Depth distribution of organic carbon sources in Arctic Chukchi Sea sediments

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ABSTRACT

Climate-induced changes in the composition of organic matter sources in Chukchi Sea sediments could have major implications on carbon cycling, carbon sequestration, and food sources for lower benthic trophic levels. The aim of this study was two-fold: (1) to identify the proportional contributions of organic matter from various primary producers (phytoplankton, terrestrial, and bacterial) to depth-stratified sediments (0 - 5 cm) across the Arctic Chukchi Sea shelf using essential amino acid (EAA) specific stable carbon isotope biomarkers; and (2) to experimentally evaluate sediment bacterial production under different temperature scenarios. Proportional contributions of EAA sources to surface sediments had little relationship with environmental variables across the Chukchi Shelf and only showed noticeably higher terrestrial proportions in surface sediments in a high-deposition region in the southern study area. Across all sediment depth strata, the majority of EAA in sediments (~76 %) originated from terrestrial sources and may be indicative of accumulation over time due to slow degradation processes of this source within sediments. The different EAA sources showed no significant differences in proportional contributions with sediment depth except for phytoplankton-derived EAA, which decreased with increasing sediment depth. These patterns indicate a well-mixed upper sediment horizon, possibly from bioturbation activities by the abundant benthos. One EAA source assumed to respond quickly to changing environmental conditions are bacteria. To evaluate if and how bacterial production would respond to elevated temperatures, sediment bacterial production was measured experimentally using phospholipid fatty acid (PLFA) analysis. Bacterial production was initially (first 24 h) higher at 5°C than at 0°C; however, a drawdown of substrate or potential increase in predation activity and viral lysis resulted in bacterial production to subsequently be similar at both temperature settings. Overall results of this study suggest that terrestrial and bacterial carbon sources may become more prominent in a future, warmer Arctic. Identifying current patterns and potential shifts in organic matter sources with changes in temperature can aid in the understanding of the consequences of climate change in terms of organic matter presence and flow through benthic consumers that use these shelf sediments as feeding grounds.

Keywords: Stable isotope fingerprinting, Phospholipid fatty acids, Terrestrial organic matter, Bacterial production

1. Introduction

Marine sediments of various lithologies make up the majority of the ocean floor (Dutkiewicz et al., 2015) and, especially on continental shelves and margins, constitute >40% of carbon cycling and long-term carbon sequestration in the ocean (Muller-Karger et al., 2005; Chen and Borges, 2009; Smith et al., 2015). Sediments play vital roles in a multitude of small- and large-scale processes, for example, from understanding regional distribution of carbon sources, and their roles in benthic food webs, to global carbon budgets. Carbon provenance is essential to all these processes, with the main sources to marine shelf regions coming from marine photosynthetic production (e.g. Hedges et al., 1997). Once organic matter has settled to the sediments, sediment properties such as grain size, permeability, and porosity drive the interactions at the sediment-water interface and diagenetic processes (Klump and Martens, 1989; Santschi et al., 1990; Arndt et al., 2013). For example, water velocities influence both sediment grain size and organic carbon composition in marine sediments. These sediment properties influence exchange of O_2 and nutrients with the overlying water column and can result in steep concentration gradients of biochemical properties with increasing sediment depth (Santschi et al., 1990; Glud, 2008). All these sediment conditions influence diagenetic processes of organic matter within the sediment and, thus, patterns of long-term refractory carbon storage or the release of bioavailable carbon (Burdige, 2007).

Material derived from marine production is considered to contain large quantities of labile components, i.e. highly reactive and subject to fast degradation in sedimentary processes (Sun et al., 2007). Degradability decreases with increasing amounts of more structurally complex components, such as those frequently found in terrigenous sources (Hedges et al., 1997; Opsahl and Benner, 1997; Arndt et al., 2013). Additionally, degradation processes within the sediment are enhanced in the presence of O_2 and rapidly decrease with decreasing O_2 concentrations (Mermillod-Blondin et al., 2004, Wakeham and Canuel, 2006). While part of the deposited organic carbon on marine shelf systems is readily utilized at the sediment surface, excess or slow-degrading material can be drawn down into deeper sediment layers by bioturbation of the benthic community (Kristensen et al., 2012). Once it reaches deeper sediment layers, organic carbon provides a food source for deeper sediment-dwelling organisms and is subject to degradation processes. The interplay of deposition, bioturbation, and degradation processes within the sediment influences the quantity, quality, and distribution of different carbon sources among sediment layers. Understanding the carbon source distribution with sediment depth is important for

considerations of long-term sequestration as well as availability of food sources for benthic organisms feeding within different sediment horizons.

Despite the Arctic being the smallest of the world's oceans, it receives a disproportionately large fraction of the global river discharge (about 10 %, Aagaard and Carmack, 1989), and its immense shelf areas play a major role in carbon sequestration (Stein and Macdonald, 2004). High marine biological productivity is concentrated within a short seasonal cycle, with the highest amount of primary production deriving from phytoplankton production, especially with reduced sea-ice cover and sea-ice production over the last decade (Ardyna and Arrigo, 2020; Lewis et al., 2020). Arctic shelf regions also receive large amounts of terrestrial carbon from river discharge, permafrost erosion, and glacial melt (e.g. Guo et al., 2004; Goñi et al., 2005; Yunker et al., 2005). Terrestrial input can make up close to half of the total carbon budget in some shelf seas of the Pacific Arctic, such as the Chukchi Sea (Belicka and Harvey, 2009), although this input is typically smaller than that from marine primary production (Stein and Macdonald, 2004). Under historically cold conditions in the Chukchi Sea, a large proportion of the high marine primary production tended to be ungrazed in the water column and sank to the seafloor in tight pelagic-benthic coupling (Grebmeier and Barry, 1991). In the context of more recent years, the effects of earlier sea ice retreat and rising temperatures could include a shift in phytoplankton composition towards smaller-celled communities, reducing export to the seafloor (Hunt et al., 2002; Li et al., 2009). Although overall phytoplankton production in the Arctic has increased in recent years due to a longer growing season (Arrigo et al., 2008; Wassmann and Reigstad, 2011; Hill et al., 2018), reduced pelagic-benthic coupling could strongly affect the proportion of this carbon source in sediments and shift the proportional contributions of marine versus terrestrial production on the seafloor (Lalande et al., 2007). Increase in river discharge, permafrost melt, and coastal erosion could further increase amounts of terrestrial carbon on the shelf (Lantuit et al., 2012). Food webs in areas with increased amounts of terrestrial matter have shown an increase in trophic steps due to additional bacterial degradation of the refractory material, decreasing the amount of carbon availability to higher trophic levels and reducing trophic efficiency of the whole food web (Dunton et al., 2006; Bell et al., 2016). Although the high refractory components such as lignin and cellulose in terrestrial matter reduce the digestibility and assimilation of this matter to marine invertebrates (Cividanes et al., 2002), a number of aquatic invertebrates contain enzymes that are able to hydrolyze these materials (Antonio et al., 2010), and recent studies have shown terrestrial sources to be common in Arctic marine invertebrate diets (Bell et al., 2016; Harris et al., 2018; Zinkann et al., 2021).

Among the plethora of possible bacterial metabolic pathways, conversion of particulate and dissolved organic carbon (POC and DOC, respectively) into bacterial cells (bacterial production) is especially important to build bacterial biomass in marine sediments that can be utilized by benthic organisms as food (Jiao et al., 2010). Among others, bacterial degradation processes are especially important in the processing of terrestrial matter, although bacterial production based on terrestrial matter is lower than on marine microalgal material (Dyda et al., 2009). Generally, bacterial biomass decreases with sediment depth as labile carbon availability decreases and more refractory portions increase (Fabiano and Danovaro, 1994). In addition to the carbon quality, O_2, and nutrients to support redox-reactions, bacterial production is also reliant on temperature (Mermillod-Blondin et al., 2004; Kristensen et al., 2012; North et al., 2014). While Arctic bacterial communities are adapted to low *in situ* temperatures, their optimal production rate is typically above polar temperatures (Knoblauch et al., 1999). Bacterial degradation of POC requires production of extracellular enzymes; however, at low temperatures hydrolyzing efficiency decreases, resulting in less substrate made available (Arnosti and Jorgensen, 2003). Bottom water temperatures on Arctic shelves are predicted to increase to 5°C by 2050 (Wang et al., 2012), which may increase bacterial production and biomass in sediments substantially (Kirchman et al., 2009; Wiklund et al., 2009; Kritzberg et al., 2010). A higher proportion of bacterial biomass in marine sediments could increase their role in digesting terrestrial matter, as a food source for benthic organisms, and ultimately change the proportions of the various carbon sources in Arctic shelf sediments.

A method that can reliably distinguish among different carbon sources is essential to the goal of determining biosynthetic sources contributing organic carbon to sediments. Biomarker approaches have been commonly applied to distinguish multiple sources in benthic food webs from the Arctic, employing bulk stable isotope analysis (e.g. Iken et al., 2010; Divine et al., 2015; Bell et al., 2016; McTigue and Dunton, 2017; Harris et al., 2018) or fatty acid analysis (Mohan et al., 2016; Schollmeier et al., 2018). A combination of these two methods has been used to distinguish sea-ice and phytoplankton production and separating terrestrial from marine sources (Budge et al., 2007; Oxtoby et al., 2016; Oxtoby et al., 2017; Paar et al., 2019). Highly branched isoprenoids (HBI) are an emerging tool to specifically trace sea-ice algal production in benthic consumers (Koch et al. 2020). Although each of these methods allow determination of specific production sources in marine consumers, few are able to distinguish among all production sources present in a system and entering the food web (Majdi et al., 2018). We applied essential amino acids (EAA) carbon stable isotope fingerprinting, which allowed us to complement these other biomarker methods and address some of the limitations of other approaches (Post, 2002; Larsen

et al., 2013; Close, 2019). EAA stable isotope fingerprints only show marginal variations among phylogenetically close groups (i.e. carbon source endmembers) (Larsen et al., 2013; Larsen et al., 2015), making this method a highly source-specific biomarker to distinguish marine, terrestrial and bacterial production. Another benefit of this method is that EAA stable isotope values are conserved across environmental conditions (Larsen et al., 2013).

The aim of this study was to identify the proportional contributions of various organic matter sources (phytoplankton, terrestrial, and bacterial carbon) within the top 5 cm horizon of sediments across the Chukchi Sea shelf. We hypothesized that the relative proportions of carbon sources across the shelf would vary spatially in response to environmental conditions. We further predicted that the proportions of phytoplankton-derived carbon would be highest in surface sediments while proportions of bacterial and terrestrially derived carbon would be higher in deeper sediment layers. Additionally, we hypothesized that higher temperatures (5°C over ambient 0°C) would result in higher bacterial community production within sediments.

2. Materials and methods

2.1. Sample collection

Sediment samples used to examine carbon sources were collected at 14 stations between 30 and 54 m water depths across the Chukchi Sea shelf during the Arctic Marine Biodiversity Observing Network (AMBON, www.ambon-us.org) cruise in August 2015 (Fig. 1). Single sediment samples were collected with a Haps core at stations where the core could penetrate the sediment. The top 5 cm of each core were sliced into 1 cm sections, each layer was then homogenized with a spatula, and frozen at -20°C in whirl packs. Deeper sediment layers (to 10 cm depth), mostly composed of condensed clay, were also analyzed for some stations to determine whether EAA depth trends could be detected in deeper sediments that may be less affected by bioturbation. However, EAA source contributions did not change over this additional sediment depth range and data are not presented. Sediment samples were transported frozen to the University of Alaska Fairbanks (UAF) for later processing.

Environmental variables (Table 1), measured concurrently by collaborators at each station, included bottom temperature, bottom salinity, bottom oxygen, sediment grain size, sediment chlorophyll *a* content, total organic carbon (TOC), bulk sediment carbon to nitrogen ratios (C/N), and bulk stable carbon and nitrogen isotope compositions (expressed as $\delta^{13}C$ and $\delta^{15}N$ values). Environmental data are available through the Marine Biodiversity Observing Network (MBON) Data Portal (https://mbon.ioos.us/, https://doi.org/10.25921/zqwr-at45). Bottom temperature, salinity and oxygen ranged from -1.7°C to 7.5°C, 31.0 to 32.7, and 230.0 – 335.3 µmols kg^{-1}, respectively. The majority of the sediments consisted of silt (phi ≥5, 17.5 – 97.1 %, median 74.3 %) with varying proportions of sand (phi 1-4, 2.7 – 82.3 %, median 24.6 %). Chlorophyll *a* concentration of the upper 2 cm sediment layer ranged from 5.5 to 17.4 mg/m^2 and TOC ranged from 0.25 to 1.35 %. Surface sediment bulk C/N (wt/wt) ratios ranged from 4.01 to 8.74, and $\delta^{13}C$ and $\delta^{15}N$ values ranged from -21.2 to -24.4 ‰ and 4.8 to 9.8 ‰, respectively.

Sediment samples for microcosm experiments of bacterial production were collected at one location in the northern Bering Sea (63.316643 °N, -168.467905 °W) during the Arctic Shelf Growth, Advection, Respiration, and Deposition Rate Measurements (ASGARD) cruise in 2017 (Baker et al., 2020; https://www.nprb.org/arctic-program). The upper 1 cm of eight Haps cores were taken and homogenized. Bottom water from the sediment sampling site was collected using a CTD rosette and filtered through GF/F filters (Whatman, approx. pore size 0.7 µm) to remove particles. Homogenized sediments in whirl packs were topped off with filtered seawater and stored at 0°C onboard the vessel for three days before returning back to the UAF for experimental set up.

2.2. Determining organic matter sources using essential amino acid stable isotope analysis

EAA specific stable isotope fingerprinting was used to identify carbon sources in sediments. This approach is based on the EAA of phylogenetically close groups (e.g. marine microalgae, terrestrial plants, bacteria) conserving specific stable isotope values that form characteristic patterns (fingerprints) for these primary producer groups (Larsen et al., 2013; Larsen et al., 2015). This makes it a highly source-specific biomarker and a powerful tool to trace primary production sources.

For EAA extraction, homogenized sediment layers were freeze-dried for 24 h and dry weight per sample determined (150-220 mg). Dried sediments were transferred into culture tubes, 1 mL of 6-N

hydrochloric acid (HCl) added, flushed with N_2 to prevent oxidation, sealed and hydrolyzed at 110°C in a heating block for 20 h (following Larsen et al., 2013). The liquid phase containing amino acids (AA) was transferred into a 3 mL BD syringe™ connected to a 0.2 µm Millex-GP™ filter to remove any excess sediment material. The syringe filter was rinsed with approximately 0.25 µl of 0.1-N HCl to remove remaining AA. At this stage, norleucine (25 µl, Sigma-Aldrich, batch number BCBQ0497V) was added as an internal standard to each filtrate sample, and samples were evaporated to dryness under constant N_2 flow in a 60°C water bath. A cation exchange column equipped with Dowex 50WX8-400 ion exchange resin was prepared for each sample, rinsed with 0.01 N HCl, and each sample resuspended in 1 mL 0.01-N HCl, and added to its respective column. Amino acids in the sample solution remained on the resin. Bound AA were rinsed from the column with 4 mL 2-N ammonium hydroxide (Na_4OH) in 1 mL increments and the combined eluents collected. These samples were then dried under constant N_2 flow in an 80°C water bath for 2-4 h. Amino acid in samples were re-protonated by adding 1 mL 0.2-N HCl, the sample then flushed with N_2, heated for 5 min at 110°C, and evaporated to dryness. Dried samples were acetylated using 2 mL acidified 2-propanol to convert non-volatile AA into volatile N-acetyl methyl ester derivatives, and samples capped and heated to 110°C on a heating block for 60 min. After cooling, samples were evaporated to dryness under constant N_2 flow at 60°C. Samples were washed twice with 0.5 mL dichloromethane (DCM) and evaporated to dryness at room temperature under a constant stream of N_2. Samples were derivatized by adding 0.5 mL trifluoroacetic acid (N-TFA) and 0.5 mL DCM, heated at 100°C for 10 min, cooled, and evaporated to dryness at room temperature under a constant stream of N_2. Then, 2 mL phosphate-buffer (PB) and 2 mL chloroform were added to each sample, shaken for 60 sec, and centrifuged for 5 min at 600 g (3000 rpm). The chloroform layer (bottom layer) containing AA was transferred into new vials, while the remaining PB (top layer) was re-extracted twice with 1 mL chloroform each (repeat shaking and centrifuging). Derivatized AA were then dried at room temperature under N_2. To ensure full derivatization, 0.5 mL N-TFA and 0.5 mL DCM were added to each sample vial, heated at 100°C for 15 min, and then rinsed with DCM as described above. Ethyl acetate (250 µl) was added to each sample and transferred into 2 mL vials. $\delta^{13}C_{AA}$ values of AA were determined on a gas chromatograph isotope ratio mass spectrometer (GC-IRMS) equipped with an HP ULTRA-1 column (Agilent, 50 m x 0.32 mm x 0.52 µm) at the UAF Alaska Stable Isotope Facility. The following temperature program was used: 60°C (3 min), 110°C (3°C min^{-1}) for 5 min, 190 °C (3°C min^{-1}) for 5 min, then increasing at a rate of 10°C min^{-1} to 280°C (8 min). Samples were injected using a split/splitless inlet (280°C): injection volume 0.3 µL, carrier flow 0.8 min^{-1}, split flow 50 mL min^{-1}, purge flow 5.0 min^{-1}, split flow 50 mL min^{-1}, splitless time 1.0 min.

Stable isotope ratios are reported in delta (δ) notation as $((R_{sample}/ R_{standard}) -1) \times 1000$ ‰, where R is the ratio of heavy to light isotope, and the standard for carbon was Vienna Pee Dee Belemnite (VPDB). To account for the addition and fractionation of carbon during the AA derivatization process, correction factors for each AA were calculated from known reference values for $\delta^{13}C$ of pure AA according to O'Brien et al., (2002). Average reproducibility for the internal standard (norleucine) from all analyses was ≤1.46 ‰. Corrected AA $\delta^{13}C$ values were normalized for each sample to their respective mean $\delta^{13}C$ ($\delta^{13}C_{EAA} = \delta^{13}C_{EAA} - \text{mean } \delta^{13}C_{EAA}$) to create $\delta^{13}C_{EAA}$ fingerprints (e.g. Rowe et al., 2019) for each sediment layer and allow for direct comparison of fingerprints among samples.

All AA samples were analyzed in triplicate and the following five essential AA separated: isoleucine (Ile), leucine (Leu), phenylalanine (Phe), threonine (Thr), valine (Val). The additional EAA lysine (Lys) and tyrosine (Tyr) were not consistently detected in all samples due to low concentrations. Additionally, to account for analytical variability among different extraction batches, an external AA standard (norleucine Sigma-Aldrich, BCBQ0497V) was analyzed with each extract batch.

2.3. Sediment bacterial production incubations

Phospholipid fatty acid (PLFA) analysis was used to determine bacterial production at different temperatures in sediment microcosm experiments. PLFAs are a major component of bacterial cell membranes and a common biomarker used to identify the bacterial community and their biomass (Boschker et al., 1998; He et al., 2015). The objective was to track assimilation of labeled microalgal carbon into bacterial PLFAs under different temperature treatments. This allowed us to assess whether the bacterial community showed higher productivity at increased temperatures that are predicted for the Chukchi Sea shelf. Only PLFAs known to be bacterial markers were included in the analysis.

A ^{13}C-labeled and non-labeled microalgal stock was grown prior to the ASGARD cruise at UAF according to Weems et al., (2012), to be used as substrate in microcosm experiments. An 8-L monoculture of the marine diatom *Chaetoceros muelleri*, supplied by Dr. R. Hopcroft (UAF), was incubated at 5°C with 24 h light over a one-month period. Artificial seawater (Instant Ocean, S=32) served as a medium to grow algal culture, and nutrient fertilizer (Guillard's f/2 marine water enrichment + silicate, concentration 50x) was added weekly (160 mL). Aeration and mixing were provided by bubbling the culture with an aquarium pump. The culture was subsampled weekly, at which time half of

the batch was removed and replaced with artificial seawater and f/2 nutrients. The removed algal stock (4 L) was subsampled, with 2 L being centrifuged (4000 rpm, 2647 g, 5 min) and resulting pellets frozen at -20°C for the non-labeled algal stock. The remaining 2 L were incubated for another 24 h with 1 mL of ^{13}C-enriched sodium bicarbonate solution (1.7 g of 98 % ^{13}C sodium bicarbonate in 100 mL distilled water added to 2 L culture) and afterwards centrifuged (4000 rpm, 2647 g, 5 min), and frozen at -20°C for the isotopically labeled algal stock. Multiple harvested batches of algae were homogenized to ensure a consistent algal food stock supplied to the microcosm treatments. Bulk carbon stable isotope values of algal stocks were determined using a GC-IRMS to ensure sufficient isotopic enrichment and for later calculation of carbon incorporation into bacterial PLFAs. The average bulk stable isotope value (δ^{13}C) for the labeled algal stock was 2300.0 ‰, while the non-labeled algal stock averaged -14.9 ‰.

About 35 g (wet weight) homogenized natural sediment were placed into 50 mL Erlenmeyer flasks, and each flask was covered by approximately 30 mL of ambient filtered seawater. Erlenmeyer flasks were loosely covered with aluminum foil to prevent contamination and then randomly assigned to one of two temperature treatments. Temperature settings were chosen to be 0°C (Treatment 1), representing current bottom water temperature on the Chukchi Sea shelf for much of the annual cycle (Weingartner et al., 2013), and 5°C as a predicted increased bottom water temperature on the shelf by 2050 (Treatment 2) (Wang et al., 2012). Flasks were then placed on a shaker in the incubator at the respective temperatures to ensure sufficient O_2 supply during the experiment. Isotopically labeled algal stock was supplied to half the 0°C and half the 5°C treatment flasks, while the other respective half received non-labeled algal stock. Algal stock was added at time zero (T_0) at the beginning of the experiment at a concentration of 458 mg C m^{-2}, reflecting typical *in situ* daily organic carbon deposition rates in the Chukchi Sea at the time of sampling (Moran et al., 1997). Both temperature treatments were run concurrently with labeled and non-labeled algal food in parallel for 8 days; experiments were destructively sampled at eight times (0, 3, 6, 12, 24, 48, 96, and 192 h), when one flask per temperature and isotope label treatment was removed and contents frozen (-20°C) for later PLFA analysis. Each temperature treatment was conducted as a single replicate experiment.

Sediment PLFA extraction followed methods described by He et al., (2015). Sediment samples from the experiments were freeze-dried for 24 h and approximately 5.0 g sample sequentially extracted with 3.2 mL citric acid buffer, 4.0 mL chloroform, and 8.0 mL methanol. Then, 4.8 mL citric acid and 6.0 mL chloroform were added to the combined supernatants per sample, well shaken, and the sample kept at 4°C in the dark overnight for phase separation. The bottom chloroform layer containing lipids was

isolated, washed with methanol, and dried under constant N_2 flow in a water bath (25-35°C). Through solid phase extraction (SPE) gel chromatography, both neutral lipids and glycolipids were removed using chloroform and acetone, respectively. Remaining polar PLFAs were collected using methanol and dried under constant N_2 flow in a water bath (25-35°C). PLFAs were esterified into fatty acid methyl esters (FAMEs) using methanol:toluene, potassium-hydroxide:methanol, n-hexane:chloroform, acetic acid, and deionized water, and 80 µL of internal 19:0 fatty acid standard (nonadecanoate, Sigma Aldrich, batch number BCBT3339) was added at this stage for later PLFA quantification of PLFA concentrations. The top organic layer was retained, dried with N_2, and stored at -20°C until analysis. The following temperature program was used: 60°C (3 min), 110°C (3°C min^{-1}) for 5 min, 190 °C (3°C min^{-1}) for 5 min, and increasing at a rate of 10°C min^{-1} to 280°C (8 min). Samples were injected using a split/splitless inlet (280°C): injection volume 0.3 µL, carrier flow 0.8 min^{-1}, split flow 50 mL min^{-1}, purge flow 5.0 min^{-1}, split flow 50 mL min^{-1}, splitless time 1.0 min.

Nomenclature A:Bn-C as defined in Budge (1999) was used to describe PLFAs, where A represents the number of carbon atoms in a given PLFA, B refers to the number of double bonds, and C the position of the double bond closest to the terminal methyl group. A bacterial acid methyl ester mix (BAME, Sigma-Aldrich, batch number BCBT4956) was used to identify bacterial PLFAs in samples. The BAME mix was analyzed using a GC-IRMS to identify peaks. Both BAME mix and extracted samples were run on a GC-IRMS to identify (using BAME mix) and quantify (using 19:0 nonadecanoate FA standard) peaks and determine $\delta^{13}C$ values of PLFAs. For ease, PLFA were labeled with numbers referring to their sequence in the chromatograms (Table 2).

Concentrations for each bacterial PLFA per gram of sediment in microcosm experiments were calculated as follows:

$$\text{PLFA } \left(\frac{\mu g}{mL}\right) = \frac{\left(\frac{19{:}0 \text{ concentration}}{19{:}0 \text{ peak area}} \bullet \text{PLFA peak area}\right)}{\text{dry weight sediment (g)}}$$

where, 19:0 concentration is the concentration of the internal standard added to each sample (230 µg/mL), and dry weight sediment refers to the total amount of freeze-dried sediment used for PLFA extraction in grams. In addition, isotope tracer assimilation into each bacterial PLFA over time was determined using a stable isotope mixing model (McMahon et al., 2006; Weems et al., 2012) as follows:

$$X_{tracer}(\%) = \left[\frac{\delta^{13}C_{sample} - \delta^{13}C_{initial}}{\delta^{13}C_{algal\ tracer} - \delta^{13}C_{initial}}\right] \bullet 100$$

where, X_{tracer} refers to the fraction (%) of the tracer incorporated into bacterial PLFA, $\delta^{13}C_{sample}$ being the $\delta^{13}C$ value of the PLFA at the time of sampling, $\delta^{13}C_{initial}$ is the initial $\delta^{13}C$ value of PLFA at t_0, and $\delta^{13}C_{algal\ tracer}$ is the mean labeled algal $\delta^{13}C$ value.

2.4. Statistical analysis

EEA values of endmembers were taken from Rowe et al., (2019) for diatoms and terrestrial plants (samples analyzed in the same lab and instrumentation as in this study), while bacterial $\delta^{13}C_{EAA}$ were used from Larsen et al., (2013). While some of the data obtained from Larsen et al. (2013) were obtained from a different lab, all $\delta^{13}C_{EAA}$ measures were made relative to standards and were consistently expressed relative to the same primary standard (VPDB). Analytical precisions are very similar between labs for $\delta^{13}C_{EAA}$ measures (see Rowe et al., 2019 and Larsen et al., 2013). Also, the data analyses involved normalization of the actual $\delta^{13}C_{EAA}$ relative to the means of the amino acids, which practically eliminates the importance of $\delta^{13}C$ as the actual data used are the difference in per mil between amino acids. Average reproducibility for the internal standard (norleucine) from all analyses was ≤0.7 ‰.

$\delta^{13}C_{EAA}$ values were distinct among these sources. A stable isotope mixing model in R (SIMMR, https://cran.r-project.org/web/packages/simmr/vignettes/simmr.htmL) was used to determine proportional contribution of EAA carbon from the various endmembers to sediments. This model is a commonly used tool to infer dietary proportions, based on various carbon sources (here phytoplankton, bacteria, terrestrial), assuming that all potential sources are considered in the mixing model and endmembers are isotopically distinct. Five EAA $\delta^{13}C$ values (see above) were used to estimated proportional contributions using mass balance mixing equations within a Bayesian framework to determine the proportional (%) EAA carbon contributions of endmembers for each sediment depth section at each station (Appendix A). The upper two sediment layers (0-2 cm) were averaged to account for uneven sediment surfaces. Here, we used EAA source contributions in statistical analyses as a proxy for overall carbon contribution to sediments.

Most statistical analyses were performed in R using the RStudio interface version 1.1.383 (http://www.rstudio.com). Prior to parametric statistical analyses, normality of data was tested using a Shapiro-Wilks test, homogeneity of variance using Levene's test, and independence using a chi-squared

test. If necessary, data were transformed to meet assumptions. Significant differences in proportional contributions were determined of each endmember among sediment depth layers, and among endmembers within each sediment depth layer. For these analyses, stations were used as replicates. Significant differences were determined using analyses of variance (ANOVA) with Tukey's honest significant difference post-hoc test at a significance level of $\alpha = 0.05$. Differences in the proportional composition among stations was using non-metric multi-dimensional scaling (nMDS) to determine any potential grouping of stations. Environmental variables were included to determine whether any clusters were driven by environmental variables at representative stations. A BEST analysis (PRIMER version 7.0.13) determined relationships among average proportional carbon contributions of all endmember groups in surface sediments (0-2 cm layer) and environmental variables: bottom temperature, bottom salinity, bottom oxygen, sediment grain size, sediment chlorophyll *a* content, TOC, bulk sediment C/N ratios, and $\delta^{13}C$ and $\delta^{15}N$ values (Table 1). The lack of station-level replication precluded analysis of significance in multivariate analyses.

For the PLFA production of sediment bacteria under different temperature incubations, significant differences in total bacterial PLFA concentration between temperature treatments were determined using t-tests (labeled and non-labeled trials combined for n=2 per temperature treatment, significance level $\alpha = 0.05$).

3. Results

3.1. Organic matter sources across sediments depths

Normalized $\delta^{13}C_{AA}$ values of each sediment layer were averaged across stations for each EAA, and overall EAA isotope fingerprints were very consistent among depth layers (Fig. 2). Proportional contributions of EAA from the three endmember groups to sediment samples from SIMMR calculations were highly variable. On average, bacteria contributed 31.0 % (5.7 – 50.1 %), while phytoplankton averaged 30.1 % (9.9 – 64.9 %). Terrestrial carbon contributions (3.8 – 80.6 %) made up the highest average carbon contribution with 38.8 %. Visual inspection of the spatial distribution of average proportional contributions in the 0-2 cm sediment layer did not reveal a clear pattern across the shelf

385 although terrestrial contribution was especially high at the two mid-shelf stations in the southern
386 Chukchi Sea (DBO3-8 and CL3, Fig. 1 and 3). An nMDS confirmed the two mid-shelf stations to be distinct
387 (Fig. 4). There was no significant relationship between proportional carbon contributions and
388 environmental variables (BEST analysis). No significant differences in the proportional contributions
389 among sediment layers were identified within either terrestrial or bacterial EAA ($p>0.05$, ANOVA, Fig. 5).
390 Only phytoplankton contributions were significantly higher in the top layer (0-2 cm) compared to the
391 bottom layer (4-5 cm) ($p = 0.04$, ANOVA). With respect to the various EAA source composition within
392 each depth layer, proportional contributions of terrestrial carbon in the 2-3 cm and 3-4 cm depth
393 sediment layers were significantly higher compared to other carbon sources and significantly higher
394 compared to phytoplankton in the 4-5 cm depth layer ($p = 0.03$, ANOVA) (Fig. 5).

395

396 *3.2. Bacterial production at different temperatures*

397

398 Total bacterial PLFA concentrations (all other PLFA were excluded from the analysis) in
399 microcosm experiments between the 0°C and 5°C treatment (combining isotopically labeled and non-
400 labeled trials for each temperature treatment) were significantly different ($p = 0.02$, t-test) (Fig. 6). Total
401 bacterial PLFA concentrations over time were noticeably higher in the 5°C treatment at 12 and 24 h, but
402 given the low number of replicates (n=2) only the difference at 24 h was significant ($p = 0.01$, t-test). The
403 differences between the temperature treatments seemed to be driven by overall higher concentrations
404 of the individual PLFAs tested at 5°C; however, specifically C16:1 cis-9 (PLFA 14) and C17:0 (PLFA 18)
405 were higher in the 5°C treatment at 12 h and 24 h (Fig. 7, see Table 2 for PLFA identification).

406 Only five PLFAs showed incorporation of isotopically labeled material, indicated by changes in
407 individual PLFA $\delta^{13}C$ values of up to 500 ‰ throughout the experiment (Fig. 8). Other PLFAs only showed
408 marginal changes in the PLFA $\delta^{13}C$ values of ±15 ‰ and were not included in carbon incorporation
409 analyses. The proportional contribution of carbon incorporated into these five main PLFAs from labeled
410 algal material seemed to be higher in the 5°C treatment compared to the 0°C treatment. The PLFA
411 showing highest incorporation of labeled material was C16:1 “cis-9” (PLFA 14) with proportions of
412 carbon incorporation ranging from 0.16 – 33.56 %. C15:0 (PLFA 10, 0.96 – 11.00 %), C18:2w6 cis (PLFA
413 20, 0.19 – 11.41 %), C18:1w9 cis (PLFA 21, 0.65 – 4.35 %) and C18:1 (trans 9) (PLFA 22, 0.95 – 8.03 %)
414 only showed small carbon portions to be derived from labeled material.

4. Discussion

4.1. Distribution of sediment organic matter sources

The unprecedented climate-induced changes occurring in the Arctic Ocean have the potential to influence the composition of organic matter sources in Chukchi Sea shelf sediments that are essential in carbon cycling and contribute to the base of the benthic food web. The goal of this study was to identify the proportional contributions of carbon sources within the top 5 cm sediment horizon of *in situ* sediments across the Chukchi Sea. Results revealed no clear spatial pattern of the three main carbon sources (phytoplankton, terrestrial, and bacterial) across the shelf in relation to environmental variables and only exhibited minor spatial patterns in terms of higher terrestrial proportional contribution at southern stations. Carbon sources in sediments were relatively well-mixed over the top 5 cm. However, phytoplankton contribution slightly decreased in deeper sediment layers and terrestrial matter was present in significantly higher proportions in deeper sediment depths (>2 cm) compared with other sources. Increased bacterial production at higher experimental temperatures indicated a potential increase in the proportion of bacterial carbon in a future, warmer Arctic.

The analysis of proportional contributions using mixing models is dependent on the source information supplied. For example, predictions of endmember contributions will only include those sources supplied to the model. Conversely, every endmember that is supplied to the model will always result in the assignment of at least some proportional contribution (Phillips et al., 2014). Here, we included marine phytoplankton, terrestrial matter, and bacterial carbon as sources and excluded macroalgal carbon that has been included in other studies (Larsen et al., 2013; Larsen et al., 2015; McMahon et al., 2016; Rowe et al. 2019). Macroalgae are uncommon along the Chukchi Sea coast (Mohr et al., 1957; Wulff et al., 2009), and while the occasional drift of algal material offshore cannot be excluded, it is unlikely to be a common carbon subsidy into Chukchi shelf sediments. In addition, the potentially high biomass and important role of fungi in the degradation of organic matter is increasingly acknowledged (Raghukumar, 2017), but isolating and characterizing this endmember as a source is currently outside our ability. In addition, mixing models provide relative contributions of EAA and not absolute concentrations of carbon sources to a given sample. Hence, results will need to be interpreted within the framework of such potential limitations, but our ecological knowledge of the system allowed

445 us to select the most likely sources, and results will be especially valuable in assessing potential shifts in
446 relative sources in the future.

447 Relative contributions of different EAA sources to sediments did not display a clear spatial
448 pattern across the shelf and did not correlate with any environmental variables tested. The Chukchi Sea
449 is characterized by distinct water masses of different temperature, salinity, and nutrient content,
450 influencing the respective productivity regimes (Walsh et al., 1989). However, all sampling sites for this
451 study were located within the salty, cold, nutrient-rich, and highly productive Bering Shelf Anadyr
452 Water, based on bottom temperature and salinity data taken during the cruise. Also, all sampling
453 locations were similar in bottom depth. Similar productivity regimes for all stations based on water mass
454 characteristics may in part explain the similarity of EAA sources across all sites.

455 Although no clear spatial pattern was detected of EAA distribution with environmental variables,
456 we observed higher contributions of terrestrial EAA at the two southern-most offshore stations in Hope
457 Basin, north of the Bering Strait. Flow regimes can differ within a water mass and influence local
458 environmental conditions, e.g. grain size, TOC content, and the deposition of suspended material.
459 Current velocities on the Chukchi shelf vary depending on topography (Winsor and Chapman, 2004),
460 season (Woodgate et al., 2005), remote atmospheric forcing (Danielson et al., 2014), and the shelf
461 isobath-density fields (e.g. Weingartner et al., 2017). Regions with lower flow variance are usually
462 associated with smaller sediment grain size and higher deposition of organic matter, as the weaker
463 currents allow smaller particle sizes to settle out of the water column (Blanchard et al., 2013; Pisareva et
464 al., 2015). Within the spatial and temporal variability of the overall depositional shelf of the Chukchi Sea
465 (de Haas et al., 2002; Lepore et al., 2007), the Hope Basin in the south-central Chukchi Sea is known
466 regionally for the especially high deposition rates of organic matter (Grebmeier et al., 2015). Terrestrial
467 matter in the Chukchi Sea mostly derives from the Anadyr River in Siberia and the Yukon River in Alaska
468 (Li et al., 2017) with smaller contributions of the Kobuk and Noatak rivers in Kotzebue Sound (McManus
469 and Smyth, 1970; McManus et al., 1974; Naidu et al., 1982). For example, the Yukon River alone
470 discharges 2.02 10^{12} g TOC annually into the ocean (Guo and Macdonald, 2006). Sea ice also can be a
471 significant vector in the distribution of terrestrial matter beyond the coastal region farther onto the
472 shelf and even into the deep basin in the Arctic (Yunker et al., 2005). Ocean currents slow north of the
473 high-flow constriction presented by the Bering Strait, likely allowing for increased deposition of
474 terrestrial matter in the Hope Basin region (Li et al., 2017). Terrestrial matter that is partially degraded
475 during oceanic transport tends to associate with lithogenic particles, which increases their settlement in

these high depositional regions (Mayer, 1994). This could explain the observed higher proportional contribution of terrestrial EAA in sediments in this region relative to the stations farther north and regions of swifter currents found closer to the Alaskan coast (e.g. Clement et al., 2005). Increased sediment sampling in this ecologically important benthic "hotspot" region (Grebmeier et al., 2015) would be useful to discern if terrestrial deposition is indeed a consistent feature in the area as the C/N ratio and $\delta^{13}C$ values of sediments in the region, general indicators of terrestrial versus marine material (Naidu et al. 2000), were not strongly indicative of terrestrial matter.

A slight decrease in phytoplankton proportion with increasing sediment depth across the top 5 cm sediment was the only significant depth-related trend for any of the EAA sources. Such concentration gradients are dependent on consumption, transport, and decomposition of this material in the sediment (Sun et al., 1991; Sun et al., 1994). Marine microalgae (phytoplankton and ice algae) are highly labile and material deposited onto the seafloor is quickly consumed at the sediment surface by benthic consumers (Sun et al., 2007). The most labile dissolved organic portions of microalgal matter, such as lipids, are also biodegraded within days by bacteria (Newell et al., 1981; Canuel and Martens, 1996). Bioturbation from feeding activity of marine invertebrates results in the drawdown of remaining particulate microalgal fractions into deeper sediment layers, although this drawdown likely diminishes in deeper sediment layers (Kristensen et al., 2012). The Chukchi Shelf, including the locations of sediment collections for this study, are characterized by high benthic invertebrate biomass with a variety of feeding types that contribute to bioturbation (Iken et al., 2010; Iken et al., 2019). These subducted particulate fractions of phytoplankton are typically more refractory and have degradation times on the order of weeks to months (Newell et al., 1981; Garber, 1984; Kristensen and Holmer, 2001), which could lead to higher proportions of microalgal EAA at greater depth. The observed decrease in phytoplankton EAA proportions with depth, however, suggests that degradation rates in deeper layers in our study region exceeded the rate of particle transport from surface sediment down to depth. These observations match previous observations that chlorophyll *a* and POC concentrations can show an exponential decrease with sediment depth (Sun et al., 1991; Sun et al., 1994). Hence, high deposition of microalgae onto the sediment surface, combined with some subduction from bioturbation and continued degradation within the sediments, can cause the depth-related gradient in relative proportions of phytoplankton we hypothesized and observed.

Terrestrial EAA contributions also were relatively consistent over sediment depth horizons, and were present in significantly higher proportions compared with the other two sources in sediment

depths >2 cm. This is consistent with findings from Svalbard fjords, which showed higher amounts of lighter carbon isotope bulk organic material in sediments deeper than 1 cm, which was attributed to increases in terrestrial matter (Koziorowska et al., 2016). The initial, and rate-limiting, step of degradation of organic matter is the extracellular enzymatic hydrolysis of the high-molecular-weight organic matter common for terrestrial matter (Arnosti et al., 1998; Arndt et al., 2013). Terrestrial matter contains a high amount of structurally highly complex components, e.g. macromolecules like lignin and cellulose, and other molecules with high numbers of double bonds (Hedges et al., 1997; Opsahl and Benner, 1997; Baldock et al., 2004; Garneau et al., 2009). While this typically renders terrestrial material as less labile than marine-derived matter, overall degradability of terrestrial matter also differs depending on its age. Ancient terrestrial carbon is highly recalcitrant, while modern material is somewhat more labile (Goñi et al., 2005; Kim et al., 2011). During the transport from shore onto of the labile fraction of terrestrial matter is already subject to degradation, increasing the refractory proportion of the residual material when finally deposited onto the seafloor (Canuel and Martens, 1996; Lee et al., 2004). Hydrolysis rates in subsurface sediments can actually be higher than in surface sediments, but efficiency ultimately depends on how recalcitrant the material is (Teske et al., 2011). The remaining refractory portion of terrestrial matter after initial degradation in the water column and ancient carbon, which can make up the majority of total terrestrial carbon influx from Arctic rivers (Goñi et al., 2005), could have long degradation times, leading to accumulation in the deeper sediments (Canuel and Martens, 1996). These processes fit well with the observed pattern of higher proportion of the organic matter at these deeper layers being of terrestrial origin.

The relatively high proportions of terrestrial EAA found in Chukchi Sea sediments are not unusual for Arctic sediments. Most terrestrial matter comes from discharge of large Arctic rivers as well as groundwater seepage (McClelland et al., 2006). Permafrost and its accelerated melting due to climate warming also contribute substantial amounts of terrestrial matter to river discharge (Guo et al., 2007; Loiko et al., 2017). Terrestrial matter contributed 70 % (Winkelmann and Knies, 2005) and up to 80 % (Koziorowska et al., 2016) to the bulk organic carbon in fjords in the European Arctic, based on sediment bulk stable isotope analyses. The higher percentage values from the fjord systems likely derive from higher glacial input in such systems (Winkelmann and Knies, 2005; Koziorowska et al., 2016). While comparability of studies based on different methodology is limited, our values of about 50 % terrestrial matter of the EAA sources are lower than those for overall carbon sources from fjord environments, but suggest that our values are likely not overestimated and that terrestrial contributions to sedimentary carbon exceeding those from marine phytoplankton is common.

539 Contrary to our hypothesis, the proportional contributions of bacterially-derived EAA did not
540 show any change with sediment depth. This is in contrast to studies conducted elsewhere (e.g.
541 Mediterranean Sea), where bacterial biomass decreased with sediment depth because of a decline in
542 concentration of labile compounds and relative increase of more refractory compounds less prone to
543 bacterial degradation (Fabiano and Danovaro, 1994). Conversely, others have suggested that deeper,
544 paleo-sedimentary archives can contain higher proportions of bacterial carbon compared to other
545 carbon sources based on EAA fingerprinting (Larsen et al., 2015). In part this can be due to the overall
546 dynamic nature of sediments in the shallow Chukchi Sea based on storms, ice scour, shelf currents, etc.
547 (e.g. Toimil and Grantz 1976). This leads to overall shallow sediment accumulations of 2-6 m in the
548 study region, of which the upper ~50 cm are of Holocene origin, overlying deeper Quaternary and
549 Cretaceous layers (Phillips et al. 1988). Net sedimentation rates are low with estimated <0.05 cm yr^{-1}
550 since the last ice age (Keigwin et al. 2006). Low net sediment accumulation and upper layer sediment
551 mixing is also evident from the lack of layering of sediment trace metal distributions (Trefry et al., 2014).
552 Bioturbation, in addition to dynamic hydrography, are likely reasons for this. Bioturbation subducts
553 organic matter into deeper sediment layers, which also enhances ventilation rates within the sediment
554 and influences physical, chemical and biological properties within the deeper sediments (Mermillod-
555 Blondin et al., 2004; Kristensen et al., 2012; North et al., 2014). For example, degradation processes are
556 dependent on the availability of electron acceptors, which are directly influenced by processes such as
557 bioturbation and can govern the types of diagenetic processes occurring with depth (Nealson, 1997;
558 Fenchel, 2008). The increased O_2 penetration into sediment depths from bioturbation (Kristensen and
559 Holmer, 2001; Mermillod-Blondin and Rosenberg, 2006) supports bacterial degradation of labile matter
560 within the bioirrigated layer (Hulthe et al., 1998; Kristensen et al., 2012). O_2 penetration also increases
561 the typically slow, thermodynamically limited anaerobic degradation rates of refractory matter buried in
562 these deeper sediment layers (Hulthe et al., 1998; LaRowe and Van Cappellen, 2011). Despite O_2
563 availability, the buildup of bacterial carbon is highly reliant on the amount and specific lability of the
564 buried material (Legendre and Le Fevre, 1995; Pomeroy and Wiebe, 2001). A “priming” effect has been
565 suggested for labile organic matter in deeper layers, where either the breakdown of this labile matter
566 stimulates the production of extracellular enzymes that are active in degrading the more refractory
567 material, or where the labile matter provides energy for a bacterial community that is then able to
568 degrade the refractory matter (van Nugteren et al., 2009). Bacteria can assimilate available carbon in a
569 matter of hours (Moodley et al., 2000), and cell lysis of dead bacterial cells releases nutrients and
570 substrate that living bacteria are able to utilize to maintain bacterial community biomass. These

processes may cause relatively constant bacterial degradation and production in all sediment depths and, therefore, the observed consistent bacterial EAA contribution across sediment depths.

4.2. Sediment bacterial activity in a warming climate

Bacterial activity in degradation processes is not only dependent on the degradability of the organic matter but also on temperature. While polar bacteria are physiologically well adapted with high specific metabolic rates that support activity at low *in situ* temperatures (Arnosti et al., 1998; Knoblauch et al., 1999), their activity is sensitive to increases in water temperature. In fact, metabolic rates increase at optimal temperatures that are typically above *in situ* temperatures in polar systems (Rysgaard et al., 2004; Kirchman et al., 2005, 2009; Robador et al., 2009). As hypothesized, our microcosm experiment showed increased bacterial production, although intermittent, at the higher temperature (5°C) compared to the 0°C treatment. This is similar to another Arctic study that found a six-fold increase in bacterial production at incubations 6°C above ambient conditions (Kritzberg et al., 2010). Thus, despite physiological adaptations to low temperatures, optimal growth rates are not achieved at *in situ* temperatures in Arctic bacteria and, bacterial community activity is lower compared to those in temperate regions (Pomeroy and Deibel, 1986; Middelboe and Lundsgaard, 2003; Kirchman et al., 2005, 2009). Higher bacterial production at higher temperatures has been attributed to increased substrate affinity of extracellular enzymes at warmer temperatures as well as increased substrate assimilation within the cell (Nedwell, 1999). As substrate availability in our incubation experiment was equal across both temperature treatments, the increase in sediment bacterial production between treatments is attributable to temperature effects. This is similar to global (López-Urrutia and Morán, 2007) and Arctic (Kritzberg et al., 2010) studies that found clear increases in bacteria production in response to higher temperature if resource availability was equal.

The higher bacterial community productivity at the higher temperature treatment (5°C) peaked at 12-24 h, after which bacterial PLFA concentrations started to level with those of the 0°C treatment. The decrease in overall PLFA concentration (bacterial production) after 24 h in the 5°C treatment could have been related to the availability of substrate (Thingstad et al., 2002). The substrate may become rapidly depleted in sediment incubation experiments that are not supplied with any additional nutrients, resulting in a rapid decrease in overall activity of the bacterial community within hours (Novitsky and

601 Morita, 1977; Goldman et al., 1987; Lopez et al., 1998). For our experiment, no additional substrate was
602 provided past the initial addition, likely leading to an increase in bacterial production from the higher
603 rates supported by high temperatures. Once labile substrate was drawn down, resources were too
604 limited to support the higher bacterial production rates at 5°C. A similar decline in bacterial production
605 was not observed at the 0°C treatment, possibly because the lower production rates had not yet led to
606 substrate limitation. Finally, increased predation of bacteria by flagellates or meiofauna and viral lysis
607 (Almeida et al., 2001) could contribute to the decrease in bacterial PLFA concentration after 12-24 h at
608 higher temperatures.

609 Changes in bacterial PLFA concentrations between the temperature treatments seemed to be
610 largely driven by two PLFAs: C 16:1 (cis 9) (PLFA 14) and C 17:0 (PLFA 18). C 16:1 (cis 9) is produced by
611 both Gram-positive and Gram-negative bacteria, while PLFA 18 is usually produced only by Gram-
612 positive bacteria (Kaur et al., 2005). Although PLFA analysis is a widely applied tool enabling us to trace
613 the fate of specific substances, such as methane and contaminants through bacterial communities
614 (Kaplan and Bott, 1989; Evershed et al., 2006; He et al., 2015), the use of PLFAs as a biomarker for
615 taxonomic resolution of the bacterial community is still debated (Ruess and Chamberlain, 2010;
616 Frostegård et al., 2011). A good biomarker is defined by being highly source specific; however, while
617 some PLFAs are assigned to specific groups of bacteria, they often are produced by multiple groups of
618 bacteria, making taxonomic distinction of the bacterial community based on PLFA patterns difficult
619 (Frostegård et al., 2011; Yao et al., 2014). Higher taxonomic resolution, such as from DNA-stable isotope
620 probing (Radajewski et al., 2000), is needed to make detailed inferences about the specific groups of
621 bacteria responsible for the differences observed. Although taxonomic resolution is coarse, overall PLFA
622 presence and concentrations showed high overlap between the 5°C and 0°C treatments, indicating that
623 the differences in production were not due to major changes in community composition.

624 Only five out of eleven bacterial PLFAs incorporated the isotopically labeled substrate
625 throughout the incubation period (Table 3). Incorporation of labeled material into newly formed PLFAs
626 seemed to be slightly higher in the 5°C treatment, although only a small fraction (0.16 – 33.56 %) of
627 isotopically labeled carbon was incorporated during PLFA synthesis. This supports findings in previous
628 studies of only marginal assimilation of labeled substrate into bacterial PLFAs (Boschker et al., 1998;
629 Moore-Kucera and Dick, 2008). Labeled material is slightly higher in molecular weight and, therefore,
630 may not be taken up preferentially and incorporated into all PLFA by bacteria (Cifuentes and Salata,
631 2001). The incorporation of only small fraction of labeled PLFAs indicates that the majority of the

bacterial community derived carbon from other substrates than the provided microalgae. These other substrates probably included organic matter and dissolved organic carbon (DOC) present in the sediment, porewater and water supplied to the experimental set up, as well DOC released from predation and viral lysis of bacteria (Qiu et al., 2009) or internal carbon turnover in bacterial cells. In summary, these results suggest that expected elevated water temperatures in a future Arctic will increase bacterial production, which could be supported by the predicted higher phytoplankton production with the loss of sea ice (Arrigo et al., 2008).

5. Conclusions

In conclusion, carbon sources in Chukchi Sea sediments were relatively well-mixed over the top 5 cm horizon with large proportions of terrestrial carbon. The effects of climate-driven changes in temperature are predicted to be especially prominent on Arctic shelves. Resulting changes in the strength of pelagic-benthic coupling and increases in riverine input have the potential to shift the composition of carbon sources in Arctic sediments. Additionally, temperatures higher than current *in situ* conditions will increase bacterial metabolism and production in sediments, indicating a likely increase in this bacterial carbon source in a future, warmer Arctic. These potential shifts in carbon source contributions to the sediments could have strong implications for carbon storage or mobilization in sediments and the carbon flow through the Chukchi Sea benthic food web.

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Figures and tables

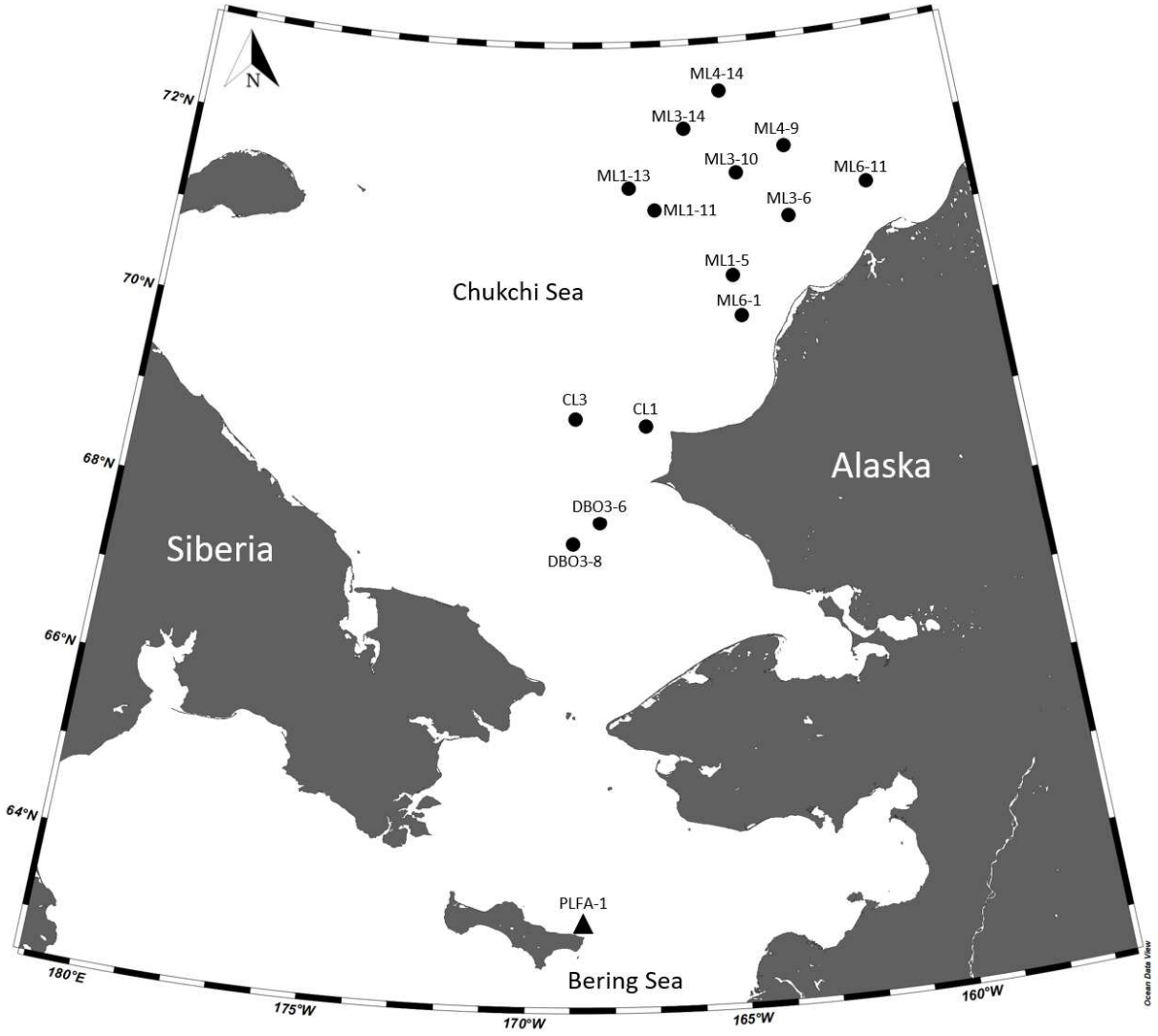


Fig. 1. Chukchi Sea stations (black dots – essential amino acid analysis) and Bering Sea station (black triangle – phospholipid fatty acid analysis - PLFA) sampled for sediment during the AMBON 2015 and ASGARD 2017 cruise, respectively.

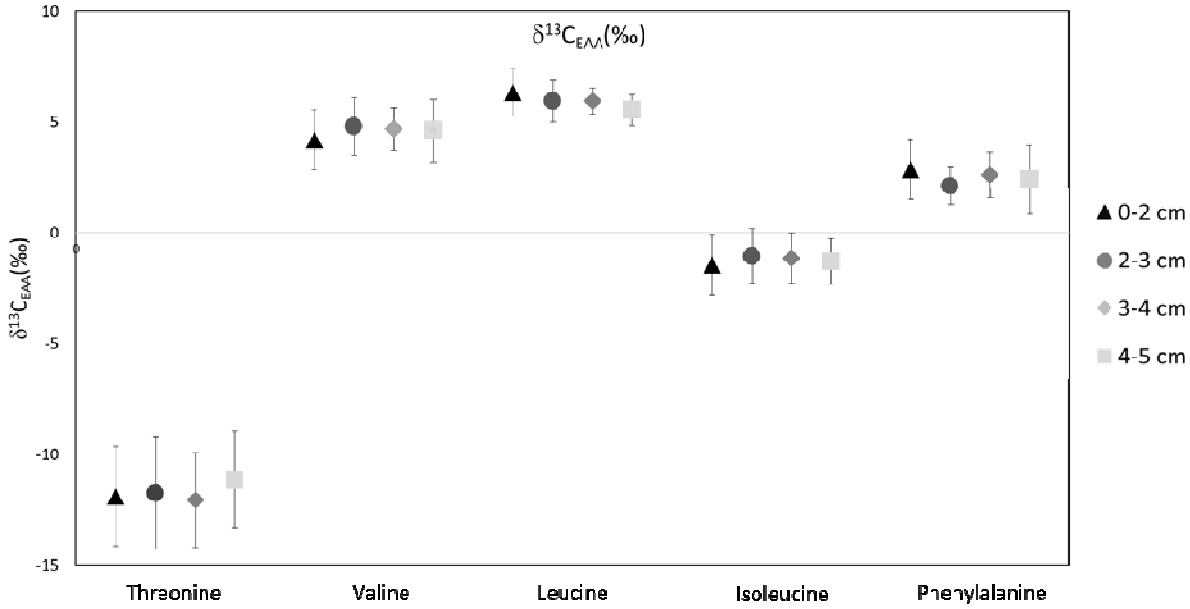
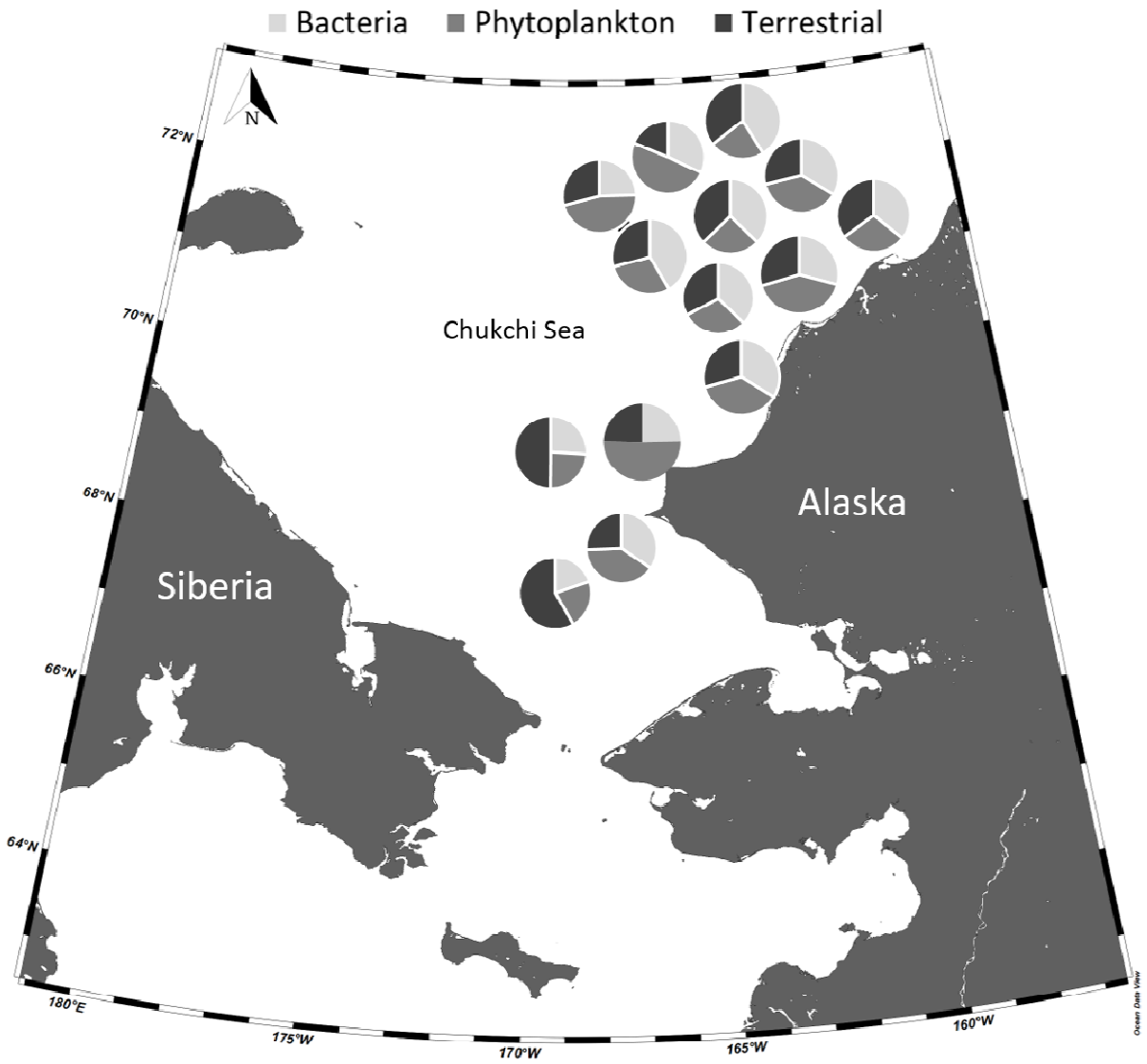


Fig. 2. $\delta^{13}C$ values of five essential amino acids (EAA), averaged across Chukchi Shelf sediment depth layer sampled (n=14) across all stations.



1067

1068 Fig. 3. Mean proportional contributions (%) of three essential amino acid sources (bacteria,
1069 phytoplankton, terrestrial) for the 0-2 cm sediment layer across the Chukchi Sea Shelf.

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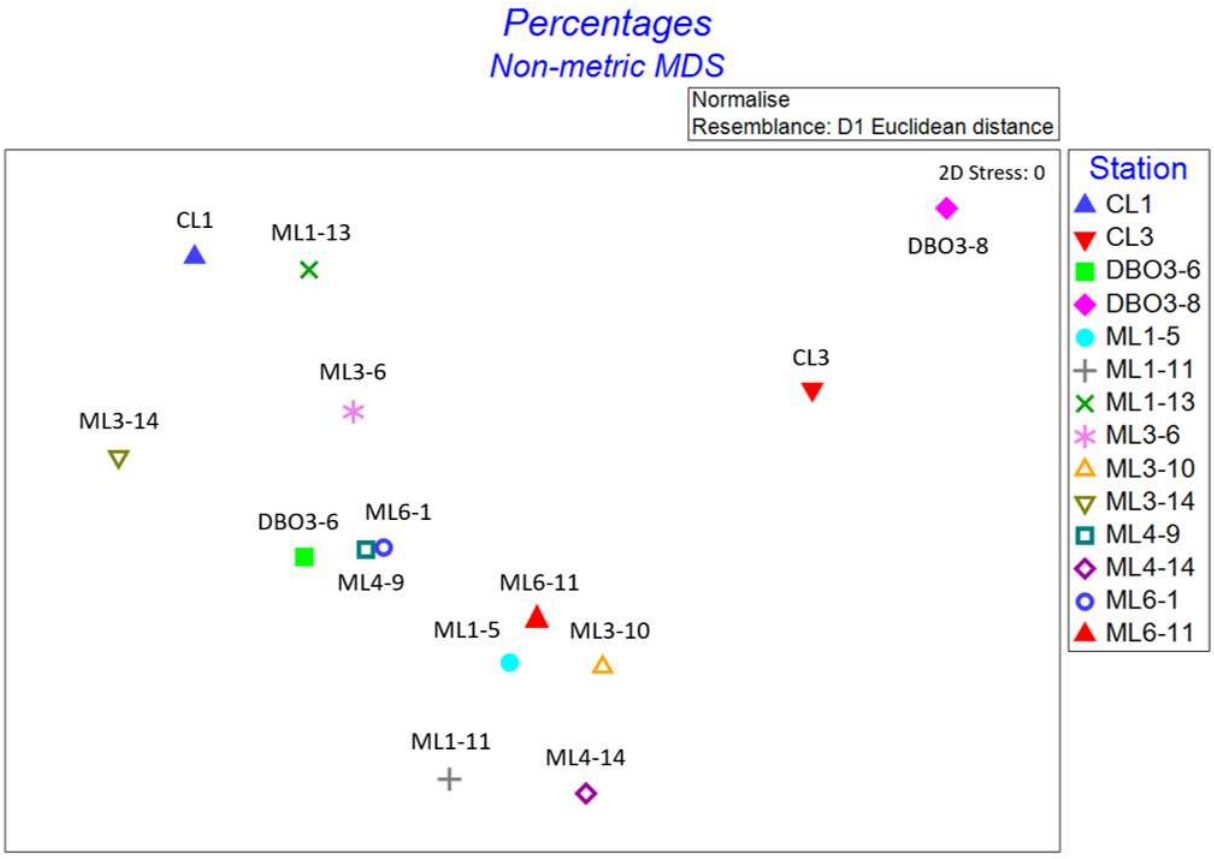

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1072 Fig. 4. nMDS mean proportional contributions (%) of three essential amino acid sources (bacteria,
1073 phytoplankton, terrestrial) for the 0-2 cm sediment layer across the Chukchi Sea Shelf.

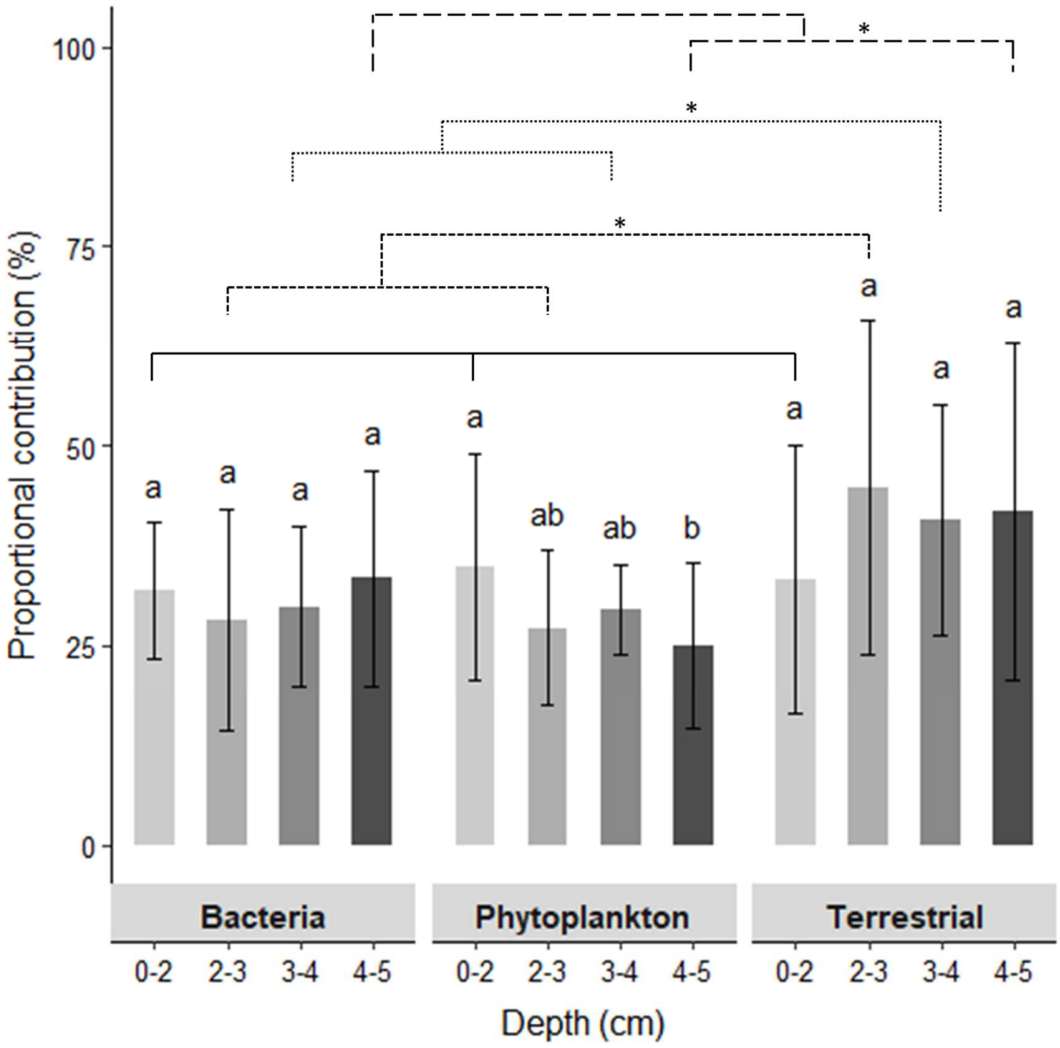


Fig. 5. Mean proportional contributions (%, mean ± 1 SD) of three essential amino acid (EAA) sources (bacteria, phytoplankton, and terrestrial) for each Chukchi Shelf sediment depth interval (cm, gray shades). Different letters above bars indicate significantly ($p<0.05$) different contributions among depth layers (n=14 per sediment layer), separately for each EAA source. Lines above bars indicate significant differences of proportional EAA contributions among sources for each sediment depth layer (n=14 per sediment layer and source). Different line types indicate statistical results for each sediment depth layer (solid: 0-2 cm; small dash: 2-3 cm, dotted – 3-4 cm; long dashed – 4-5 cm). Asterisks above connecting lines represent significant differences ($p<0.05$) between the sources within that sediment layer.

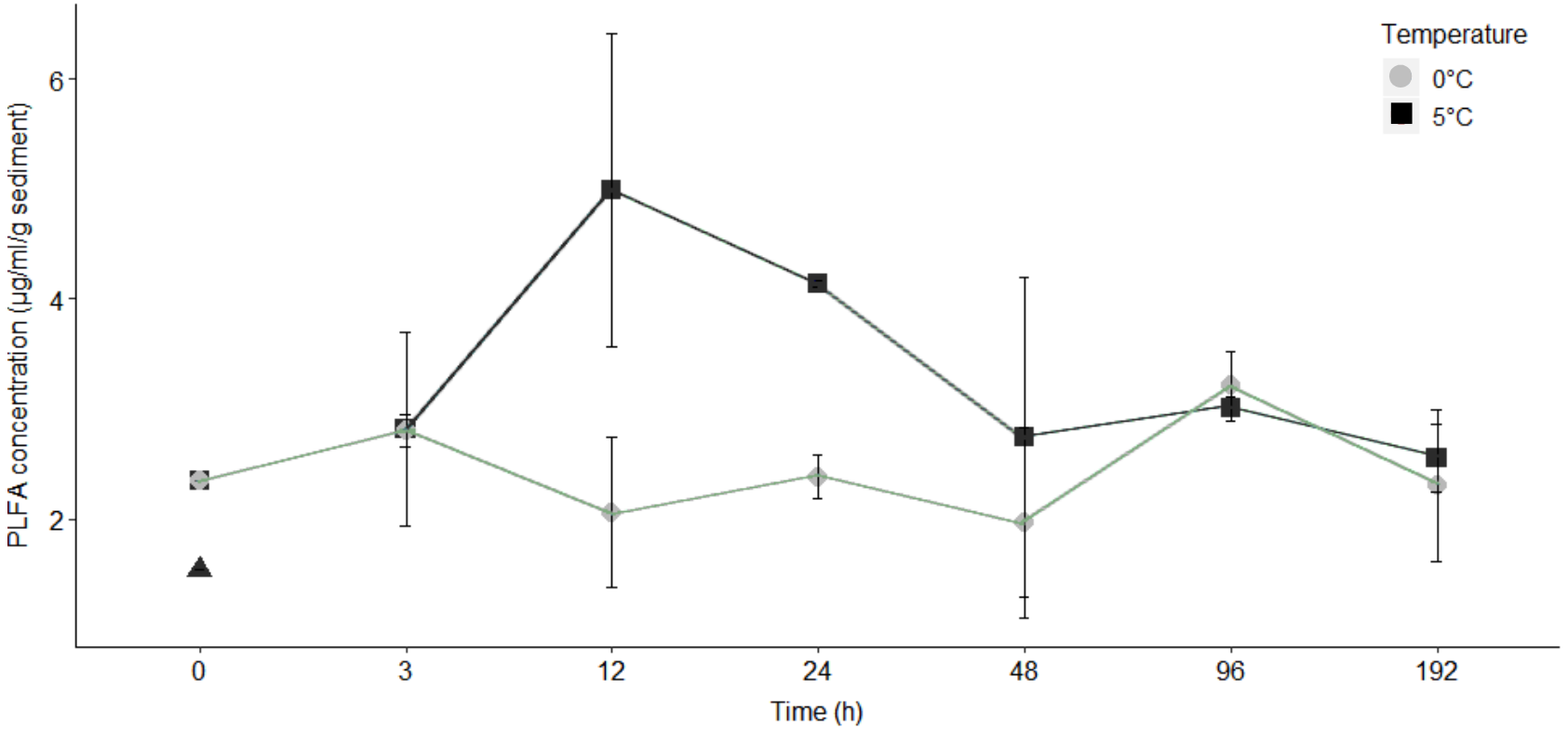


Fig. 6. Total phospholipid fatty acid (PLFA) concentration attributed to bacteria in marine sediments over 192 h for two temperature treatments, 0°C (light gray circle) and 5°C (dark gray square) (mean ± 1 SD, n=2 per treatment and time). The triangle at 0 h represents the sediment sample without addition of algae.

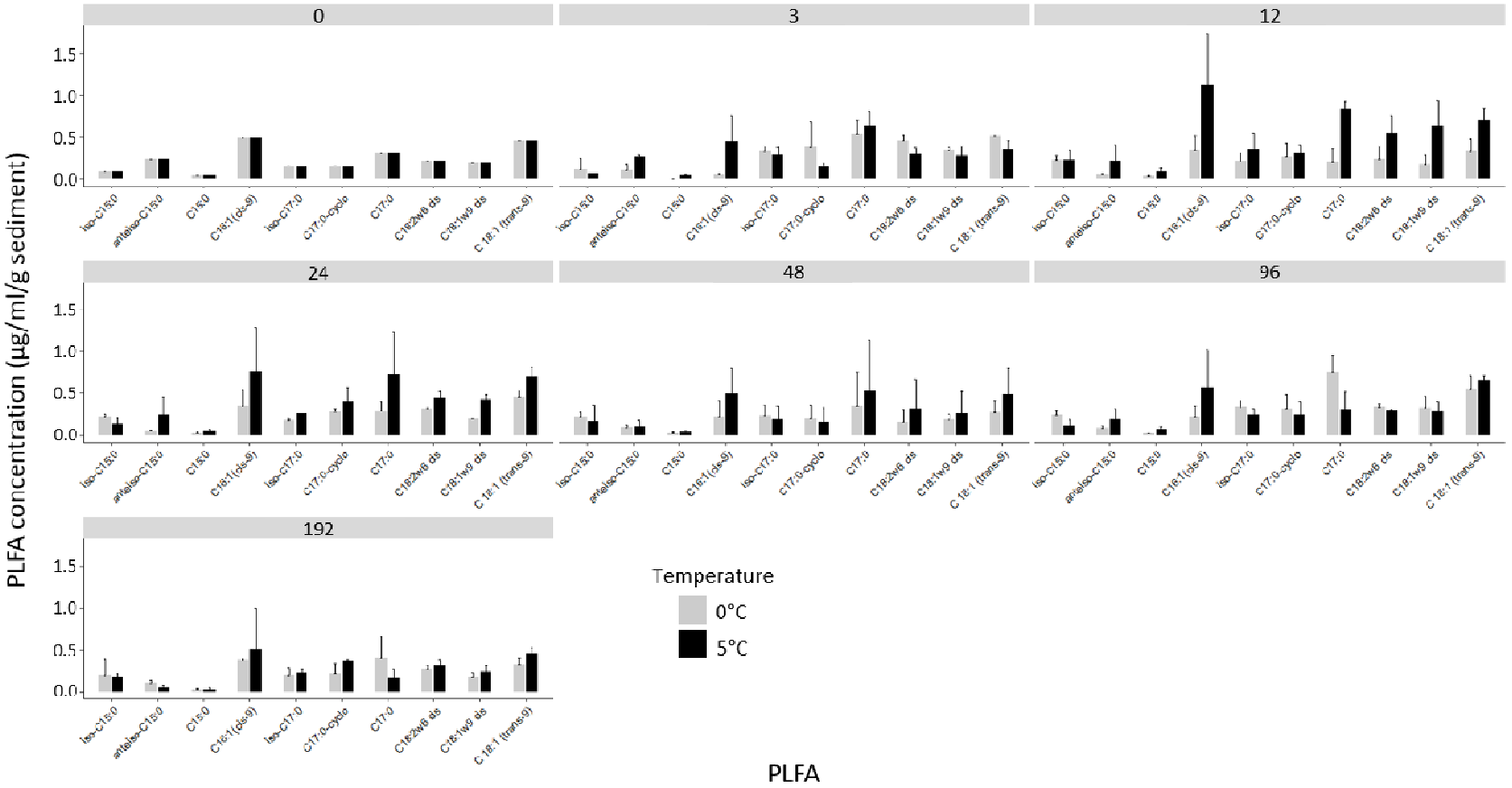


Fig. 7. Phospholipid fatty acid (PLFA) concentrations in marine sediments over 192 h (time given in bars above graphs) at two temperature treatments (mean ± 1 SD, n=2 per treatment and time, except at 0 h), 0°C (light gray) and 5°C (dark gray). Specific PLFAs are listed on the x-axis with additional information given in Table 1.

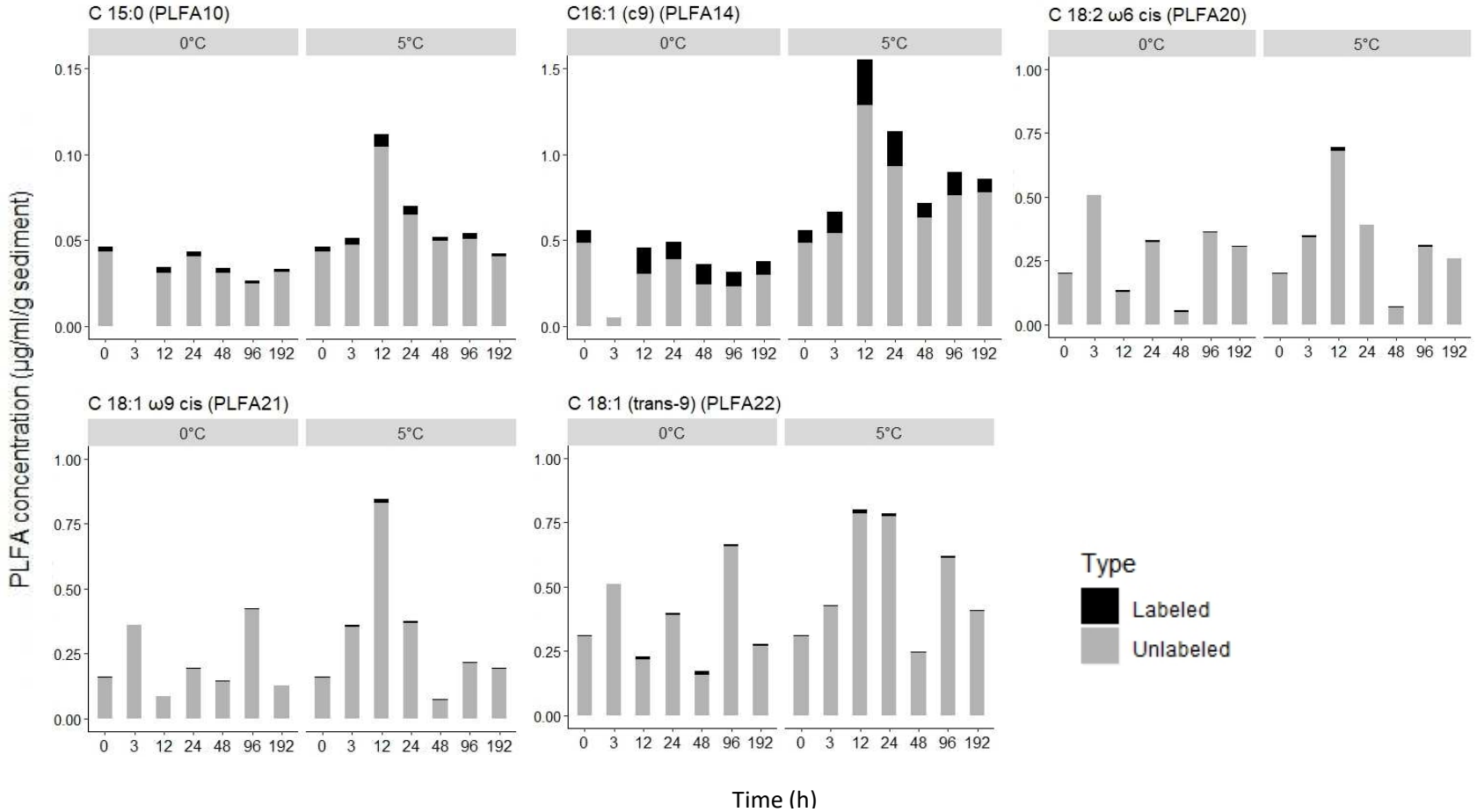


Fig. 8. Isotopically labeled (^{13}C, black) and unlabeled (gray) portion of phospholipid fatty acid (PLFA) concentrations in marine sediments over time (h) at two temperature treatments (0°C and 5°C, n=1 per treatment) for selected PLFA.

Table 1. List of environmental variables at all sample stations on the Chukchi Sea shelf during AMBON 2015 cruise including bottom depth (m), bottom water temperature (°C), bottom water salinity, bottom water oxygen (µmols kg^{-1}) sediment grain size (% phi), surface sediment chlorophyll-a content (mg/m^2), surface sediment $\delta^{13}C$ (‰), $\delta^{15}N$ (‰), total organic carbon (%), and carbon to nitrogen (mass of C:mass of N) ratio. Data obtained from https://doi.org/10.25921/zqwr-at45.

Station	Depth (m)	Temp	Sal	O_2 (µmols kg^{-1})	>5 phi (%)	Sed Chl a (mg/m2)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	TOC (%)	C/N
CL1	41	7.47	31.70	276.663	75.93	7.13	-23.5	6.6	1.09	8.74
CL3	42	4.73	32.14	255.831	97.19	12.21	-22.2	7.6	1.24	6.94
DBO3-6	54	4.18	32.60	236.325	70.11	17.38	-21.5	7.2	1.04	6.41
DBO3-8	44	3.82	32.75	255.018	74.65	16.42	-21.2	7.8	1.08	6.23
ML1-5	37	5.59	31.70	279.308	36.84	7.6	-24.4	7.7	0.46	4.01
ML1-11	38	0.10	32.40	330.706	80.28	5.48	-22.5	9.5	1.02	6.48
ML1-13	42	-0.14	32.38	265.578	92.85	7.58	-22.6	9.8	1.12	6.01
ML3-6	42	-1.19	32.27	335.298	63.43	14.45	-22.9	7	1	7.57
ML3-10	36	0.71	32.21	320.443	50.14	12.53	-22	7.4	0.65	7.05
ML3-14	40	1.63	32.23	318.266	93.09	13.73	-22.1	7.6	0.98	7.18
ML4-9	36	-1.44	32.14	312.192	67.34	11.1	-22.2	7.4	0.87	6.72
ML4-14	44	-1.15	32.48	269.068	94.58	16.59	-21.9	8.1	1.35	6.75
ML6-1	30	5.88	31.03	234.804	17.55	6.14	-23.2	4.8	0.25	6.52
ML6-11	46	-1.66	32.47	229.964	73.95	9.97	-22.7	7.6	0.95	7.16

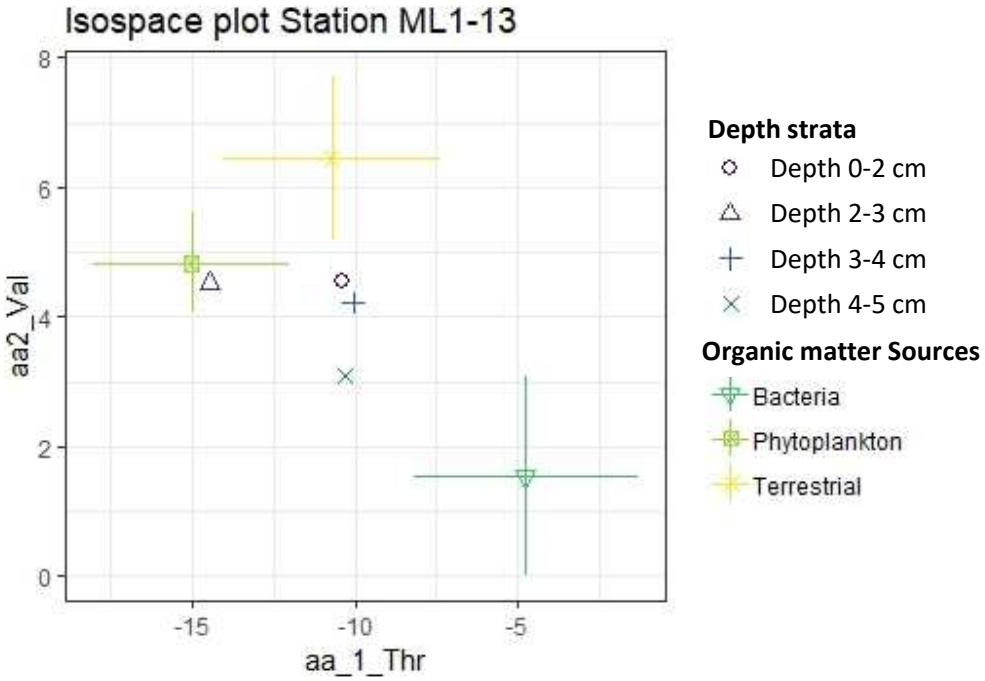
Table 2. List of phospholipid fatty acid (PLFAs) detected in microcosm marine sediment samples, respective PLFA numbers assigned in this study, and their source affiliations. Fatty acid nomenclature, e.g. 18:2n6, refers to the number of carbon atoms (18), number of double bonds (2), and position of first double bond.

PLFA #	PLFA name	Nomenclature	Source	Literature
7	Methyl-myristate	C 14:0	Eukaryotes & Prokaryotes	Crossman et al., 2006; Ding et al., 2009
8	Methyl-13-methyltetradecanoate	iso- C 15:0	Gram-positive bacteria	Crossman et al., 2006; Moore-Kucera 2008
9	Methyl-12-methyltetradecanoate	anteiso- C15:0	Gram-positive bacteria	Crossman et al., 2006; Moore-Kucera 2008
10	Methyl-pentadecanoate	C 15:0	Gram-positive & Gram-negative bacteria	Bååth&Anderson 2003
14	Methyl-cis-9-hexadecanoate	C16:1 (cis-9)	Gram-positive & Gram-negative bacteria	Crossman et al., 2006; Zelles 1999
15	Methyl-palmitate	C 16:0	Eukaryotes & Prokaryotes	Crossman et al., 2006; Zelles 1999
16	Methyl-15-methylhexadecanoate	iso C 17:0	Gram - positive bacteria	Crossman et al., 2006; Moore-Kucera 2008
17	Methyl-cis-9,10-methylenehexadecanoate	C 17:0 cyclo	Gram - negative bacteria	Crossman et al., 2006; Grayston 2004
18	Methyl-heptadecanoate	C 17:0	Bacteria	Grayston 2004; Bååth&Anderson 2003
19	Methyl-2-hydroxyhexadecanoate	2-OH C 16:0	Unknown	
20	Methyl-linoleate	C 18:2ω6 cis	Fungi	Grayston 2004; Zelles 1999
21	Methyl-oleate	C 18:1ω9 cis	Gram - negative bacteria	Crossman et al., 2006; Grayston 2004
22	Methyl-trans-9-octadecanoate	C 18:1 (trans-9	Gram - negative bacteria	Crossman et al., 2006; Grayston 2004
23	Methyl-stearate	C 18:0	Eukaryotes & Prokaryotes	Crossman et al., 2006; Bååth&Anderson 2003
25	nonadecanoate	C 19:0	Standard	
26	Methyl-eicosenoate	C 20:0	Eukaryotes & Prokaryotes	Crossman et al., 2006; Zelles 1999

Table 3. List of overall average (± 1SD) individual phospholipid fatty acid (PLFA) $\delta^{13}C$ values in marine sediments. Gray areas indicate PLFAs where incorporation of labeled material into newly formed PLFAs was detected (see Fig. 7).

PLFA #	Nomenclature	0°C labeled	0°C unlabeled	5°C labeled	5°C unlabeled
8	iso C15:0	-18.0 ± 6.7	-23.5 ± 2.5	-20.8 ± 7.4	-23.5 ± 0.7
9	anteiso C15:0	-11.8 ± 11.5	-23.7 ± 0.7	-14.0 ± 8.8	-25.7 ± 2.4
10	C15:0	149.2 ± 49.8	-20.3 ± 3.6	116.6 ± 34.3	-19.3 ± 3.1
14	C16:1 (cis-9)	466.8 ± 267.0	-22.0 ± 1.4	320.8 ± 77.7	-23.4 ± 1.8
16	iso C17:0	-27.4 ± 2.8	-25.1 ± 1.4	-24.7 ± 1.3	-25.9 ± 0.8
17	C17:0 cyclo	-30.1 ± 4.9	-28.3 ± 2.2	-26.0 ± 3.2	-27.4 ± 1.9
18	C17:0	-23.6 ± 7.7	-26.7 ± 0.6	-25.6 ± 1.3	-26.9 ± 0.9
19	2-OH C16:0	-25.0 ± 4.7	-26.3 ± 1.2	-27.8 ± 3.7	-27.8 ± 2.0
20	C18:2ω6 cis	45.6 ± 93.2	-26.4 ± 1.2	2.2 ± 18.9	-26.9 ± 0.9
21	C18:1ω9 cis	24.1 ± 36.7	-26.1 ± 0.8	30.7 ± 21.4	-26.4 ± 1.2
22	C18:1 (trans-9)	40.9 ± 64.2	-25.0 ± 0.8	11.9 ± 8.7	-25.5 ± 0.6

8 Appendix



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10 Appendix A. Stable isotope mixing model plot (displayed in two dimensions) based on the $\delta^{13}C$ values
11 of five essential amino acids (EAA; $\delta^{13}C_{EAA}$) of three organic matter sources bacteria,
12 phytoplankton and terrestrial plants (mean ± standard deviation). Shapes were used to
13 represent the four depth strata of sediment samples at station ML1-13 (see Figure 1).

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