have an unpredictable impact on the benthic C budgets through changes in C supply and demand. While novel under-ice (Mundy et al. 2009, 2014, Lowry et al. 2014, Assmy et al. 2017) and autumn (Brugel et al. 2009, Ardyna et al. 2011, 2014) phytoplankton blooms or possible mismatch of the blooms and zooplankton reproduction (Søreide et al. 2010, Leu et al. 2011) have the potential to increase POC export to the seafloor, increased zooplankton biomass and

grazing due to warm surface water temperatures could significantly reduce it (Coyle & Pinchuk 2002, Hunt et al. 2002). Additionally, C export to the seafloor could be altered if future conditions in the Arctic Ocean favour the growth of picoplankton species at the expense of larger nanoplankton (Li et al. 2009, Tremblay et al. 2012, Blais et al. 2017), or benefit *Phaeocystis pouchetii* instead of diatoms (Lovejoy et al. 2004). Benthos may thus struggle to meet their energetic needs if POC export to the seafloor decreases, or if their C demand increases with increased food availability (Morata et al. 2015) or due to the transition from ice algal to phytoplankton organic matter (this study). It should be noted that as only axenic cultures of *Synedropsis hyperborea* and *Thalassiosira nordenskioeldii* were used to represent ice algal and phytoplankton communities in this study, it is difficult to assess to which extent the patterns observed are dependent on the algal species used. Future work should therefore focus on how the species composition of ice algal and phytoplankton communities impacts the C cycling rates described here. As *S. hyperborea* and *T. nordenskioeldii* are among the most commonly encountered ice algal and phytoplankton species, respectively (Hegseth 1998, Lovejoy et al. 2002, von Quillfeldt et al. 2003, Tamelander et al. 2009), we are confident that the conclusions of this study also apply *in situ.* Finally, while some C budgets have been calculated for the Arctic Ocean (Hirche et al. 2006, Tremblay et al. 2006, Wassmann et al. 2006, 2008, Forest et al. 2011), the seafloor component is often reduced to only downward POC export, despite the active role sediment communities have in C respiration. We therefore highlight the need for better integration of benthic C cycling processes to Arctic biogeochemical models.

CONCLUSIONS

Climate change has the potential to alter Arctic benthic C cycling through changes to timing, quality and quantity of POC exported to the seafloor. The present study tested the hypothesis that ice algae are the preferred C source for benthic communities, and therefore C_{IA} is more readily processed by the benthos in LS and NOW than C_{PP}. Contrary to previous studies and our hypothesis, the processing rate of the phytoplankton species *Thalassiosira nordenskioeldii* was higher than that of the ice algal species *Synedropsis hyperborea* at both sites. The main pathway for processing of the added C was respiration, with

18–34 % higher respiration of C_{PP} than C_{IA}. The sediment community oxygen consumption, indicative of the total sediment C respiration, was not significantly changed by the algal addition, suggesting that this method is not sensitive enough to detect the impact of different C sources on sediment respiration. Bacteria rapidly and non-preferentially incorporated both C_{IA} and C_{PP}, and bacterial biomass was rapidly increased following addition of both algal types. Overall, 33 and 37 % higher processing of C_{PP} than C_{IA} was recorded in NOW and in LS, respectively. During the peak summer growth season, the total daily sediment C demand either closely matched or exceeded the estimated POC supply, suggesting the sediments are unlikely to act as major C sinks at this time due to high water column retention and increased benthic C turnover. However, as the type of sinking phytodetritus appears to influence the C residence time at the seafloor, the future changes to magnitude and quality of POC sinking to the seafloor could influence the proportions of C being remineralized and sequestered.

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