MICROBIAL DYNAMICS IN THE AMUNDSEN SEA POLYNYA, ANTARCTICA: HETEROTROPHIC BACTERIAL RESPONSES TO INTENSE SEASONAL BLOOMS OF THE MARINE HAPTOPHYTE *PHAEOCYSTIS ANTARCTICA*

by

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(Under the Direction of Patricia L. Yager)

ABSTRACT

Bacteria play a significant role in elemental cycling in the ocean. The Amundsen Sea Polynya International Research Expedition (ASPIRE) sought to better understand how heterotrophic bacteria respond to intense austral summer blooms, dominated by the haptophyte *Phaeocystis antarctica*. Bacterial production (BP) rates were measured using ^{3}H-leucine incorporation and bacterial respiration (BR) was estimated with carbon dioxide changes in dark-bottle 48-hr incubations. When combined, BP and BR yield average bacterial growth efficiencies (9.6% ± 0.6 with a range from 5 to > 20%, depending on assumptions and conversion factors). One explanation for low BGE is low macro- and micro-zooplankton abundances in the upper 100 m compared to oligotrophic systems, resulting in reduced DOM flux to the bacteria from minimal grazing of organic rich *P. antarctica*. Bacterial production correlates with particulate organic matter concentration (R^2=0.76), and size fractionation experiments show 70% of BP is particle-associated. Exoenzyme hydrolysis also correlates with high POM concentrations, suggesting strong particle-association of bacterial activity in the Amundsen Sea Polynya.

INDEX WORDS: Heterotrophic, Bacteria, Productivity, Antarctica, Amundsen Sea, Polynya, Organic Matter

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TABLE OF CONTENTS

LIST OF TABLES

Page

LIST OF FIGURES

Page

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Purpose of the Study

This research examines pelagic microbial dynamics in the highly productive Amundsen Sea Polynya (ASP). It combines measurements of both organic and inorganic matter with analyses of microbial activity and abundance. Measuring these different parameters provides insight into factors that control microbial loop dynamics in high-latitude marine systems. While similar measurements have been made in the neighboring Ross Sea Polynya (RSP) (Carlson et al. 1999; Ducklow et al. 1999; Kirchman et al. 2009), very few studies have been conducted in the ASP (Yager et al. 2012). This study investigates controls on rates of bacterial and primary production, proposes to organize research stations along a logical 'bloom progression' dominated by *P. antarctica*, and applies these insights to infer the ultimate fate of this productive bloom.

Thesis Structure

This thesis is formatted as an introductory Chapter (1), a manuscript thesis chapter (2), and a conclusion chapter (3). Chapter 2 will be submitted to the open source journal *Elementa* as part of a special feature on the ASPIRE project.

Background Information

Inorganic Nutrients

In marine systems inorganic nutrients provide compounds necessary for primary production, and, in combination with light availability, have been shown to limit phytoplankton activity (Laws and Bannister 1980; Zehr and Kudela 2011; Moore et al. 2013). The major inorganic nutrients in marine systems are nitrate (NO_3), nitrite (NO_2), ammonium (NH_4), phosphate (PO_4), and silicate (SiO_4) (Raimbault et al. 2008). Dissolved inorganic carbon (DIC) is also important for phytoplankton photosynthesis, and is directly related to CO_2 exchange with the atmosphere and the marine carbon cycle (Luecker et al. 2000). The demand for major nutrients is constrained by the "Redfield ratio" of 106C:16N:1P, which represents the average molar composition ratio for typical marine phytoplankton (Redfield et al. 1963; Hecky et al. 1993). Minor elements and trace metals such as iron (Fe) are also needed by phytoplankton and can be limiting in some marine systems (Cullen 1991).

Upwelling and wind-driven mixing contribute significantly to nutrient input to the surface ocean. This is especially true for the Southern Ocean, where riverine input is minimal (Holm-Hansen 1985). In the relatively low-productivity Southern Ocean, polynyas represent localized hot spots of nutrient-rich water and light that fuel intense phytoplankton blooms (Sweeny et al. 2000; Smith and Gordon 2012).

Chlorophyll a and Primary Production

Marine phytoplankton account for almost half of global primary production: 35-65 Gt C yr^{-1} (Ducklow 1995; Field et al. 1998; Boyce et al. 2010). Primary production in the ocean is often limited by one or both of two main factors: light and nutrients (Cloern

1999). Oligotrophic systems show generally lower productivity (~ 0.3 g C m^{-2} d^{-1}), primarily due to nutrient limitation (Marañón et al. 2003). Primary productivity in coastal upwelling zones can far exceed oceanic averages, with rates up to 6 g C m^{-2} d^{-1} (Cai 2011). Primary productivity in the coastal Southern Ocean (Ross Sea Polynya) shows similarly high rates, with a springtime average of 3.5 g C m^{-2} d^{-1} and a maximum rate of 6 g C m^{-2} d^{-1} (Smith and Gordon 2012).

Dissolved Organic Matter

In both Antarctic coastal zones and oligotrophic waters, heterotrophic bacteria rely on phytoplankton production of organic matter, as there is negligible terrestrial input (Ducklow et al. 2007). Since bacteria have not been shown to lyse algal cells, heterotrophic communities rely on phytoplankton extracellular release (PER) of DOM (Billen and Becquevort 1990). PER in blooming phytoplankton averages 2-10% of total DOM and can range up to 60% (Myklestad 2000). Nutrient limitation and other environmental factors, such as temperature stress, exacerbate PER (Myklestad 2000). DOM is also released as a result of cellular breakage or lysis: viral lytic cycling and grazing by microzooplankton present two likely pathways for DOM release to heterotrophic bacteria in marine systems (Glibert and Bronk 1994). In addition to releasing dissolved organic carbon (DOC) and nitrogen (DON), some phytoplankton, e.g., *Phaeocystis spp.,* release other energetically favorable compounds such as dimethylsulfoniopropionate (DMSP) (Yoch 2002).

DMSP is produced by phytoplankton primarily for use as a grazing deterrent, for osmotic balance, and as an antioxidant (Howard et al. 2006). This DMSP is released by phytoplankton cells via one of the pathways of DOM exudate mentioned above, and can

be degraded by heterotrophic bacteria to form dimethylsulfide (DMS) (González et al. 2003). This DMSP degradation can support up to 10% of bacterial carbon demand (BCD) (Kiene et al. 2000; Mou et al. 2008). The most common phytoplankton species in Antarctic coastal waters, *P. antarctica*, produces large quantities of DMSP (Liss et al. 1994; DiTullio and Smith 1996; Alderkamp et al. 2012). DMSP flux could account for a significant portion of microbial DOM cycling within coastal Antarctic waters, especially during intense austral summer phytoplankton blooms (Vance et al. 2013).

Particulate Organic Matter

Particulate organic matter (POM) produced in the photic zone can sink and provide a potentially significant source of organic matter and energy to the deep pelagic or benthic ecosystems (Veit-Köhler et al. 2011; Henley et al. 2012). It is also a way to remove carbon from the surface ocean and atmosphere via the "biological pump" (Falkowski 1997; Falkowski et al. 2000). POM can form aggregates (≥ 0.5 μm) that then sink out of the surface ocean. These particle aggregations are commonly comprised of dead or dying cellular matter from algal or bacterial cells, larger size fractionations include fecal pellets from higher trophic levels, and marine snow (Volkman and Tanoue 2002). As these organic particles sink, bacterial colonies attach to the particles; up to 20% of the bacterial community is attached to phytoplankton or particulate matter (Teeling et al. 2012). Heterotrophic bacteria achieve this particle-associated lifestyle by producing extracellular enzymes that can break down organic matter that would otherwise be too large for uptake (Billen, 1984; Thurman 1985; Huston and Deming 2002). The majority of these enzymes hydrolyze complex molecules such as proteins to more labile DOM such as amino acids, which can then be used by bacteria for energy

or biomass production (Smith et al. 1992; Martinez et al. 1996). Hydrolytic enzyme activities, and enzyme speciation, are directly related to the bacterial species composition for a given particle (Long and Azam 2001; Ortega-Retuerta et al. 2013).

Organic matter concentration, composition (dissolved vs particulate), and fate are highly dependent on the productivity of the ecosystem and the stage of the algal bloom (Riemann et al. 2000). Coastal zones represent ~7% of total ocean surface area, yet account for 80% of organic matter burial and 90% of sedimentary mineralization (Teeling et al. 2012). For coastal Antarctic polynyas, particle flux is highest during peak bloom periods (late December – January) and corresponds with high surface primary productivity and biomass (Asper and Smith 2012).

Bacteria

Prokaryotic microbial heterotrophs play a significant role in biogeochemical cycling in the global ocean (Herndl et al. 2005). Prokaryotes are ubiquitous throughout the ocean, with global averages of approximately $1x10^6$ cells ml^{-1} (Church et al. 2003). 16S rRNA studies have shown that a group of alpha-proteobacteria (SAR11) is often, although not always, the most ubiquitous and abundant group, accounting for up to 50% of the total surface community (Morris et al. 2002; Fuhrman et al. 2006). Most operational taxonomic units (OTUs) in polar oceans belong to Gammaproteobacteria, Alphaproteobacteria, and Flavobacteria, with summertime coastal communities dominated by the OMG-Ant4D3-Cluster1, Gammaproteobacterium HTCC2207-Cluster 1, and Sulfitobacter, with fewer Polaribacter- and Loktanella-affiliated OTUs (Ghiglione et al. 2012). In high-latitude environments, psychrophiles are often most abundant due to cold adapted enzyme activity (Bowman et al. 1997; Feller and Gerday 2003). For the

ASP surface waters specifically, the most abundant clades are *Polaribacter* (20-64%) and uncultivated *Oceanospirillaceae* (7-34%); *Pelagibacter* were also observed (7-42%) (Ghiglione et al. 2012; Kim et al. 2013; Richert et al (personal communication). Uncharacterized Roseobacter NAC11-3 are present but not highly abundant in coastal Antarctic summer waters (Ghiglione et al. 2012).

Heterotrophic Productivity

Heterotrophic bacteria play a vital role in aquatic ecosystem cycling. Bacteria consume organic matter (often produced by primary producers), and convert a portion of the uptake to increasing biomass (Cole et al. 1988; Bjørnsen and Kuparinen 1991). Bacterial production (BP) is usually directly linked to organic matter availability. Inorganic nutrients and other trace metals, however, can also become limiting to overall bacterial productivity (Ducklow 2008). BP is commonly measured using a radio-labeled tracer, most commonly [^{3}H]-labeled thymidine (Fuhrman and Azam 1980) or leucine (Kirchman et al. 1985). In this study, all BP measurements were made according to established ^{3}H-leucine protocols.

^{3}H-leucine incorporation works under the assumption that leucine is a critical building block in the formation of bacterial proteins, and ultimately, bacterial biomass (Simon and Azam 1989). This approach also assumes that bacteria contribute the only significant uptake of ^{3}H-leucine in a given sample, and that the added tracer concentration was great enough that there is negligible uptake of non-labeled leucine (Kirchman et al. 1985). To convert from ^{3}H-leucine incorporation to a production rate (g C m^{-2} d^{-1}), standard conversion factors are used (Simon and Azam, 1989). These

conversion factors can vary across different environments and conditions, so some uncertainty is involved if they are not measured directly in each experiment.

In oligotrophic systems, BP is limited by seasonal fluxes of DOM (Malmstrom et al. 2005), and there is often high interannual variability; average BP in these systems is ≤ 2 μg C L^{-1} d^{-1} (Steinberg et al. 2001). In coastal upwelling zones, and in Antarctic polynyas such as the RSP, BP rates average 1.48 μg C L^{-1} d^{-1} during spring, and can exceed 3.0 μg C L^{-1} d^{-1} during peak summer blooms (Carlson et al. 1999).

Bacterial Respiration: Connections to BCD and Growth Efficiency

Remineralization of organic matter through bacterial respiration represents a significant portion of total respiration in marine systems (del Giorgio and Duarte 2002). In oligotrophic environments, estimates of bacterial respiration rates can exceed those of primary productivity, potentially providing a CO_2 source to the atmosphere (del Giorgio et al. 1997; Rivkin and Legendre 2001). While it can be methodologically difficult to separate bacterial respiration from other microbial community respiration, it is still important in discussions of heterotrophy to distinguish them as total community respiration (TCR) and bacterial respiration (BR).

By measuring BP, and BR, an estimate on bacterial growth efficiency (BGE) can be made, allowing for cross-system comparisons. BGE is calculated using the following equation:

$$BGE = ((BP) / (BCD)) * 100$$

BGE has a wide range in marine systems, from < 5% up to 60% in some regions (del Giorgio and Cole 1998). Several factors have been suggested to limit BGE, including the chemical characteristics of available organic matter, temperature, and

availability of trace nutrients and metals (del Giorgio and Davis, 2003; Valliéres et al. 2008). While temperature was previously held to be the primary factor controlling bacterial productivity and BGE in cold oceans, Pomeroy and Wiebe (2001) show that psychrotolerant and psychrophilic bacteria are limited by affinity for a given substrate, not solely water temperature (Weibe et al. 1992, 1993). High rates of BP observed in Antarctic waters with perennially cold temperatures (-1.8 ºC) confirm that while temperature is important, it is not the sole limiting factor of bacterial productivity (Leakey et al. 1996, Ducklow et al. 2000).

Heterotrophic Grazers: Zooplankton and Microzooplankton

Microzooplankton are heterotrophic (phagotrophic) organisms in the 20-200 µm size class that represent a significant source of predation to both prokaryotic and eukaryotic microbes in marine systems (Sherr and Sherr 2007). Microzooplankton are a trophic link between microbial producers and mesozooplankton and fish (Thompson et al. 1999; Landry and Calbet 2004). Microzooplankton also graze on detrital POM. The production of fecal pellets by micro and mesozooplankton represents a separate component of POM flux from the surface ocean to the benthos (Landry and Hassett 1982; Turner 2002). Intense microzooplankton grazing can consume ~ 52% of primary production per day in some environments, and grazing of bacterioplankton by larval zooplankton (nauplii), particularly copepods, cannot be discounted as a top-down control on bacterial productivity (Landry and Hassett 1982; Turner 2004).

Viruses in Marine Systems

On average, viral abundances are an order of magnitude higher than bacterial abundances in global marine systems and they are ubiquitous throughout most water

columns ($1x10^7$ – $1x10^8$ ml^{-1}) (Suttle and Chen 1992; Swanson et al. 2012). Viral infections play a key role in organic matter cycling, with up to 20% of the microbial community lysed each day by phage particles (Suttle 2007). It is important to note that not all viruses are bacteriophages: some viruses will infect archaeal and eukaryotic organisms (Rohwer and Thurber 2009; Philosof et al. 2011; Monier et al. 2011). By lysing nutrient rich eukaryotic cells, viruses faciltate a significant supply of dissolved organic matter for other microorganisms; this process is referred to as the 'viral shunt' of the traditional microbial loop (Wilhelm and Suttle 1999; Middelboe et al. 2003; Sheik et al. 2013). *Phaeocystis spp.*, demonstrated to form robust blooms during austral spring and summer in coastal Anarctic polynyas, can be susceptible to viruses; the viral lytic cycle could present a high supply of organic matter to microbial heterotrophs in these productive regions (Sheik et al. 2013).

Summary

Since its initial conceptualization (Pomeroy 1974), the marine microbial loop and its importance to global carbon and nutrient cycling have been well studied and significantly extended to include the complex suite of components and activities described above (Azam 1998; Pomeroy et al. 2007; Fenchel 2008). Its role in the high-latitude ocean is thought to be key to understanding the high carbon fluxes there (Azam et al. 1991). Here, we report a brief but thorough examination of these processes in a remote coastal Antarctic ecosystem significant to global cycles and sensitive to climate change.

Chapter 2

PELAGIC MICROBIAL HETEROTROPHY IN RESPONSE TO A HIGHLY PRODUCTIVE BLOOM OF THE MARINE HAPTOPHYTE *PHAEOCYSTIS ANTARCTICA* IN THE AMUNDSEN SEA POLYNYA [1]

[1] Williams, C.M., A. Dupont, A. Post, L. Riemann, and P.L. Yager. To be submitted to *Elementa.*

Abstract

Heterotrophic bacteria play a key role in marine carbon cycling and understanding their activities in polar systems is important for considering climate change impacts there. One of the goals of the Amundsen Sea Polynya International Research Expedition (ASPIRE) was to examine the relationship between extensive *Phaeocystis antarctica* blooms and pelagic bacterial heterotrophy in the polynya. Microbial parameters such as bacterial production (BP; by ^{3}H-leucine incorporation), respiration, and gross growth efficiency were measured in the open waters (7 ± 3 weeks after the retreat of sea ice) along with inventories of inorganic and organic carbon, nitrogen, phosphorous, and chlorophyll *a,* as well as rates of primary productivity (PP) and exoenzyme hydrolysis. The opening of the polynya during the early austral summer stimulated large blooms of *P. antarctica,* and chlorophyll *a* concentrations in the surface polynya exceeded 20 mg m^{-3}. Bacterial production (from 0.25 to > 9 μg C L^{-1} d^{-1}) and respiration (from 3 to 95 μg C L^{-1} d^{-1}) had a wide potential range based on assumptions and conversion factors. Despite this range of rates, a general trend was observed of higher productivity in open-water areas particularly in the central polynya where chlorophyll *a* concentrations and primary productivity were greatest. Bacterial growth efficiency in the upper 10 m was low compared to oligotrophic systems, averaging 9.6 ± 0.06 % (with a range of 5 to > 20%). Average ratios of BCD:PP were 0.76 ± 0.1 (with a range of 0.41 – 1.4), this ratio appears to be inconsistent with the obvious dominance of autotrophy in surface as indicated by undersaturated pCO_2 and high net community production measurements. Despite this dominance, rates of microbial heterotrophy were high compared to the neighboring Ross Sea Polynya, and were also found to be

cold adapted and particle associated. With rapid losses in seasonal sea ice and nearby glacial ice, the Amundsen Sea Polynya (ASP) is a climate-sensitive ecosystem with an active microbial community.

Introduction

As air and ocean temperatures rise due to global climate change, polar systems are particularly vulnerable (Schofield et al. 2010) and changing rapidly (Stammerjohn et al. 2008). In the Southern Ocean, phytoplankton production is the primary source of organic matter to the marine system and heterotrophy is directly tied to the annual bloom of primary producers. Coastal polynyas are hot spots for both primary productivity and air-sea exchange. Productivity in Antarctic coastal waters typically exceeds 78 g C m^{-2} yr^{-1} (Arrigo et al. 2012) while productivity in the open Southern Ocean (south of 50 ºS) averages 57 g C m^{-2} yr^{-1} (Arrigo et al. 2008). In coastal areas, the seasonal sea ice reduction from climate change is expected to enhance light penetration, but also deepen the upper mixed layer (UML) due to increased surface wind stress (Ducklow et al. 2013). This deeper UML can result in decreased phytoplankton abundance and productivity (Montes-Hugo et al. 2009). Thus, the carbon cycle of these ecosystems is sensitive to climate change.

Primary productivity in Antarctic polynyas is dominated by diatoms along the marginal ice zone, and by the haptophytic alga *Phaeocystis antarctica* in the open polynya (Arrigo et al. 1999; Alderkamp et al. 2012). Although *P. antarctica* does have a unicellular life stage, it is most commonly found in dense colonial assemblages in the photic zone of Antarctic waters (Kennedy et al. 2012). Key questions relevant to the carbon cycle impact of these polynyas is whether potentially high rates of PP are

matched by comparably high rates of heterotrophic activity, and what impact the microbial heterotrophs have on the export flux. In the Ross Sea polynya (RSP), a high particulate concentration has been shown to yield large vertical fluxes (Smith et al., 2011).

The Amundsen Sea hosts the most productive polynya (per unit area) in the Southern Ocean (Arrigo, et al., 2012), yet it is one of the most remote and least studied. The ASP covers approximately 38,000 km^2 (on average; up to 80,000 km^2 at its maximum extent mid-January) and is only accessible by icebreaker for a few months during the austral summer (Arrigo and van Dijken, 2003). While iron (Fe) concentrations have been shown to limit phytoplankton growth throughout the Southern Ocean (Martin et al. 1990; Smith et al. 2013), the ASP receives significant Fe from ice-sheet-ocean interactions (Yager et al. 2012; Sherrell, personal communication).

As part of the ASPIRE project (Dec 2010-Jan 2011), our goal was to determine the influence of pelagic heterotrophic microorganisms on net community production (NCP), how bacterial communities are responding to dense, seasonal blooms, and the ultimate fate of this productivity within the polynya. While there is some evidence of rate limitation due to temperature (Pomeroy and Wiebe 2001), psychrophilic bacteria are primarily limited by DOM flux in Antarctic waters (Williams et al. 2012). Unlike in the Arctic, which receives large dissolved organic matter (DOM) supply from rivers (Feng et al. 2013), Antarctic DOM supply is linked primarily to primary productivity, with secondary sources from ice sheet degradation and deep-water current dynamics (Dubnick et al. 2010). DOM flux is also influenced by macro- and micro-zooplankton

(Steinberg et al. 2004), which can be spotty and low in these regions (Dolan et al. 2013).

Here we report bacterial production (BP), respiration (BR), and bacterial carbon demand (BCD) in the context of an early season algal bloom in the ASP, and comment on the impact of these activities on the fate of the bloom.

Methods

The ASPIRE expedition took place aboard the RVIB *Nathaniel B. Palmer* from December 2010 to January 2011. A powerful icebreaker was required to reach the Amundsen Sea Polynya, as heavy sea ice surrounds the coastal polynyas near the ice shelf (Yager et. al., 2012). Over the course of the expedition, 68 stations were sampled across an average open water area (<50% ice cover as observed from daily unprojected AMSR-E 12.5 km images) of 48 ±10 x 10^4 km^2, while the *Palmer*'s underway system continuously measured surface water properties: temperature, salinity, phytoplankton fluorescence, and oxygen and carbon dioxide concentrations (Yager et. al., 2012).

Discrete water samples for all microbial biomass and activity experiments were collected from individual stations and depths (Figure 1) using a conventional shipboard conductivity-temperature-depth (CTD) sensor with a 24 x 10 L Niskin bottle rosette. Samples were focused in the upper 400 m of the water column, with < 25% collected below 400 m. Shelf water depths in this area range from 300 to 1000 m (Nitsche et al. 2007).

Water samples were collected and processed according to standard protocols (Knap et al. 1996) for dissolved inorganic nutrients, as well as particulate and dissolved

organic carbon and nitrogen. Briefly, inorganic nutrients, including nitrate, nitrite, ammonium, phosphate, and silicate were measured using a Lachat Nutrient Auto-Analyzer (Zellweger Analytics, QuickChem 8000 Series). Samples were pre-filtered (GF/F), kept refrigerated, and run onboard ship within 1 day of sampling.

Particulate organic matter (POM) was collected by cleanly filtering ~1-2 L of seawater from the Niskin onto a combusted GF/F (nominal pore size of 0.7 um). Samples were processed at Rutgers using CHN analyzer (Hedges and Stern 1984).

Samples for dissolved organic matter (DOM) were collected cleanly from the filtrate of the POM samples and stored frozen until processed at Georgia Tech by Shimadzu TOC analyzer with NOx box (Yager et al. 2001).

Biological inventories and rates

Discrete pelagic samples were collected with the CTD and analyzed shipboard for Chl*a* using acetone extraction and a spectrofluorometer (Yager et. al., 2012). Shipboard values were crosschecked against similarly collected samples analyzed with HPLC (e.g., Wright et al. 1991).

Bacterial abundance samples were collected in triplicate from the Niskin bottles or from the underway system, preserved using 1% paraformaldehyde, and deep frozen (-80 ºC) until processed in Georgia. Flow cytometry was used to count bacterial cells, with SYBR Green nucleic acid stain (Marie et al. 1997). Flow cytometer abundance was calibrated with polystryene beads and values were crosschecked using DAPI and epifluorescence microscopy (Porter and Feig, 1980).

Bacterial production was measured using ^{3}H-Leucine incorporation into protein as a proxy for production (Kirchman, et al., 1985). Initial experiments identified 20 nM

additions adequate for saturation. Samples were incubated with 20 nM ^{3}H-leucine for 4 hours at in situ temperature and then compared to killed controls. Following protein extraction in microcentrifuge tubes (Smith and Azam, 1992), Ultima Gold scintillation cocktail was added and allowed to stand overnight. Incorporated radiation was determined using a Beckman LS 6500 liquid scintillation counter for 5 minutes per sample. Reported dpm values were then converted using specific activity to pmol leucine incorporated (pmol leu L^{-1} hr^{-1}), then to bacterial production (μg C L^{-1} d^{-1}) using standard conversion factors (Ducklow et al. 1992; Ducklow et al. 2002).

Total community respiration was measured by examining changes over time in dissolved inorganic carbon (DIC) in the dark and at in situ temperature (Fransson et al. 2011). Briefly, whole seawater was collected into a sterile 2-L bottle and then dispensed aseptically without bubbling into six identical, sterile, 200-ml pyrex bottles with ground glass stoppers, sealed, and incubated at −1°C in the dark. Pairs were fixed by adding 200 μl saturated mercuric chloride solution at 0h, ~24h and ~48 h, sealed with Apiezon L grease and thick silicone rubber bands, and then stored dark at 2°C until processed in Georgia. Total DIC was measured using a SOMMA and coulometer (Johnson et al. 1993; Cooley and Yager 2006) with accuracy established with Certified Reference Material and a precision of <1 μmol C kg^{-1} based on duplicate sample runs (Dickson et al. 2007). Respiration rates were calculated by linear regression using all six points, except when the best linear fit and smallest error was accomplished using the first four points.

To determine the extent of particle association, a size-fractionated experiment was conducted at Site 50. Water was gravity-filtered through a 3-μm filter to calculate

the contribution to production by free-living bacteria. This value was then compared with the whole water sample and the difference is presumed to account for the production due to particle associated bacteria.

A temperature sensitivity experiment was also run for bacterial production at Station 35. Here, triplicate samples were incubated at -1.5, 5, 10, and 20°C and compared to killed controls.

Extracellular enzyme activity was measured at several stations and depths according to Huston and Deming (2002) to assess the potential for bacterial hydrolysis of particulate organic matter. Four enzyme activities were measured: methylumbellipherone glucosidase (MUF-G), methylumbellipherone beta-glucosidase (MUF-B), methylumbellipherone protease (MUF-P), and methyl-coumarinyl-amide-leucine (MCA-L). A size fractionation experiment was conducted at Station 57, and examined four main size groups: < 20 μm, < 3 μm, < 1 μm, and < 0.2 μm. For each size fractionation, water samples were filtered according to the size classes above.

Data analysis

Net community production (NCP, mmol N m^{-2}) was calculated by estimating a missing nitrogen concentration from an initial wintertime concentration. Wintertime baselines were estimated by examining DIN concentrations at ~100 m, the base of the mixed layer where Winter Water was usually found (Tynan 1998; Prézelin et al. 2000). Observed DIN concentrations were subtracted from the wintertime DIN to calculate 'missing' nitrogen. Missing nitrogen (mmol N m^{-3}) was depth integrated over the upper 100 m, and the summation of integrated values was considered NCP.

Bacterial growth efficiency (BGE) values were calculated for the surface (upper 10 m) waters in the polynya (BGE = BP / (BP+BR); del Giorgio and Cole, 1998).

Respiration samples were not pre-filtered, and due to difficulty in distinguishing bacterial respiration from total community respiration, for the purpose of this paper BR was considered to equal half of total respiration, according to Ducklow et al. (2000).

Bacterial carbon demand (BCD) was calculated by converting both BP and BR to μg C L^{-1} d^{-1}, and represented as BCD = BP + BR (Ducklow et al. 2002; Alonso-Sáez et al. 2007).

Statistical Analysis

All R^2 values were calculated using linear best-fit regression using reduced major axis (RMA) statistical modeling in both MATLAB and Microsoft Excel. All color profiles were produced using MATLAB statistical analysis software (2012b), and the *contour(f)* function. Interpolation between data points was allowed for casts that did not follow the exact sampling depth profile of the previous, or proceeding station. Unless otherwise mentioned, all data analyzed is for the upper 100 m water column in the ASP. Sample analysis for this manuscript was limited to the upper 100 m due to a significant decline in primary and secondary productivity below 100 m. All standard deviations and standard error of the mean reported were calculated using Microsoft Excel analysis tools (Microsoft Excel for Macintosh 2011, ver. 14.3.9). Standard error (reported below as ± 1 SE) was calculated as $SE = \sigma / \sqrt{n}$, where σ is equal to the standard deviation, and n is the number of samples collected.

Results

Site Description

Over the entire austral spring-summer season of ASPIRE, October 1, 2010 and March 31, 2011, the mean daily open water area of the ASP was 27,707 ± 22,072 km^2. When ASPIRE entered the area on December 14, the open water area was 41,388 km^2, when we departed the area on January 3, it was 63,277 km^2. The open water area peaked at 76,081 km^2 on January 12. Seawater temperature and salinity varied with depth and were strongly associated with specific water masses (modified Circumpolar Deep Water, Winter Water, and Antarctic Surface Water; Yager et al. 2012). Surface waters exhibited temperatures ranging from -1.8 to -0.2 °C. With the influence of Circumpolar Deep Water, sub-surface water samples had higher temperatures (~2°C). The melting of seasonal sea ice, as well as that from icebergs and surrounding ice sheets, caused a freshening of surface waters within the ASP, which then likely led to stratification and warming by the sun. In such areas, mixed layer depths ranged from 10 to 30 m. Strong winds generated deeper upper mixed layers (75-100 m) in regions less recently influenced by ice melt.

With the complex dynamics of changing sea ice cover, light regime, and wind, stations across the polynya region appeared heterogeneous, not following linear spatial gradients, and instead exhibited a spatial mosaic of productivity. Thus, for the purposes of this analysis, stations were arranged as a proposed bloom sequence, in order of increasing nitrogen drawdown (net community production; NCP) over the upper 100 m. A total of 13 stations from ASPIRE were "long" stations, with a full suite of microbial rates, abundances, and chemical inventories. A bloom progression of these13 stations

was established; stations were arranged based on increasing depth integrated NCP (mmol N m^{-2}). By establishing this progression, spatio-temporal trends of chemical inventories, and activity rates can be better visualized within the ASP.

Nutrients

Dissolved inorganic nitrogen (DIN = NO_3 + NO_2 +NH_4) ranged from 7.3 to 31.9 µmol N L^{-1}, with the highest values found near the surface at Station 5 and a deepwater (80 – 100 m) peak at Stations 29 and 57. The greatest drawdown was observed in the upper 30 m during the peak bloom, with observed concentrations of < 10 µmol N L^{-1} (Figure 2). Calculated NCP values ranged from 58.9 to 736 mmol N m^{-2}. NCP for all thirteen stations averaged 500 ± 57 mmol N m^{-2}. There was a general trend in NCP that indicated higher depth-integrated values at central, open-water stations (Stations 25, 29, 35, 50, 57) compared to ice-edge or marginal ice zone stations (5, 66, 68).

Dissolved inorganic phosphate (DIP) concentrations ranged from 0.63 to 2.10 µmol P L^{-1}. Average concentrations of DIP were 1.56 ± 0.36 µmol P L^{-1} for the upper 100 m. General distribution patterns of DIP were similar to those observed for DIN (Figure 3).

Chlorophyll a

Chlorophyll *a* concentrations averaged 5.73 ± 0.6 µg chl *a* L^{-1} and were highest within the surface waters of the central polynya. Peak bloom stations had the highest concentrations, constrained to the upper 50 m with values up to 21.8 µg L^{-1} (Figure 4). Chlorophyll *a* decreased significantly with depth below the upper mixed layer.

Particulate Organic Matter

Particulate organic carbon (POC) concentrations were highest in the upper 30 m of the ASP (Figure 5). Concentrations exceeded 200 μmol C L^{-1} at peak bloom stations. Points of high concentrations corresponded positively with chlorophyll *a* peaks (with the exception of station 57, all stations had $R^2 > 0.8$, up to 0.99). Particulate organic nitrogen (PON) concentrations showed similar trends as POC within the ASP, with POC:PON values averaging 7.41 ± 0.54. (Figure 6).

Dissolved Organic Matter

Dissolved organic carbon (DOC) concentration in the ASP ranged from 47 to 122 μmol kg^{-1}. There was a general spatial trend of high DOC (~100 μmol kg^{-1}) in the surface waters at peak-bloom stations (Figure 7).

Residual dissolved organic nitrogen (rDON) was calculated by subtracting measured total dissolved nitrogen (TDN) from total dissolved inorganic nitrogen (TDIN). While overall rDON was relatively low at most stations, there was a trend of higher concentrations in the surface and subsurface at high productivity stations (Figure 8).

Some stations showed a DOC peak at depths (~ 100 m), without a corresponding DON increase. This could indicate a subsurface organic carbon input from the sediments or melting ice sheet nearby.

Microbial Abundances

Bacterial abundances averaged 6.29 ± 1.05 x 10^5 cells mL^{-1} over the upper 400 m. Bacteria were ubiquitous throughout the central polynya. Stations along the marginal ice zone (Stations 66 and 68), as well as the iceberg station (57) showed

bacterial abundances an order of magnitude higher (2.0×10^6 cells $mL^{-1} \pm 4.3 \times 10^5$) than non ice-sheet / iceberg stations.

Viruses were also abundant throughout the upper 1000 meters of the water column and ranged from 1.0 to 8.2×10^9 particles L^{-1}. Virus to bacterium ratios (VBR) averaged 8.3 ± 0.6 in the ASP. There was a significant linear correlation between viral and bacterial abundance ($R^2 = 0.42$, $p < 0.01$). Viral abundance also correlated significantly with chl *a* ($R^2 = 0.40$, $p < 0.01$) and inverse depth ($R^2 = 0.20$, $p < 0.01$), with a general trend of higher viral abundances in the upper 200 m.

Microzooplankton abundances were low throughout the ASP, with ciliates averaging $1.8 \pm 0.31 \times 10^4$ cells L^{-1}. Ciliates were most abundant at sea-ice-covered Stations 66 and 68, with higher values also observed at the iceberg associated Station 57. Flagellate abundances were also lower than oligotrophic surface waters, with an average of $3.5 \pm 0.39 \times 10^2$ cells mL^{-1}. Macrozooplankton density was highest at subsurface depths, below the *P. antarctica* bloom (Wilson, personal communication).

Microbial Activity

Both primary and secondary productivity peaks were associated with the central, open region of the ASP. Primary production (PP) ranged up to 108 µgC L^{-1} d^{-1} at peak-bloom stations. Bacterial production (BP) followed a similar spatial trend as PP, with the highest values being observed in the central polynya (Figure 9). BP was dominant in the upper mixed layer, with values ranging from 0.20 – 4.0 µg C L^{-1} d^{-1}. Below the UML, productivity declined rapidly, with over 99% of the activity occurring in the upper 100 m. Coincident with this regionally high BP, bacterial respiration (BR) was even higher, with rates up to 53 µg C L^{-1} d^{-1}. High BR rates contributed to the low average bacterial

growth efficiency (BGE) within the ASP, with a maximum efficiency of 27%, and an average of 9.6 ± 0.06%.

Incubation experiments (at Station 25) showed that short-term warming of the water from *in situ* (-1.5 ºC) to 5 ºC approximately doubled bacterial production rates. Continued warming to 10 ºC did not affect rates, and production rates dropped significantly with continued warming to 20 ºC, indicating a classical psychrophilic temperature response (Figure 10).

Size fractionation experiments conducted at station 50 showed that particle-associated activity was high: whole water bacterial production (4.0 µg C L^{-1} d^{-1}) was significantly higher than that measured on the size-fractionated sample (1.0 µg C L^{-1} d^{-1}) (Figure 11).

Bacterial production correlated strongly with particulate organic matter in the ASP. For the upper 100 m, BP was significantly, positively correlated with both POC (R^2 = 0.752, $p < 0.01$) (Figure 12) and PON (R^2 = 0.714, $p < 0.01$) (Figure 13). BP showed similar but weaker relationships with DOC (R^2 = 0.47, $p < 0.01$) and DON (R^2 = 0.261, $p < 0.01$).

Exoenzyme Analysis

Exoenzymatic activity rates were measured at a total of five ASPIRE stations (13, 14, 35, 50, 57). Of the four enzymes, MCA-L had the highest rates observed in the ASP at station 13. MCA-L ranged up to ~ 250 nmol L^{-1} h^{-1}, with an average of 32.7 ± 14.9 nmol L^{-1} h^{-1}. MUF-G, MUF-B, and MUF-P were all ubiquitously low throughout the ASP, with averages of 0.173 ± 0.04 nmol L^{-1} h^{-1}, 0.175 ± 0.06 nmol L^{-1} h^{-1}, and 0.109 ± 0.07, respectively. Size fractionated rates show an approximately even division of

exoenzymatic rates between larger size classes (< 3 μm) and free-living (0.2 - 1 μm) (Figure S.2). MCA-L activity shows strong, significant correlations with BP (R^2 = 0.75, p < 0.05), Chl *a* (R^2 = 0.95, p < 0.05), and POC (R^2 = 0.96, p = 0.05).

Heterotrophy vs Autotrophy in the ASP

Both PP and BP were high in the ASP. The BP:PP ratio was consistently low across all stations in the ASP, with an average of 0.05 ± 0.004. BCD:PP averaged 0.76 ± 0.1, reflecting high BR. Statistically significant correlations were observed between both BP and Chl *a*, and BP and PP. A linear regression of Chl *a* and BP yielded a significant relationship (R^2 = 0.76, p < 0.01) (Figure 14). A reduced major axis regression between BP and PP shows a strong, initial linear trend (R^2 = 0.802, p < 0.01), with a slope of 0.048, but when PP exceeds 40 μgC L^{-1} d^{-1} the slope of the relationship flattens to zero (Figure 15), suggesting saturation.

Discussion

Regional Significance

In the Amundsen Sea, surface algae blooms are significant, with the dominant blooms comprised of *Phaeocystis antarctica* that begin in December and reach peak abundance in mid-February (Arrigo and van Dijken, 2003). In the neighboring Ross Sea there is a time lag of approximately one month between the phytoplankton bloom and the bacterial bloom. This delay has been shown to not be a result of temperature inhibition (Kirchman et al. 2009), but is likely due to resource limitation (Carlson et al., 1999). Due to the lack of DOC input from rivers (Rich et al., 1997), this coupling between the phytoplankton bloom and the bacteria suggests that bacterial production rates are primarily limited by low observed DOM within Antarctic polynyas (Ducklow et

al., 2001). This relationship appears to be dependent on the time of the phytoplankton bloom, as well as labile and semi-labile DOC inventories (Ducklow and Yager, 2007).

Bacterial Production and Respiration

Despite high surface autotrophy, heterotrophic rates were still regionally significant. Leucine incorporation rates in the Amundsen Sea (0.154 – 2.587 nmol L^{-1} d^{-1}) are approximately double those calculated in the adjacent Ross Sea (0.240 – 0.940 nmol L^{-1} d^{-1}) (Ducklow et al., 1999). The regionally high production values within the polynya suggest that the microbial community is active and growing despite low ambient water temperature (-1.8 ºC). Temperature sensitivity experiments indicate an active psychrophilic community that is potentially vulnerable to ocean warming from climate change.

Linking BGE to BCD

Bacteria in the ASP are diverting, on average, 91% of total carbon uptake to BR. One explanation for this tendency is that the particulate matter is low quality, and provides a less than ideal substrate for bacterial growth. BP was found to correlate with both PON and POC and size-fractionation experiments confirmed particle-association. Particle association is generally more energetically taxing than a free-living lifestyle (Deming, 2002) and consistent with a lack of dissolved organic matter sources. The majority of organic matter in the ASP is bound inside *P. antarctica* cells (Schoemann et al. 2005), which is unable to be directly utilized by bacteria (Tang et al. 2001).

Low in situ measurements of DOM within the polynya do not, however, account for rapid production and turnover of DOM. There are three key pathways through which

DOM can be created: grazing, viral lysis, and exoenzyme hydrolysis. In the next sections we will discuss evidence to assess the importance of these mechanisms.

Zooplankton and grazer abundances

Zooplankton play a vital role in microbial loop dynamics (Azam et al. 1983; Sherr and Sherr 2002; Pomeroy et al. 2007). Zooplankton and grazing contribute significantly to dissolved and particulate organic matter flux in marine environments through sloppy feeding and excreta (Jumars et al. 1989; 1993; Steinberg et al. 2000; Steinberg et al. 2008). Flagellate and protist abundances are comparatively low in the upper 100 m. Low levels of microzooplankton grazers are also observed in the neighboring Ross Sea polynya (Tagliabue and Arrigo, 2003). While reduced grazing pressure (minimal sloppy feeding) could explain a reduction in DOM flux, the efficacy of the grazers could also play an important role. Rose and Caron (2007) suggest that temperature inhibition could constrain growth rates of protists, and that colder temperatures yield less effective feeding. *P. antarcita* have been shown to resist grazing through production of chemical compounds (DMS) or colony formation (Irigoien et al. 2005). Whether through inefficient feeding, or low abundances, microzooplankton are not observed to have a significant role in photic zone (≤ 100 m) DOM cycling in the ASP. Macrozooplankton abundances were also reported to be low in the upper 40 m. This reduced grazing could contribute to the lack of bacterial accessibility to labile DOM.

Viral cycling

Another potential source of decoupling between BP and DOM is viruses. Viral interaction and infection with bacterial communities reduces BGE (Fuhrman 1992; Middelboe et al., 1996) and its importance cannot be discounted in the polynya. Payet

and Suttle (2008) suggest that viral lysis could account for a significant proportion of cellular mortality in polar marine systems. Viral strain CCMP1871 has been shown to preferentially lyse *P. antarctica* (Brussaard et al., 2007), and while ASPIRE did not distinguish viral species, it is generally assumed that a significant proportion of free viral particles are bacteriophages (Karl et al. 1996). The lytic cycle could account for a significant portion of labile DOM flux within the polynya (Middelboe and Lyck 2002). As viruses lyse *P. antarctica* and bacteria, organic matter within the cells is released to the environment for heterotrophic utilization (Gobler et al. 1997; Middelboe and Jørgensen 2006). VBR was low in the ASP (8.3 ± 0.6) compared to Pacific ratios (~40), but similar to values in Atlantic surface waters (~10) (Suttle 2007). VBR corresponded with similar ratios observed during austral summer by Karl et al. (1996) in the West Antarctic Peninsula (WAP). Viral abundances showed a significant correlation with bacterial abundance, and chlorophyll *a* in the ASP, a trend observed by Fuhrman (1999). This could suggest that viral infection and lysis play a significant role in DOM cycling in the ASP.

Phytoplankton Extracellular Release

Since bacteria have not been shown to lyse algal cells, heterotrophic communities rely on phytoplankton extracellular release (PER) of DOM (Billen and Becquevort 1990). PER in bloom stage phytoplankton averages 2-10% of total DOM and can range up to 60% (Myklestad 2000). Nutrient limitation and other environmental factors, such as temperature stress, exacerbate PER (Myklestad 2000). Due to little evidence of nutrient limitation in the ASP (observed drawdown of nutrients never reached 0), we can assume macro-nutrient limitation was minimal in the polynya.

Constant solar input from the austral summer would also suggest light limitation is minimal, though there is some evidence of self-shading in *Phaeocystis spp.* (Shields and Smith Jr. 2009). Since the bloom was still building in the polynya at the time of ASPIRE, it is unlikely that phytoplankton were stressed and leaking significant DOM.

Extracellular Enzyme Rates

The correlation between BP and exoenzyme rates for the water column (R^2 = 0.75) show a positive, linear trend. Similar trends are observed for POC, suggesting bacteria are utilizing extracellular enzymes (particularly MCA-L) to hydrolyze POM to more labile DOM. Production of these extracellular enzymes are energetically costly, and could explain the high observed diversion of organic matter uptake to bacterial respiration (Deming 2002).

Constraining BP Conversion Factors

Measurements of ^{3}H-leucine incorporation as a measurement of bacterial production are directly linked to the methodology and conversion factors used in calculations (Kirchman 2001). For the purpose of ASPIRE standard conversion factors according to Kirchman et al. (1985), and Simon and Azam (1989) were used, as stated above. While rates listed here are considered a moderate estimate of in situ values, more conservative or liberal estimates can be made for this system based on estimates from the literature.

Theoretical conversion factors for converting leucine incorporation are established as 1.55 kg C mol_{leu}^{-1} (Simon and Azam 1989). This conversion factor assumes that isotope dilution (leucine biosynthesis or non-labeled uptake in the presence of high radiolabeled leucine concentrations) is negligible (Kirchman 2001).

The resulting bacterial production is considered to be a conservative estimate of productivity (Simon and Azam 1989; Kirchman 2001). If the theoretical conversion factor is used to calculate productivity in the ASP, rates observed are similar to those reported above, maximum productivity is slightly less at 3.88 μg C L^{-1} d^{-1} (vs 3.99 μg C L^{-1} d^{-1}). For the Southern Ocean an empirical conversion factor for calculating bacterial production is available (Bjørnsen and Kuparinen, 1991). This conversion factor is roughly twice as high (3.03 kg C mol_{leu}^{-1}) as the theoretical one. When the Southern Ocean specific conversion factor is used, ASPIRE production rates increase to a maximum of 7.8 ± 2.2 μg C L^{-1} d^{-1}, and BGE approximately doubles to 16 ± 0.01%.

Isotope Dilution

Isotope dilution in leucine incorporation experiments occurs when non-radio labeled leucine is cycled or incorporated by bacteria in a given sample. Isotope dilution is most common at low concentrations of radioisotope, where kinetics drive uptake rates (Kirchman 1985; 2001). By saturating samples with high concentrations of ^{3}H-leucine (~ 20 nM) this allows for ambient extracellular leucine to be ignored (Kirchman 2001). However, studies suggest that despite high concentrations of radio-labeled isotope, leucine biosynthesis will still occur in samples resulting in an isotope dilution (Kirchman 2001). Isotope dilution factors have been shown to range up to 11.5 (Simon 1991), however Simon and Azam (1989) present an average dilution factor of 2. For the purpose of ASPIRE, isotope dilution was assumed to be ~ 1 (or negligible, due to high concentrations of ^{3}H-leucine ~ 20 nM), and the rates presented above potentially underestimate bacterial productivity in the polynya. If an isotope dilution factor of 2 is

assumed, maximum bacterial productivity doubles from 3.99 μg C L^{-1} d^{-1} to 7.99 ± 2.25 μg C L^{-1} d^{-1}. and BGE also doubles from 9.6% to 17 ± 0.02%.

In combination, therefore, our assumptions converting to BP from leucine incorporation could be underestimating both BP and BGE by as much as a factor of 4.

Zooplankton contribution to Community Respiration

Microzooplankton respiration in marine systems has been shown to account for ~ 25% of total community respiration (Calbet and Landry, 2003). However, microzooplankton abundances are relatively low in coastal Antarctic polynyas compared to oligotrophic averages (Caron et al. 2000) so using a value of 25% is likely an upper limit. If less than 25% of TCR is attributed to microzooplankton, bacterial contribution to TCR would increase (to up to 90%), BCD would increase to 1.3 ± 0.18, and BGE would decrease to 5.7 ± 0.01%.

Phytoplankton could also be contributing from 30 - 100% of the TCR in our experiments (Lancelot et al. 1991; Robinson et al. 1999).

Bacterial contribution to Community Respiration

Heterotrophic bacterial contribution to total community respiration has a wide range in marine systems, from 50 to 90% of total community respiration (Rivkin and Legendre, 2001). For ASPIRE data analysis, bacterial contribution to TCR was estimated to be 50%, after Ducklow et al. (2000). If we asume that BR accounts for 90% of TCR, growth efficiency drops significantly, with an average BGE of 5.7 ± 0.01 %. The BCD:PP increases, with an average ratio of 1.32 ± 0.18, indicating bacteria are utilizing more organic matter than is being fixed by the primary producers. If we assume a 25% contribution of BR to TCR yields average growth efficiencies more consistent with

observed bacterial values (del Giorgio et al. 1997). BGE averaged 16.7 ± 0.9%, with maximum efficiencies of ~ 43%. BCD:PP ratios for the 25% scenario averaged 0.41 ± 0.05, with a maximum of 0.96. This low average BCD:PP would suggest a dominance of autotrophy over heterotrophy, and represents a more likely scenario in the ASP given observations of high surface Chl *a* and low pCO_2 (Yager et al. 2012).

Underestimation of Primary Production

Primary production in the ASP was measured by ^{14}C HCO_3 incubation experiments. ^{14}C methods to measure primary production have been shown to potentially underestimate productivity by only measuring POM production (Larsson and Hagström 1982; Karl et al. 1998). By only analyzing production captured on a GF/F, any DOM production is passed through the filter and is not reflected in the total rate. *Phaeocystis sp.* have been shown to produce copious amounts of DOM (Hong and Smith 2008), which is readily utilized by heterotrophic microbes (Carlson et al. 1998; 2000). This potential underestimation of primary production (up to 20%; Hansell and Carlson 1998) would explain the relatively high BCD:PP calculated for ASPIRE (0.76 ± 0.1).

Respiration Rates: Evidence for bottle effects?

Estimates of bacterial carbon demand to primary production average 0.985 ± 0.15. This ratio appears too high based on the dominance of primary production in the ASP, with ratios of PP:BP persistently ≤ 0.3. An explanation for the high BCD could be accounted for in an overestimation of community respiration. During dark bottle experiments, phytoplankton communities in a given sample become light and nutrient limited (Stefels and van Leeuwe 1998). This stress causes previously robust cells to

have increased membrane permeability, which results in increased extracellular release of organic matter, and ultimately, cellular mortality (Myklestad 2000; Stuart et al. 2009). This release of organics would stimulate heterotrophic metabolism (and presumably, respiration); this bump in cycling would be a result of a bottle effect, and not a 'true' measurement of respiration in the system.

Energetics of DMSP Degradation

A significant proportion of DOM release by *Phaeocystis sp.* is the compound dimethylsulfoniopropionate (DMSP) (Liss et al. 1994). DMSP represents a significant source of reduced sulfur in the ocean and is an energetically favorable component in protein synthesis compared to the assimilative sulfate reduction change (Kiene et al. 1999; Ruiz-Gonzalez et al. 2012). While polar marine bacterial taxonomic groups have been shown to degrade DMSP to dimethylsulfide (DMS), not all groups assimilate DMSP uniformly (Malmstrom et al. 2004). DMSP represents a small, but potentially significant proportion of BCD (0.4-6.5%), and is a major source of sulfur to marine bacteria (up to 100%) (Kiene and Linn 2000). Since DMSP (and DMS) was not measured as part of ASPIRE, its incorporation into our understanding of ASP DOM dynamics might explain some of the discrepancy.

Conclusion

Our estimates of microbial activity in the Amundsen Sea Polynya reveal high rates of bacterial and primary productivity previously unreported in polar marine systems. The range of this productivity is highly dependent upon the conversion factors used during calculation. This uncertainty is reflected in the wide range of potential bacterial growth efficiency in the ASP (5 - > 20%), as well as estimates of bacterial

production (0.25 to > 9 μg C L^{-1} d^{-1}) and bacterial contribution to community respiration (25 – 90%). Despite uncertainties in measured rates, the data range presented above represents a maxima and minima of productivity over the course of the austral spring and summer bloom. A significant finding of ASPIRE is that up to 70% of bacterial production is particle associated in the ASP, with significant correlations between [POM] and BP. Both primary and secondary production are high compared to the neighboring Ross Sea Polynya, with autotrophy in the ASP being dominated by *P. antartica*. This regionally significant PP could be underestimated based on excess DOM production not being incorporated into PP measurements via ^{14}C-HCO_3 incubations (up to 20% of PP). Despite relatively high Chlorophyll *a* and primary production, observed DOM in the ASP is low. Micro- and macro-zooplankton abundances in the upper 40 m are low, suggesting reduced DOM release. This suggests that bacteria in the ASP are utilizing a particle associated lifestyle, in conjunction with extracellular enzyme hydrolysis of POM to DOM, in order to overcome a reduced DOM flux within the ASP.

Chapter 3

Discussion and Conclusion

Discussion

Chapter 2 establishes that primary and bacterial productivity in the ASP are regionally significant compared to both the neighboring Ross Sea polynya, and the West Antarctic Peninsula. While regional comparisons are critical to better understand this remote system, a broader understanding of the ultimate fate of this productivity is of primary importance to the goals of ASPIRE (Yager et al. 2012). As stated above, we hypothesize that the ASP hosts an efficient biological pump and that a significant portion of the surface bloom is exported below the surface mixed layer to the deep.

Sediment traps deployed during ASPIRE, both moored annual traps and floating traps for 2-3 days, confirm that significant organic material is sinking to depth in this region. How such export can be consistent with high estimates of in situ BCD:PP ratios is challenging. The explanation likely has to do with temporal offsets between phytoplankton and bacterial production. Without large populations of zooplankton, we observed a large buildup of recently produced particulate organic matter at the peak bloom stations. If we assume that bacteria are the only consumers of particulate matter (an assumption which will be addressed next), if total POC content (mmol C L^{-1}) is divided by BCD (mmol C L^{-1} hr^{-1}) this will give a turnover time estimate of how long it would take bacteria to completely remineralize a given particle field. The resulting

calculation had an average degradation of 20 ± 13.9 years. The particle load is too huge for even these highly active bacteria to impact.

The assumption that bacteria are the only degraders of particulate matter is not reasonable as micro and mesozooplankton have been shown to graze sinking particles (Garzio et al. 2013), however even if bacteria are responsible for 0.01 % of particle degradation, this would correspond to a rough estimate of turnover time on the order of several months. In the Ross Sea polynya, Dunbar et al. (1998) report sinking rates of 60-400 m d^{-1}. This sinking rate, and based on the degradation rate estimated above would imply that complete bacterial degradation of particulate organic matter before reaching the benthos is an unlikely scenario in the ASP.

Based on this assumption, coupled with up to 70% of sinking matter being comprised of fecal pellets and *Phaeocystis antarctica* aggregates, potential flux rates to the benthos are high (Dunbar et al. 1998). Better constraining particle degradation and sinking rates should be the focus of future research in the ASP. Based on the calculations above, particle flux out of surface waters via the biological pump cannot be discounted (Trull et al. 2001; McDonnell and Buesseler 2010).

Conclusions

The Amundsen Sea polynya represents a highly productive coastal zone that shows regionally high rates of both primary and secondary production. These productivities are supported by high nutrient concentrations, and favorable physical conditions. While total bacterial productivity in the surface waters is significant, autotrophy dominates heterotrophy in the ASP as indicated by low pCO_2 and high organic particle loads. This trend is supported by relatively low BP:PP. The ultimate

fate of these intense blooms suggests inefficiencies in the microbial loop due to low zooplankton abundances in the upper 100 m. Although viral particle abundances are within global averages, a low VBR suggests another potential short circuit in the conversion of particulate organic matter to dissolved organic matter. This dependence on POM for bacterial productivity is reflected in high particle-associated BP (up to 70% of whole water rates).

Figures

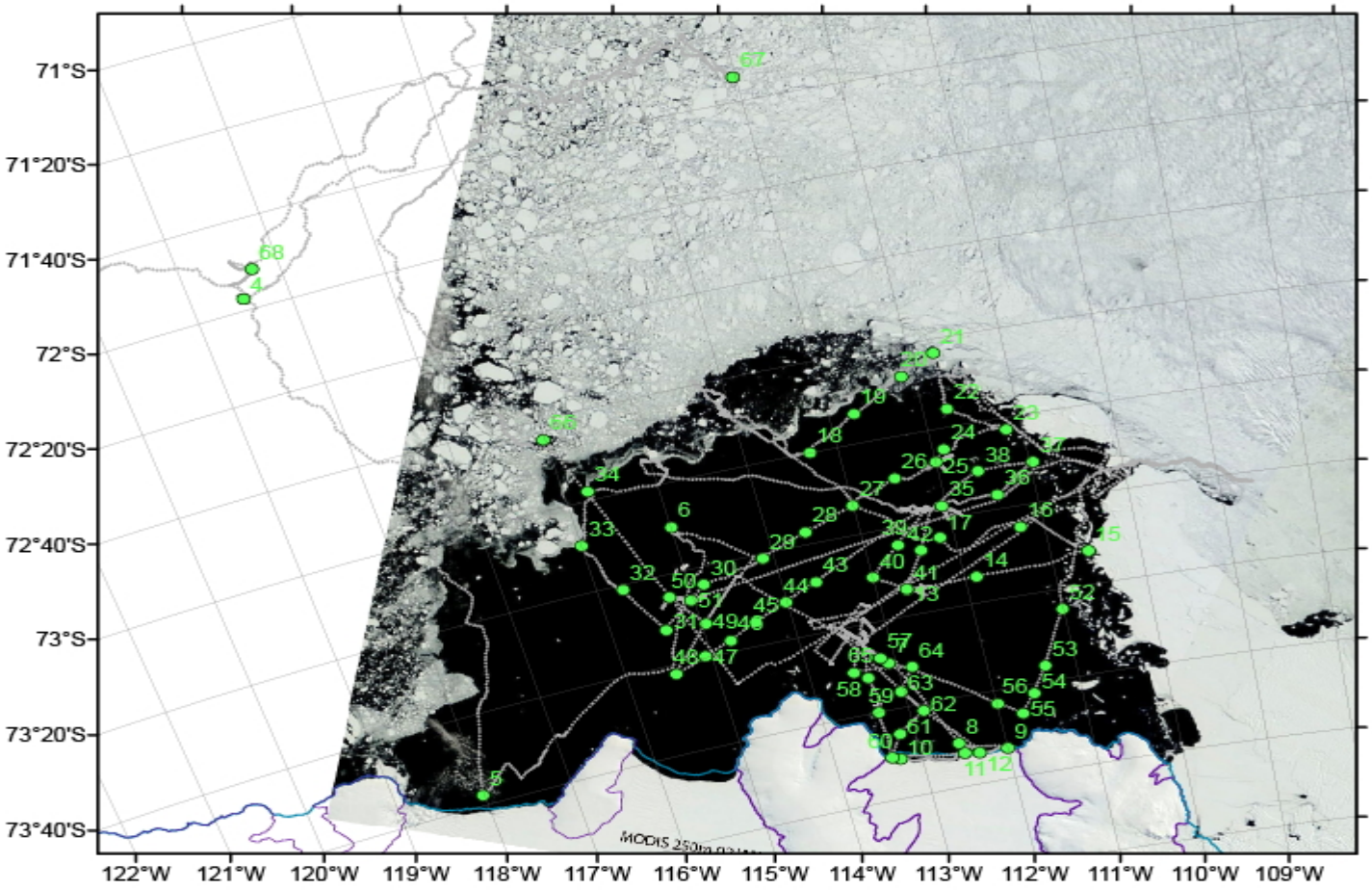

Figure 1: ASPIRE station map with cruise track. Superimposed over MODIS sea ice image from 1/2/2011.

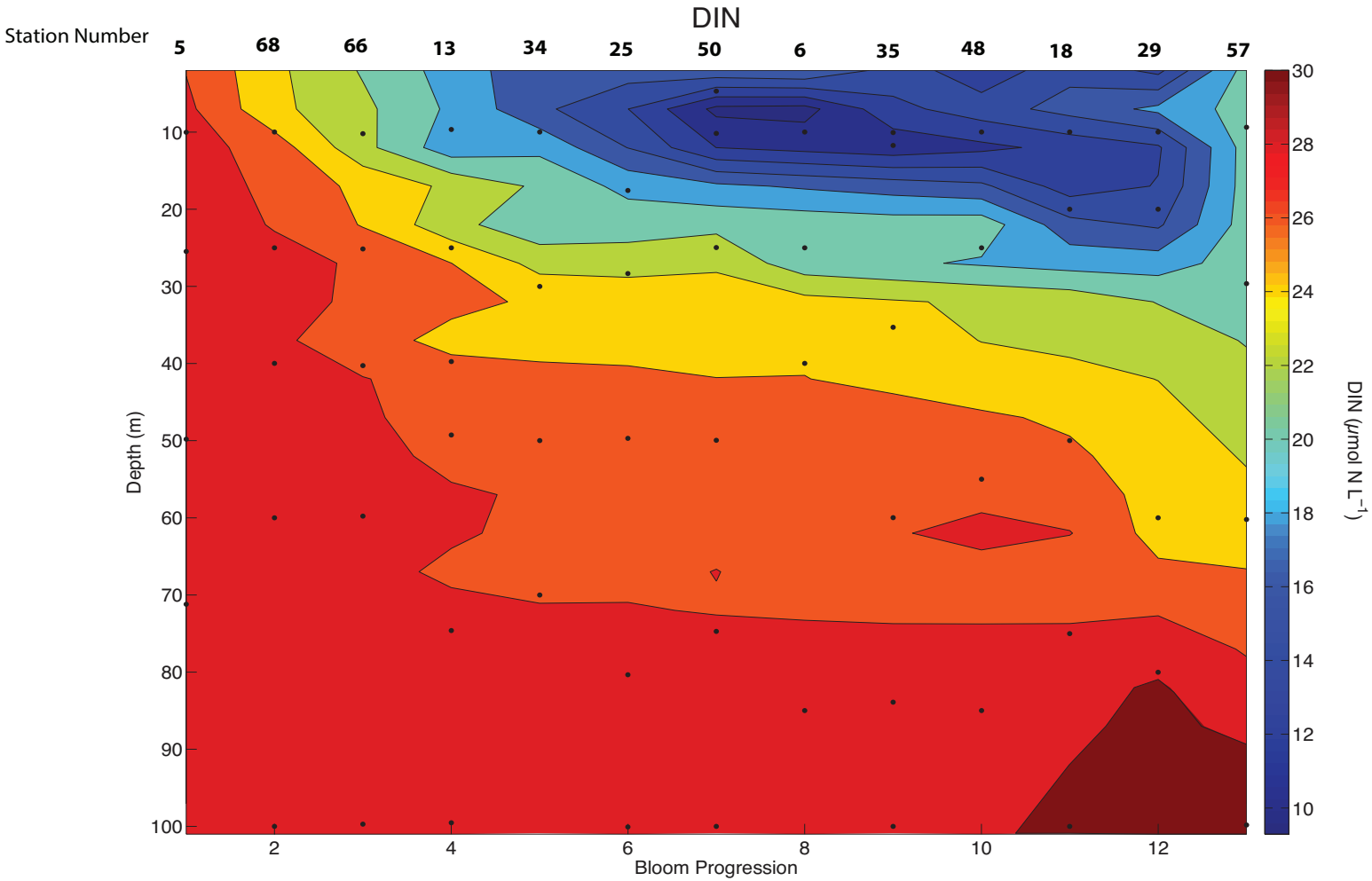

Figure 2: (DIN within the ASP arranged by bloom progression)

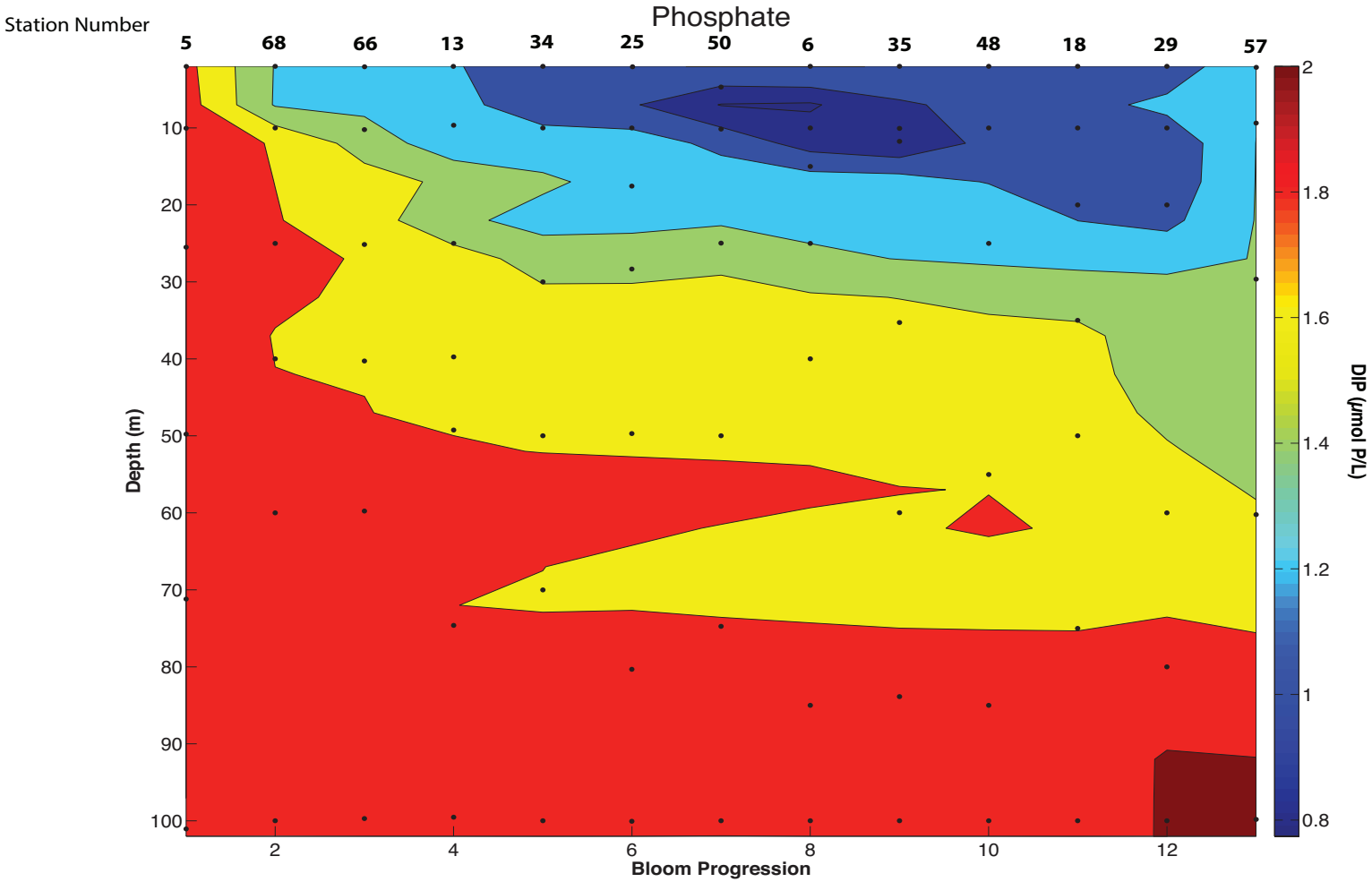

Figure 3: (DIP within the ASP arranged by bloom progression)

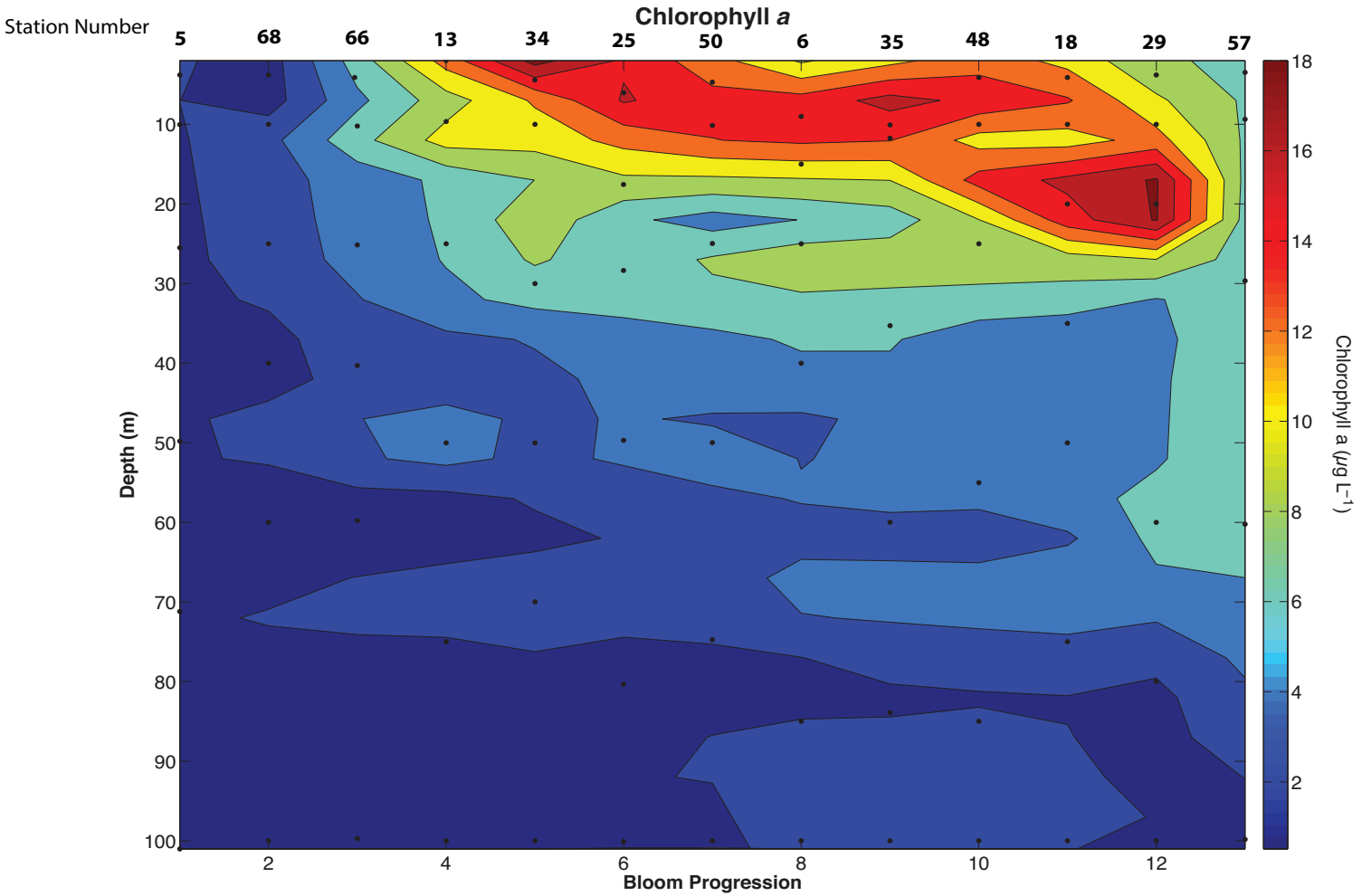

Figure 4: (Chl a concentrations within the ASP arranged by bloom progression)

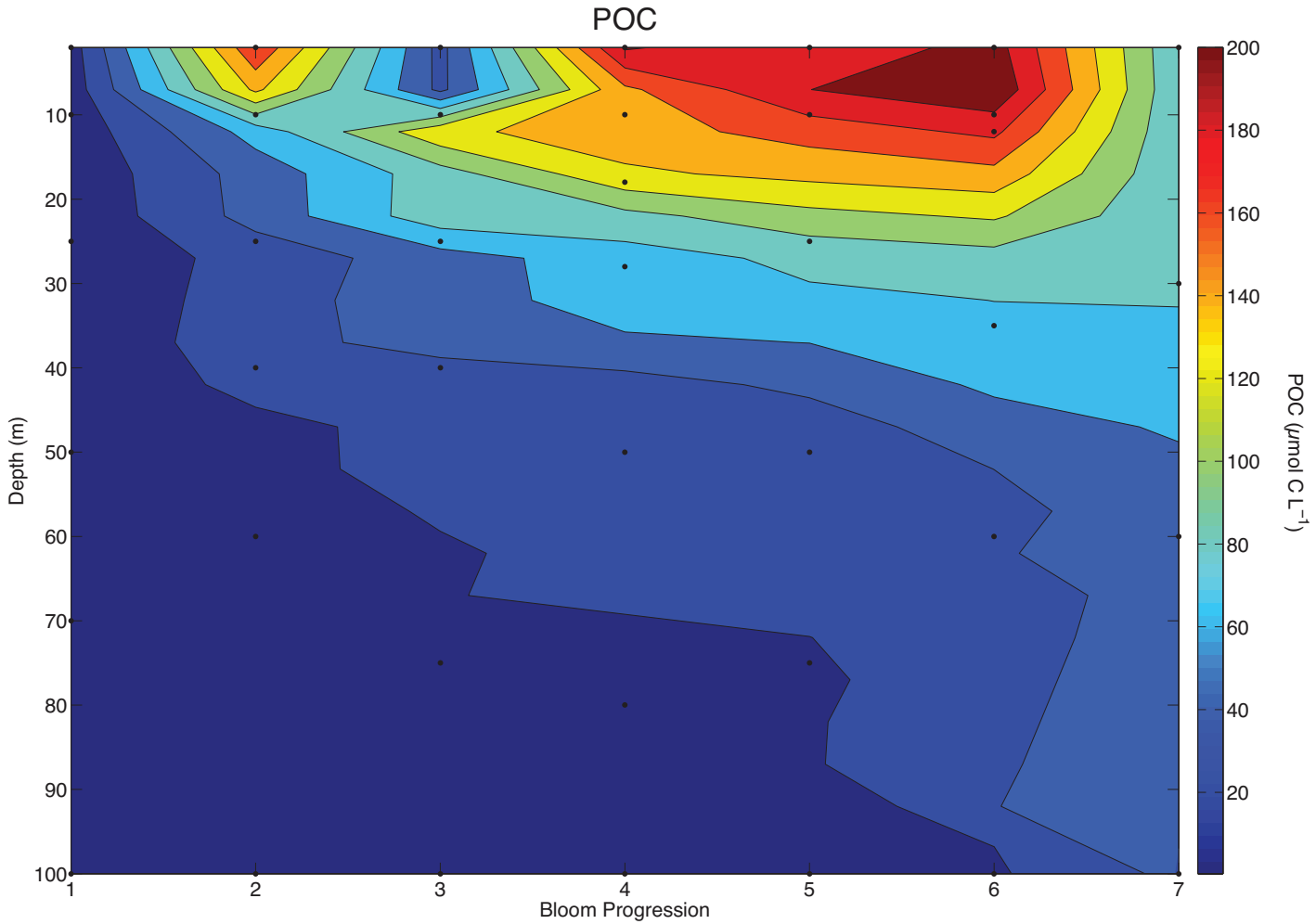

Figure 5: (POC within the ASP arranged by bloom progression)

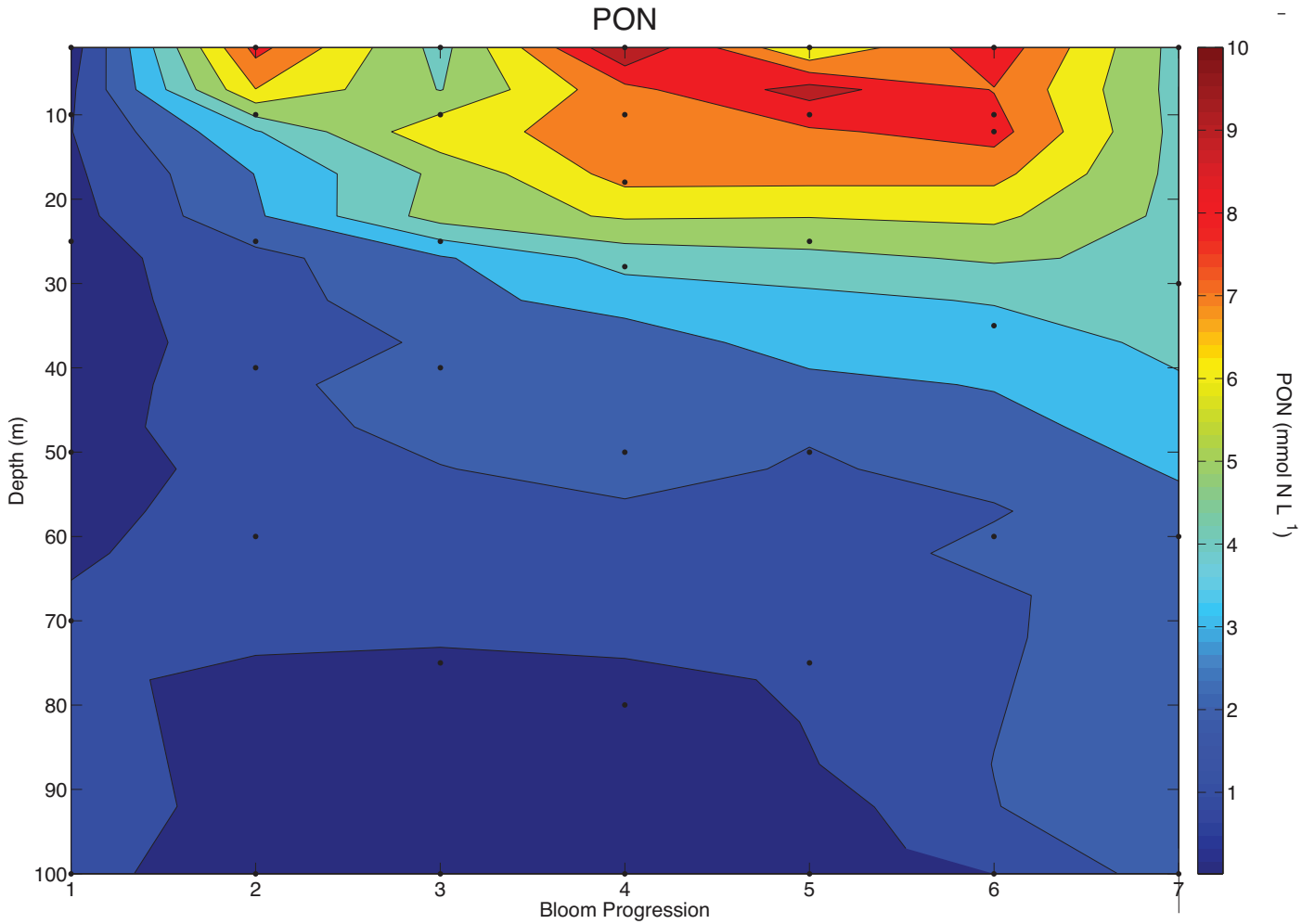

Figure 6: (PON within the ASP arranged by bloom progression)

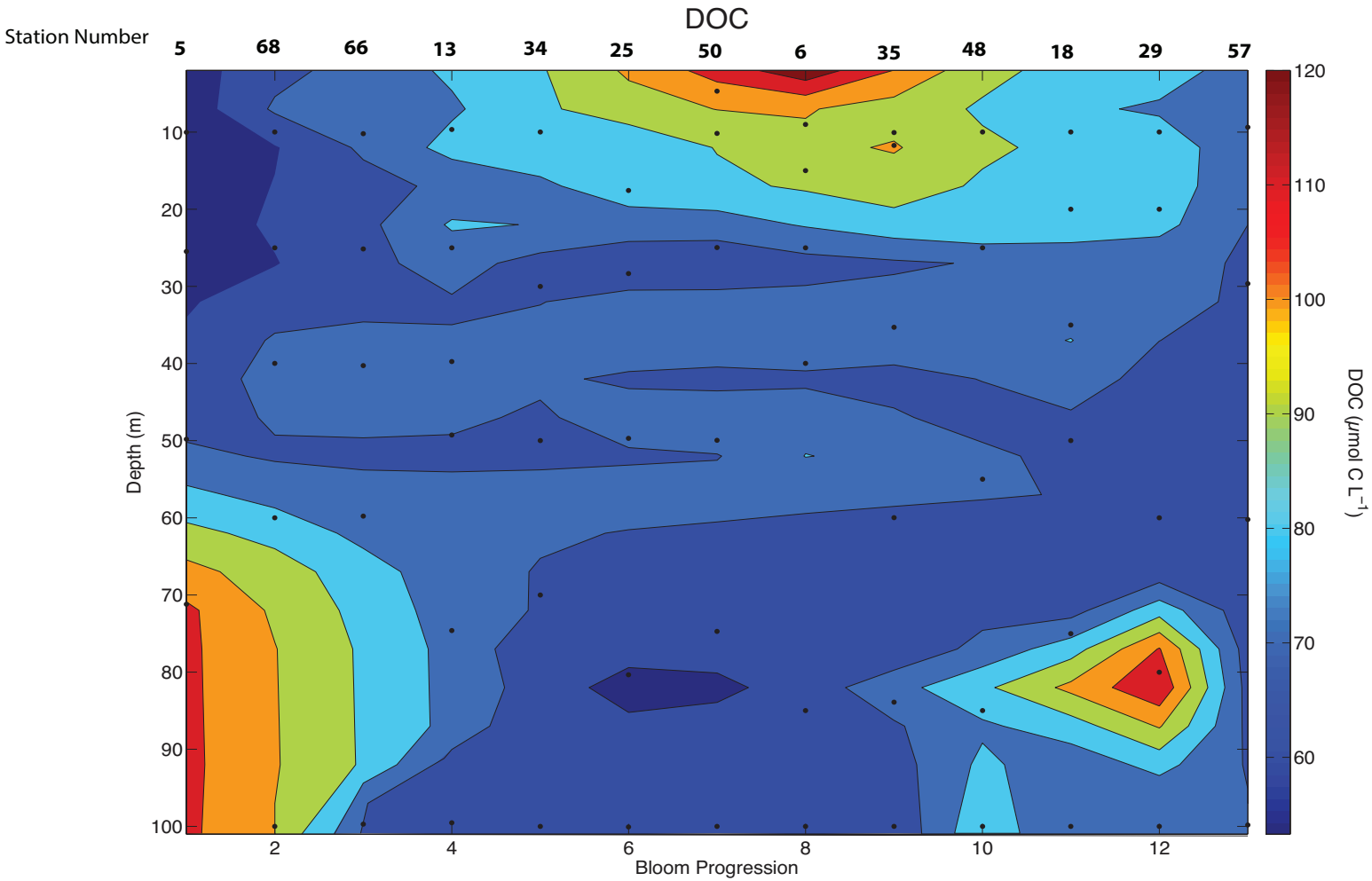

Figure 7: (DOC within the ASP arranged by bloom progression)

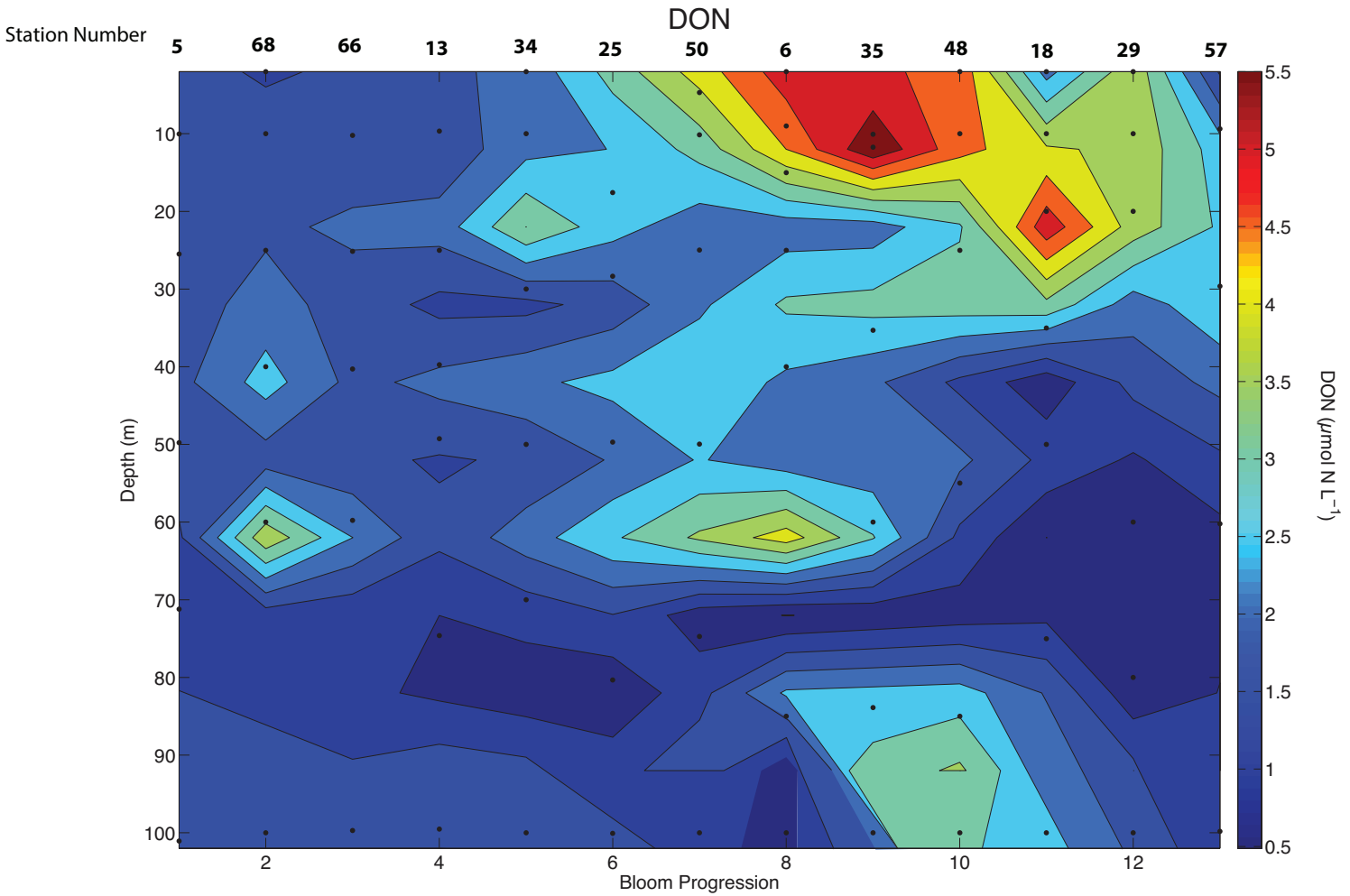

Figure 8: (DON within the ASP arranged by bloom progression)

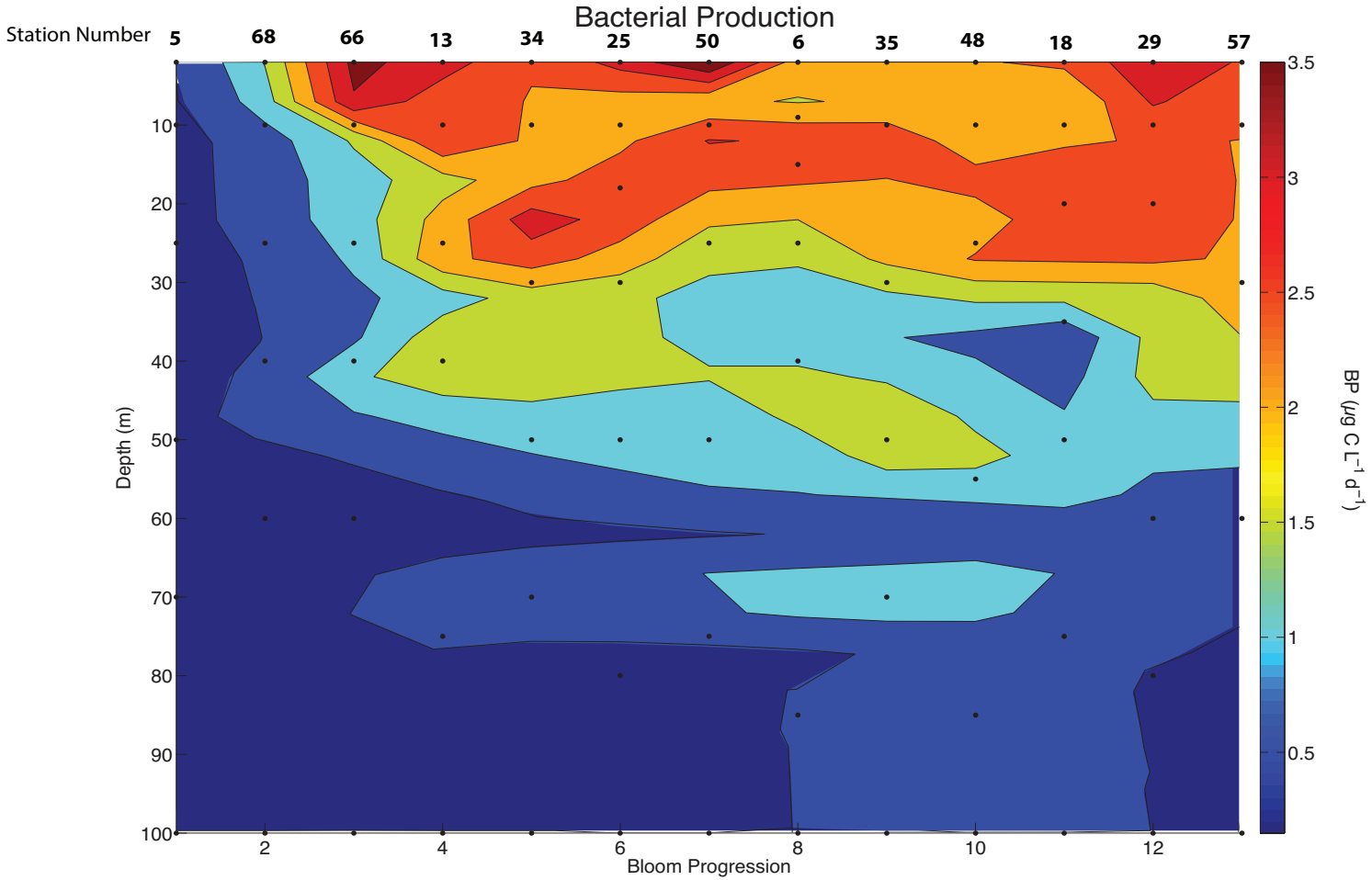

Figure 9: (BP within the ASP arranged by bloom progression)

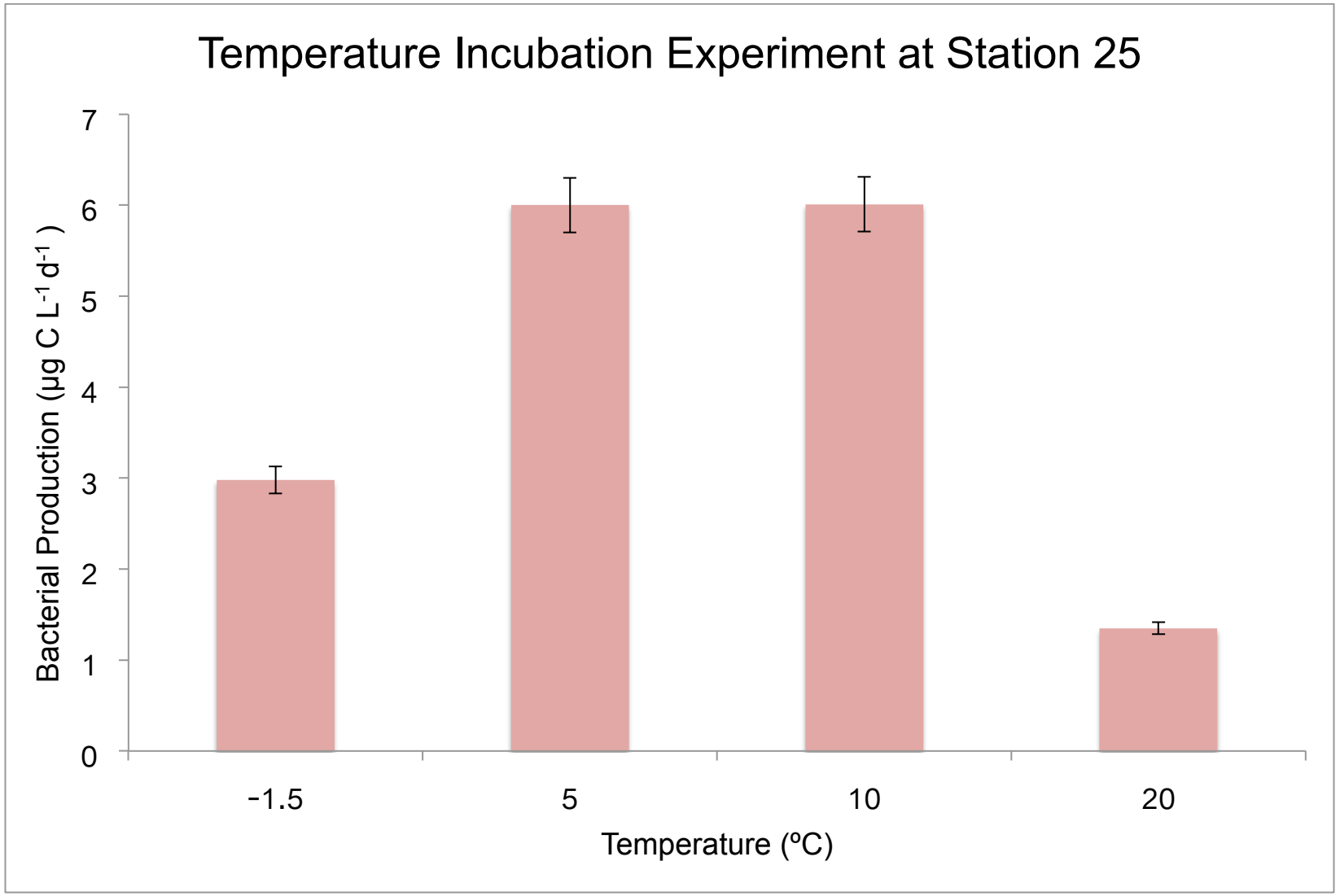

Figure 10: (BP Temperature Incubation Experiment at St. 25)

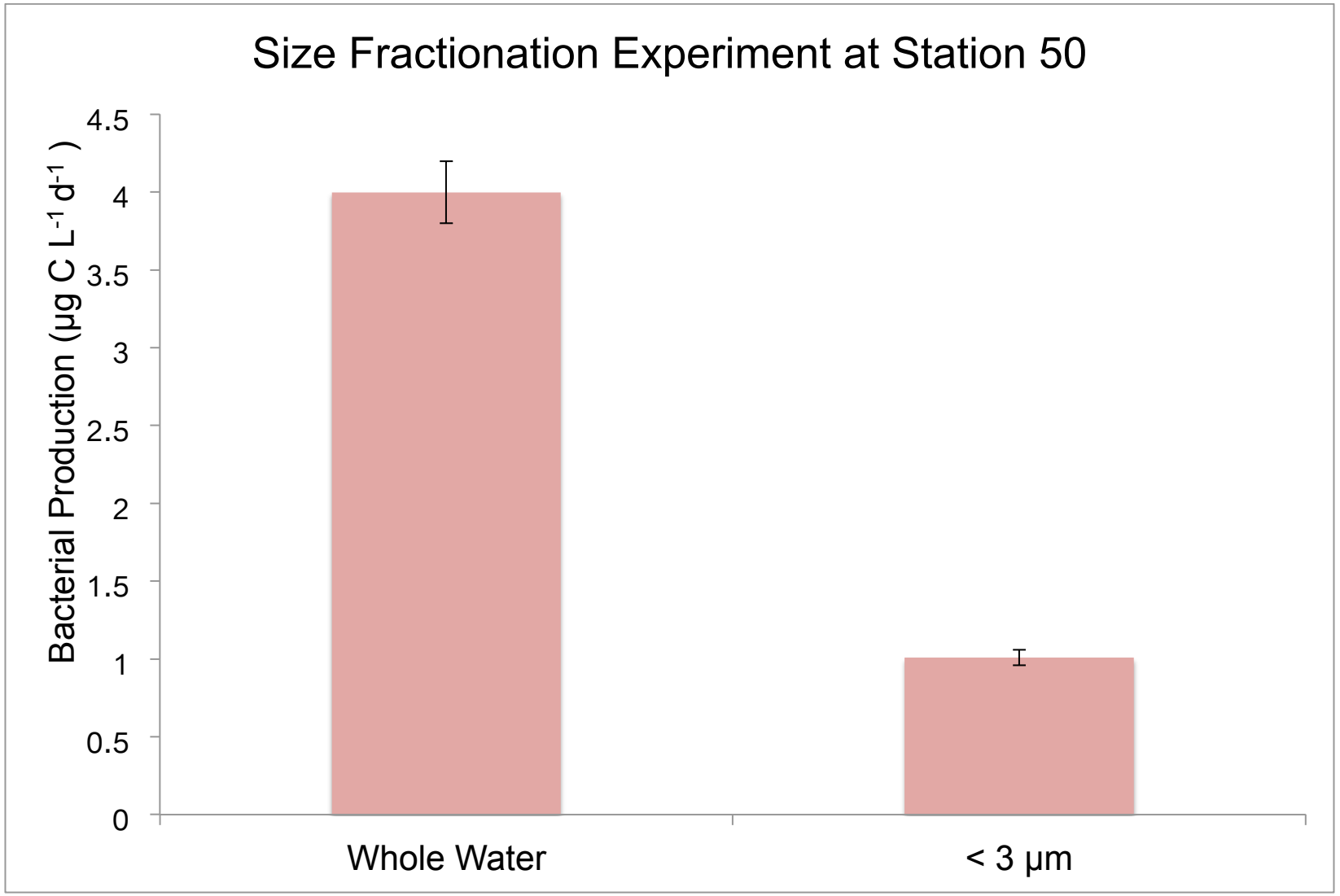

Figure 11: (Whole water vs. Particle Associated BP at Station 50)

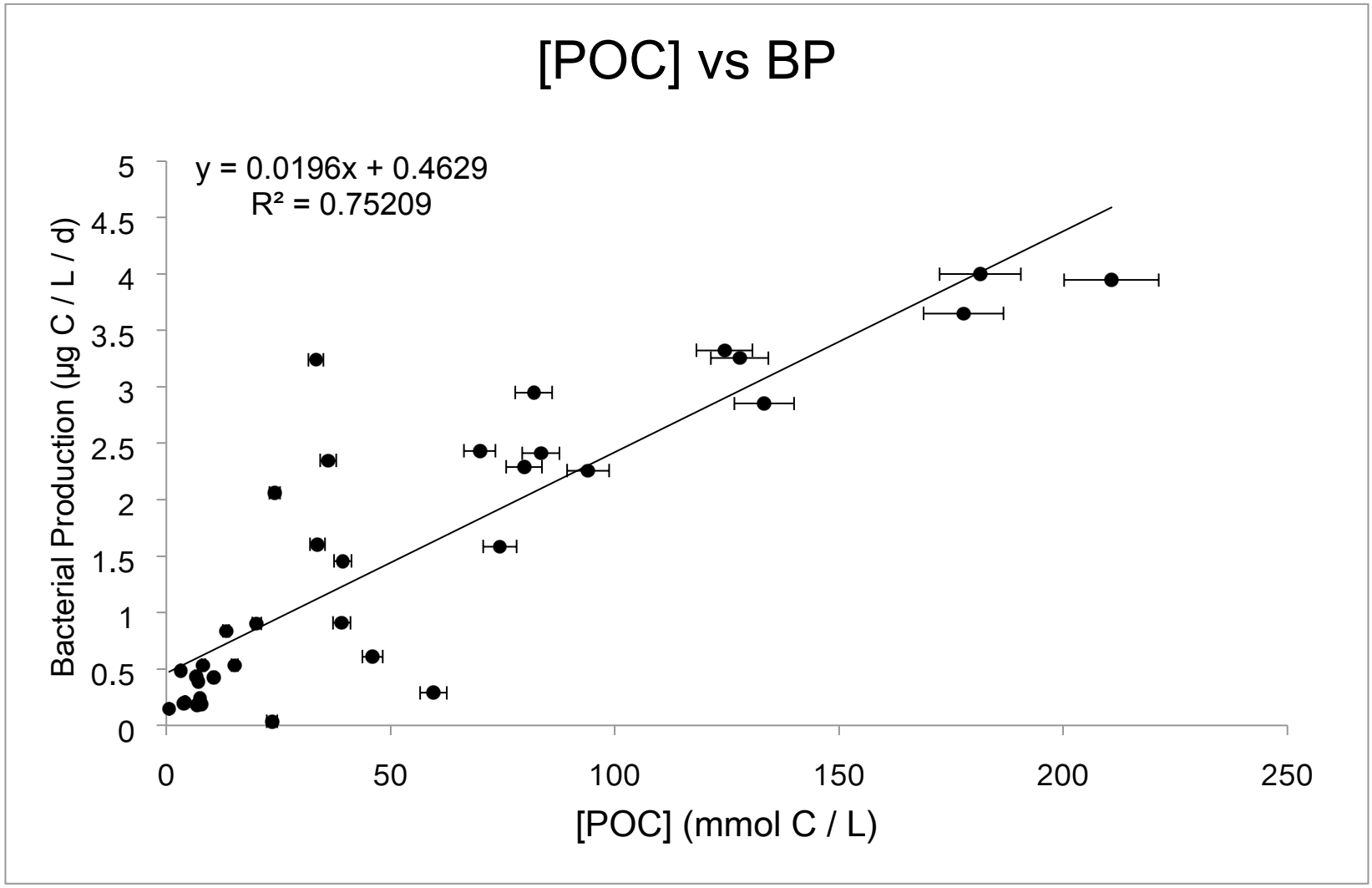

Figure 12: (Linear regression of [POC] vs BP)

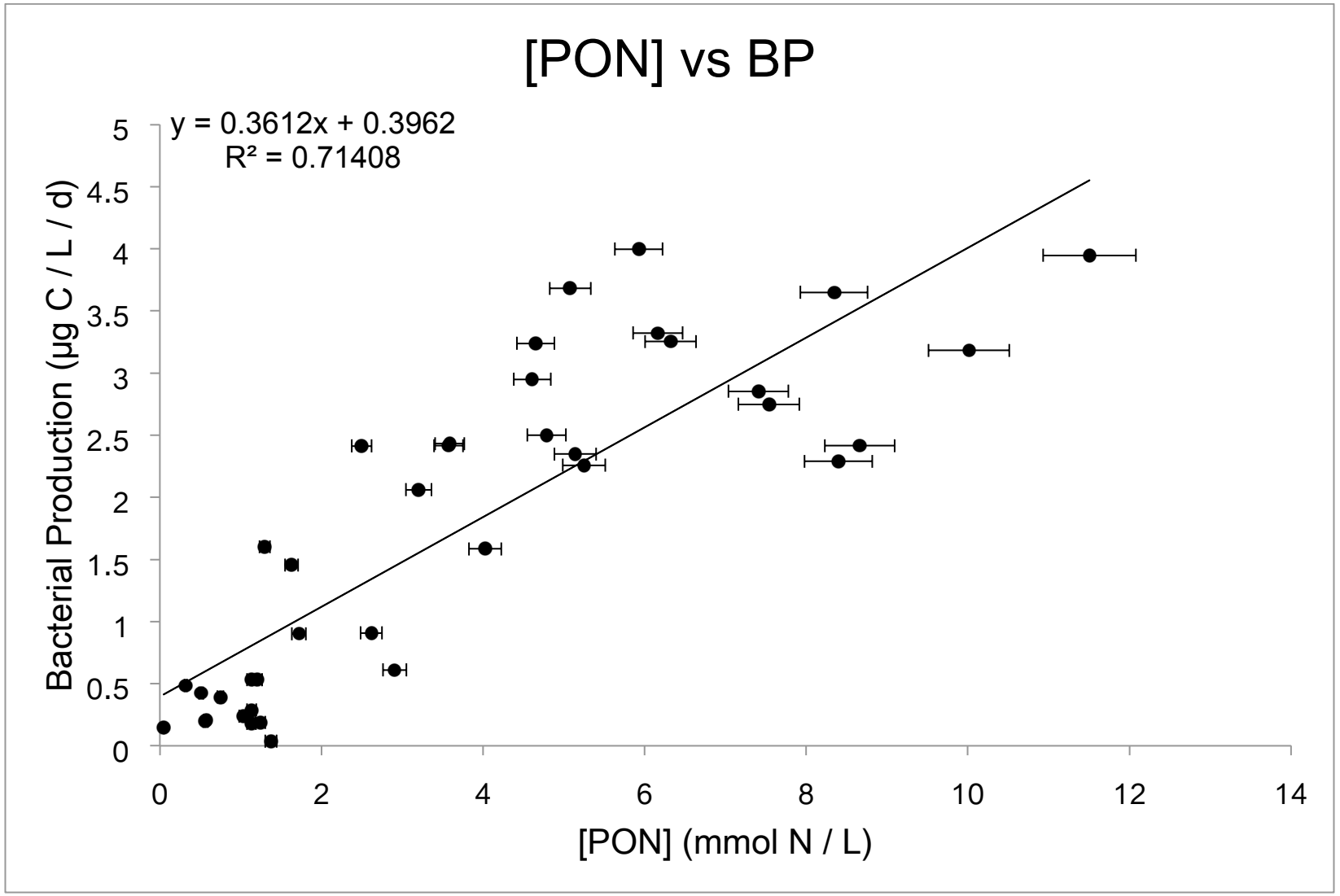

Figure 13: (Linear regression of [PON] vs BP)

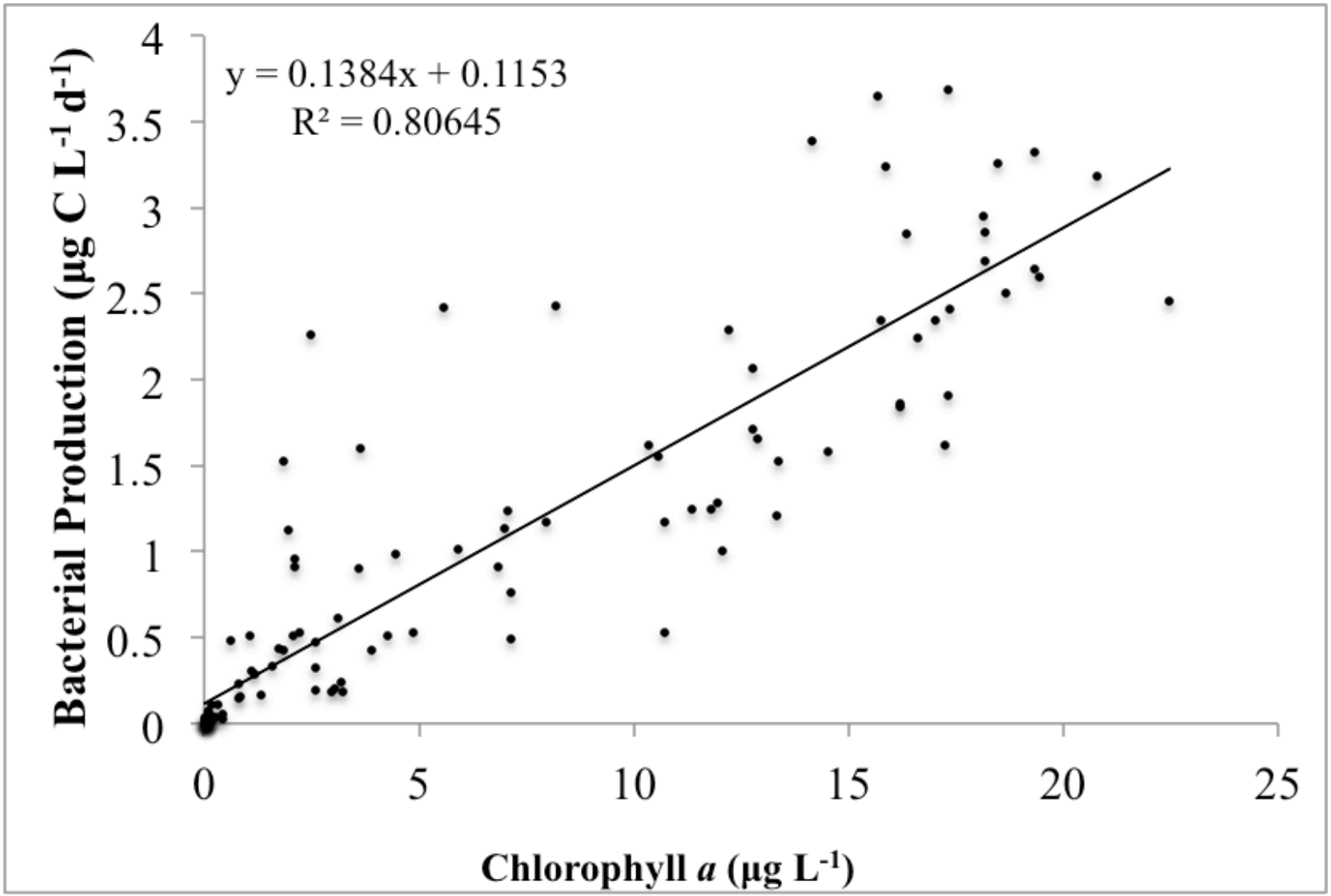

Figure 14: (Linear regression of Chla vs BP)

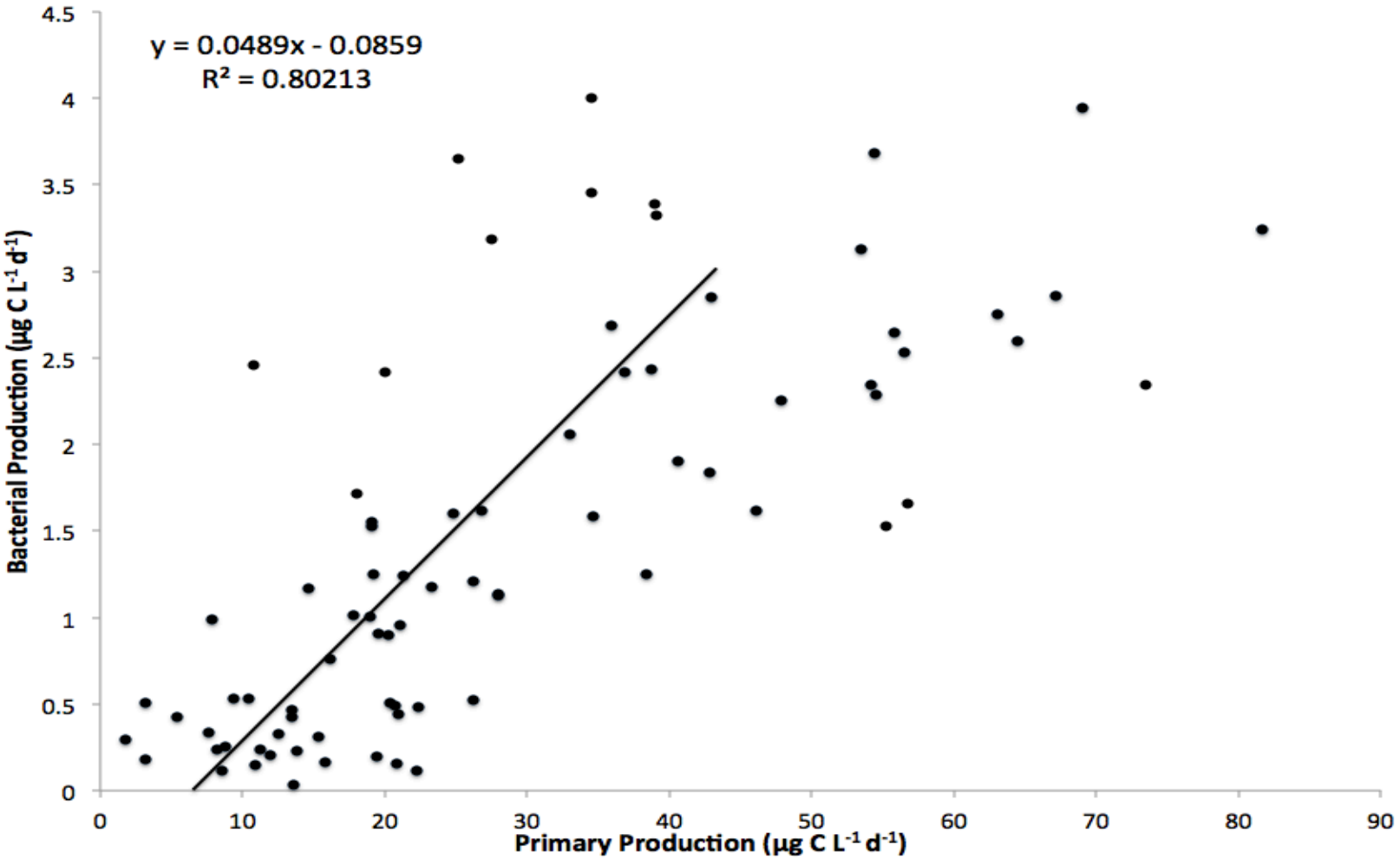

Figure 15: (Linear regression of PP vs BP)

Supplemental Figures and Tables

Table S.1 (Station data and Chemical Inventories for ASPIRE)

Station	Date	Lat / Lon (º)	Depth (m)	DOC (µmol C / L)	DON (µmol N / L)	DIN (µmol N / L)	DIP (µmol P / L)	POC (mmol C / L)	PON (mmol N / L)	Chl a (µmol / L)
5	12/15/10	-73.96, -118.04	1	55.82	1.79	27.79	1.85	10.56	0.51	2.28
5	12/15/10	-73.96, -118.04	10	52.91	1.75	28.78	1.90	7.52	1.03	1.88
5	12/15/10	-73.96, -118.04	25	55.91	1.71	29.99	1.94	3.89	0.57	1.51
5	12/15/10	-73.96, -118.04	50	67.55	1.92	29.57	1.91	4.21	0.57	1.79
5	12/15/10	-73.96, -118.04	71	111.90	1.02	29.51	1.91	6.86	1.13	1.73
5	12/15/10	-73.96, -118.04	101	112.67	2.38	29.39	1.89	7.86	1.24	1.88
6	12/15/10	-73.16, -114.99	2	126.74	5.28	17.98	1.27	--	--	9.72
6	12/15/10	-73.16, -114.99	10	95.55	4.01	18.37	1.29	--	--	9.50
6	12/15/10	-73.16, -114.99	15	90.47	4.48	--	1.30	--	--	9.23
6	12/15/10	-73.16, -114.99	25	65.31	1.88	25.59	1.66	--	--	7.01
6	12/15/10	-73.16, -114.99	40	64.11	2.84	25.53	1.65	--	--	6.07
6	12/15/10	-73.16, -114.99	85	63.31	0.59	28.73	1.84	--	--	2.49
6	12/15/10	-73.16, -114.99	100	63.04	0.75	31.21	1.89	--	--	2.33
13	12/18/10	-73.57, -112.67	1	88.86	2.91	20.94	1.32	33.38	4.65	9.29
13	12/18/10	-73.57, -112.68	10	74.31	3.18	20.45	1.31	36.11	5.14	9.96
13	12/18/10	-73.57, -112.69	25	77.48	4.33	20.84	1.31	34.49	5.08	10.15
13	12/18/10	-73.57, -112.70	40	70.63	3.70	23.97	1.54	24.14	3.20	7.49
13	12/18/10	-73.57, -112.71	50	70.21	3.27	27.53	1.76	--	--	6.22
13	12/18/10	-73.57, -112.72	75	69.09	2.12	29.29	1.83	8.26	0.00	2.84
13	12/18/10	-73.57, -112.73	100	68.16	2.21	29.40	1.88	6.64	1.21	2.30
18	12/21/10	-73.00, -113.30	2	86.42	2.31	15.42	1.07	--	--	11.39
18	12/21/10	-73.00, -113.31	10	79.10	2.77	17.54	1.17	--	--	15.90
18	12/21/10	-73.00, -113.32	20	103.31	2.50	19.58	1.29	--	--	11.32
18	12/21/10	-73.00, -113.33	35	82.55	0.72	--	1.63	--	--	4.17
18	12/21/10	-73.00, -113.34	50	65.49	0.60	26.43	1.65	--	--	4.67
18	12/21/10	-73.00, -113.35	75	67.30	0.99	28.19	1.77	--	--	4.17
18	12/21/10	-73.00, -113.36	100	68.62	0.94	30.67	1.89	--	--	3.80
25	12/22/10	-73.12, -112.00	1	90.13	4.03	14.02	0.97	202.80	10.01	12.18
25	12/22/10	-73.12, -112.01	18	84.58	2.67	19.78	1.32	127.86	6.32	9.57
25	12/22/10	-73.12, -112.02	28	57.87	2.11	23.42	1.55	133.32	7.41	8.50
25	12/22/10	-73.12, -112.03	50	82.10	1.70	26.33	1.75	74.39	4.02	4.02
25	12/22/10	-73.12, -112.04	80	53.51	0.43	29.95	1.94	39.11	2.62	0.47
25	12/22/10	-73.12, -112.05	100	53.60	0.48	30.06	1.93	0.63	0.05	0.21

Station	Date	Lat / Lon (º)	Depth (m)	DOC (µmol C / L)	DON (µmol N / L)	DIN (µmol N / L)	DIP (µmol P / L)	POC (mmol C / L)	PON (mmol N / L)	Chl a (µmol / L)
29	12/23/10	-73.35, -114.13	2	84.87	3.89	13.46	1.07	--	--	8.30
29	12/23/10	-73.35, -114.14	10	86.42	4.00	13.58	1.06	--	--	10.64
29	12/23/10	-73.35, -114.15	20	86.85	3.39	14.33	1.08	--	--	21.44
29	12/23/10	-73.35, -114.16	60	64.11	0.47	30.92	1.90	--	--	1.21
29	12/23/10	-73.35, -114.17	80	125.46	0.47	30.11	1.92	--	--	1.53
29	12/23/10	-73.35, -114.18	100	87.98	0.57	30.74	1.93	--	--	1.28
34	12/24/10	-72.96, -115.76	2	89.08	2.14	16.54	1.12	--	--	18.75
34	12/24/10	-72.96, -115.77	10	75.46	1.26	19.64	1.31	--	--	15.55
34	12/24/10	-72.96, -115.78	30	68.67	0.66	25.93	1.66	--	--	7.54
34	12/24/10	-72.96, -115.79	50	66.18	1.31	26.98	1.73	--	--	4.10
34	12/24/10	-72.96, -115.80	70	68.42	0.02	27.09	1.74	--	--	3.47
34	12/24/10	-72.96, -115.81	100	68.06	0.01	29.98	1.81	--	--	2.30
35	12/25/10	-73.29, -112.05	1	108.11	5.60	7.31	0.63	209.23	8.66	18.16
35	12/25/10	-73.29, -112.06	10	90.65	5.01	7.46	0.63	222.76	7.54	16.90
35	12/25/10	-73.29, -112.07	12	102.63	6.16	10.35	0.76	184.58	8.40	14.75
35	12/25/10	-73.29, -112.08	35	85.18	3.89	26.13	1.71	79.78	3.57	7.15
35	12/25/10	-73.29, -112.09	60	65.84	5.48	26.22	1.71	39.32	1.63	3.26
35	12/25/10	-73.29, -112.10	84	62.91	4.92	28.08	1.82	--	--	2.29
35	12/25/10	-73.29, -112.11	100	60.93	4.54	29.03	1.89	13.32	0.00	1.31
48	12/28/10	-73.70, -115.45	2	92.97	4.87	12.56	1.04	--	--	13.16
48	12/28/10	-73.70, -115.46	10	85.21	3.83	12.64	1.01	--	--	21.79
48	12/28/10	-73.70, -115.47	25	77.29	8.69	17.62	1.27	--	--	10.64
48	12/28/10	-73.70, -115.48	55	74.36	4.37	26.35	1.81	--	--	6.18
48	12/28/10	-73.70, -115.49	85	76.86	3.45	28.83	1.89	--	--	2.61
48	12/28/10	-73.70, -115.50	100	88.09	3.76	28.91	1.92	--	--	2.02
50	12/29/10	-73.42, -115.25	5	111.45	7.18	9.40	0.79	181.49	5.93	17.90
50	12/29/10	-73.42, -115.26	10	97.41	2.86	9.61	0.79	210.79	11.51	17.58
50	12/29/10	-73.42, -115.27	25	65.83	1.88	22.85	1.42	94.04	5.25	1.46
50	12/29/10	-73.42, -115.28	50	88.01	0.59	28.61	1.73	20.14	1.72	2.10
50	12/29/10	-73.42, -115.29	75	72.34	3.77	30.13	1.86	15.25	1.14	1.29
50	12/29/10	-73.42, -115.30	100	67.99	3.80	30.34	1.87	7.13	0.75	0.88

Station	Date	Lat / Lon (º)	Depth (m)	DOC (µmol C / L)	DON (µmol N / L)	DIN (µmol N / L)	DIP (µmol P / L)	POC (mmol C / L)	PON (mmol N / L)	Chl a (µmol / L)
57	1/2/11	-73.65, -113.22	1	75.76	1.19	20.82	1.37	81.93	4.61	7.49
57	1/2/11	-73.65, -113.23	9	72.94	2.71	20.84	1.40	--	--	7.83
57	1/2/11	-73.65, -113.24	30	68.23	3.06	20.94	1.41	83.48	4.79	6.91
57	1/2/11	-73.65, -113.25	60	60.87	0.81	24.88	1.61	45.98	2.50	7.07
57	1/2/11	-73.65, -113.26	100	71.23	1.18	31.84	2.10	59.55	2.91	0.77
66	1/5/11	-72.74, -116.02	2	122.90	4.59	13.97	1.02	177.79	8.34	9.18
66	1/5/11	-72.74, -116.03	10	82.09	1.04	18.26	1.26	124.48	6.16	11.32
66	1/5/11	-72.74, -116.04	25	80.30	0.60	26.70	1.73	69.89	3.59	4.80
66	1/5/11	-72.74, -116.05	40	77.91	1.64	28.01	1.79	33.73	1.30	2.14
66	1/5/11	-72.74, -116.06	60	74.79	1.58	28.74	2.07	23.55	1.38	0.02
66	1/5/11	-72.74, -116.07	100	68.41	1.46	30.24	1.99	3.20	0.32	0.36
68	1/8/11	-71.86, -118.28	2	66.83	1.39	24.45	1.39	--	--	1.07
68	1/8/11	-71.86, -118.29	10	74.24	0.85	24.54	1.38	--	--	1.14
68	1/8/11	-71.86, -118.30	25	79.52	0.76	26.42	1.65	--	--	1.23
68	1/8/11	-71.86, -118.31	40	74.53	3.33	28.06	1.77	--	--	1.02
68	1/8/11	-71.86, -118.32	60	83.58	4.57	29.18	1.94	--	--	0.47
68	1/8/11	-71.86, -118.33	100	72.30	2.84	29.37	1.91	--	--	0.20

Table S.2 (Station data and Microbial Abundances/Rates for ASPIRE)

Station	Depth (m)	ASP (Sample) #	Bact. Ab. (cells/mL) x 10^5	Viral Ab. (particles/mL) x 10^6	Flagellate Ab. (cells/mL)	BP (µg C/L/d)	BR (µg C/L/d)	BGE (%)	PP (µg C/L/d)
5	2	0126	2.79	1.97	267.78	0.424	25.056	1.7	13.43
5	10	0123	2.61	--	--	0.239	--	--	11.29
5	25	0121	2.49	1.01	--	0.197	--	--	19.48
5	50	0118	2.66	--	--	0.206	--	--	11.89
5	71	0116	2.95	2.22	127.03	0.180	--	--	3.21
5	101	0114	3.79	--	--	0.188	--	--	--
6	2	0184	2.56	4.91	388.28	2.238	16.272	12.1	105.19
6	10	0181	2.17	--	--	1.863	--	--	--
6	15	0179	2.73	5.69	--	2.342	--	--	54.14
6	25	0176	--	--	--	1.282	--	--	74.41
6	40	0175	2.46	--	--	1.619	--	--	46.06
6	85	0173	2.63	3.37	421.75	0.509	--	--	3.13
6	100	--	--	--	--	0.477	--	--	--
13	2	0375	2.95	4.95	241.0	3.239	13.248	19.7	81.68
13	10	0373	3.02	--	--	2.348	--	--	73.47
13	25	0372	3.75	--	--	3.682	--	--	54.42
13	40	0370	4.22	6.02	170.71	2.061	17.712	10.4	33.01
13	50	0366	--	--	--	--	--	--	--
13	75	0364	2.33	1.91	105.34	0.532	--	--	9.40
13	100	0362	--	--	--	0.434	--	--	--
18	2	0507	8.33	5.36	411.71	2.598	13.248	16.4	64.46
18	10	0504	3.61	--	--	1.705	--	--	--
18	20	0502	3.42	8.21	579.08	2.646	--	--	55.79
18	35	0499	5.51	--	--	0.489	--	--	20.73
18	50	0497	3.48	3.16	368.2	1.175	--	--	23.27
18	75	0495	3.19	--	--	0.758	--	--	16.21
18	100	0494	--	--	--	0.691	--	--	--
25	1	0595	7.95	1.16	391.08	3.183	26.640	10.7	27.53
25	18	0589	3.72	0.11	393.65	2.852	14.832	16.1	42.93
25	28	0596	3.84	--	--	1.584	--	--	34.63
25	50	0585	2.47	--	--	0.910	--	--	19.61
25	80	0583	2.03	0.15	130.36	0.146	--	--	10.86
25	100	0581	--	--	--	0.136	--	--	--

Station	Depth (m)	ASP (Sample) #	Bact. Ab. (cells/mL) x 10^5	Viral Ab. (particles/mL) x 10^6	Flagellate Ab. (cells/mL)	BP (µg C/L/d)	BR (µg C/L/d)	BGE (%)	PP (µg C/L/d)
29	2	0705	2.65	2.77	779.70	3.387	28.080	10.8	38.99
29	10	0702	2.09	--	--	2.856	--	--	67.21
29	20	0700	2.46	1.33	612.35	3.132	--	--	53.48
29	60	0697	1.97	--	--	0.508	--	--	20.38
29	80	0695	2.87	0.56	394.98	0.470	--	--	13.50
29	100	0693	--	--	--	0.447	--	--	--
34	2	0795	--	--	455.23	2.530	25.056	9.2	56.51
34	10	0791	2.87	2.72	497.42	2.453	--	--	107.82
34	30	0788	2.31	--	--	1.660	--	--	56.71
34	50	0786	2.18	1.03	328.03	1.137	--	--	27.93
34	70	0784	2.93	--	--	1.013	--	--	17.83
34	100	--	--	--	--	0.699	--	--	--
35	2	0882	5.04	5.48	937.24	2.416	26.640	8.3	36.86
35	10	0879	4.90	5.49	659.41	2.749	17.712	13.4	63.11
35	30	0874	3.94	--	--	2.290	--	--	54.47
35	50	0873	2.84	--	--	2.416	--	--	20.06
35	70	0872	--	--	--	1.455	--	--	--
35	100	--	--	--	--	0.837	--	--	--
48	2	1056	3.88	4.15	649.37	2.456	30.960	7.4	10.78
48	10	1053	5.01	--	--	3.455	--	--	34.55
48	25	1051	4.47	6.34	644.35	2.688	--	--	35.94
48	55	1048	3.94	--	--	1.553	--	--	19.14
48	85	1047	3.09	--	--	0.985	--	--	7.84
48	100	--	--	--	--	0.954	--	--	--
50	2	1138	3.88	3.08	920.5	3.998	28.08	12.5	34.49
50	10	1134	3.12	2.80	792.45	3.947	10.368	27.6	69.08
50	25	1131	2.76	--	--	2.572	--	--	47.84
50	50	1130	2.59	--	--	0.902	--	--	20.21
50	75	1129	2.61	--	--	0.533	--	--	10.37
50	100	1128	--	--	--	0.392	--	--	--

Station	Depth (m)	ASP (Sample) #	Bact. Ab. (cells/mL) x 10^5	Viral Ab. (particles/mL) x 10^6	Flagellate Ab. (cells/mL)	BP (µg C/L/d)	BR (µg C/L/d)	BGE (%)	PP (µg C/L/d)
57	1	1266	2.89	1.84	431.80	1.614	32.544	4.7	26.79
57	9	1261	4.48	2.40	512.13	1.838	--	--	42.83
57	30	1258	7.80	--	--	1.907	--	--	40.60
57	60	1257	5.97	--	--	1.249	--	--	19.21
57	100	1256	5.25	--	--	0.159	--	--	20.83
66	2	1409	7.07	6.85	1104.6	3.649	53.136	6.4	25.12
66	10	1406	4.07	5.67	1101.25	3.322	29.520	10.1	39.05
66	25	1402	4.42	--	--	2.432	--	--	38.76
66	40	1401	2.50	--	--	1.603	--	--	24.85
66	60	1400	1.79	--	--	0.037	--	--	13.56
66	100	1398	3.48	1.50	162.64	0.485	--	--	22.34
68	2	1469	5.13	1.67	284.73	1.527	17.712	7.9	19.06
68	10	1466	20.05	--	281.17	1.126	--	--	28.03
68	25	1464	16.50	1.76	--	0.953	--	--	21.09
68	40	1461	26.10	--	--	0.439	--	--	20.96
68	60	1460	34.20	--	--	0.232	--	--	13.80
68	100	1459	39.80	--	--	0.113	--	--	22.23

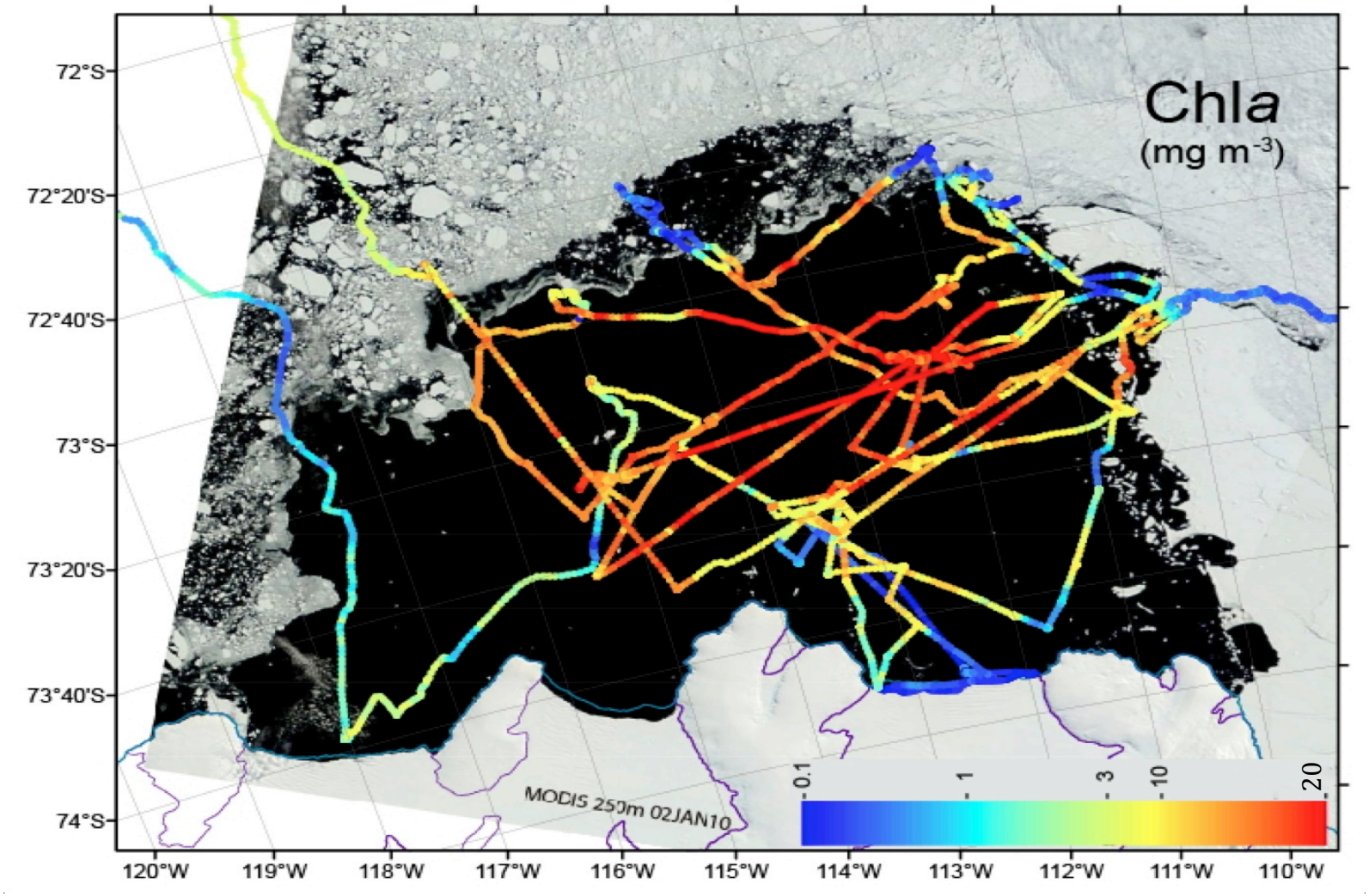

Figure S.1 (ASPIRE Cruise Track with Underway Chla data; modified from Yager et al. 2012)

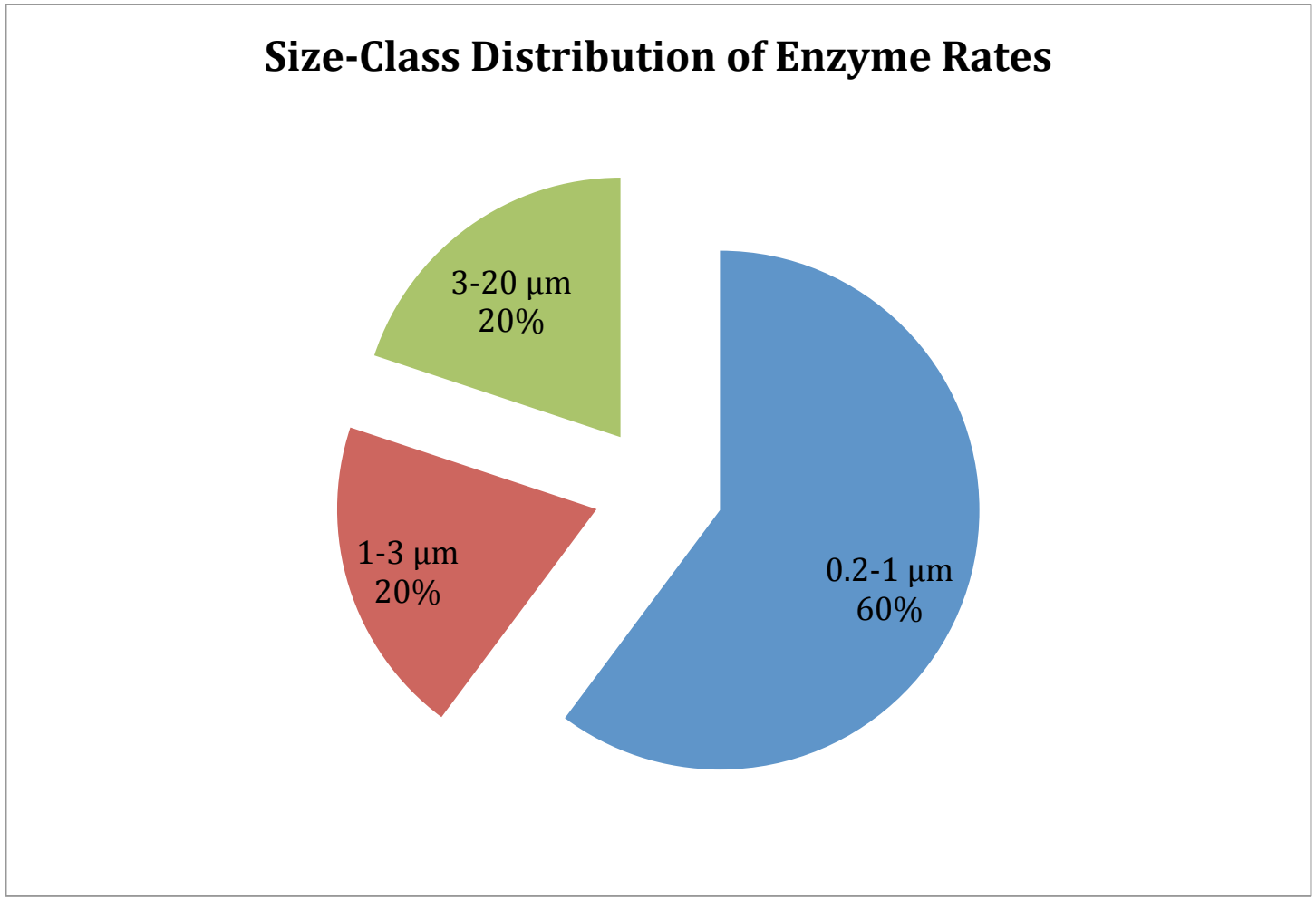

Figure S.2 (Size Class Distribution of MCA-L Enzyme Rates)

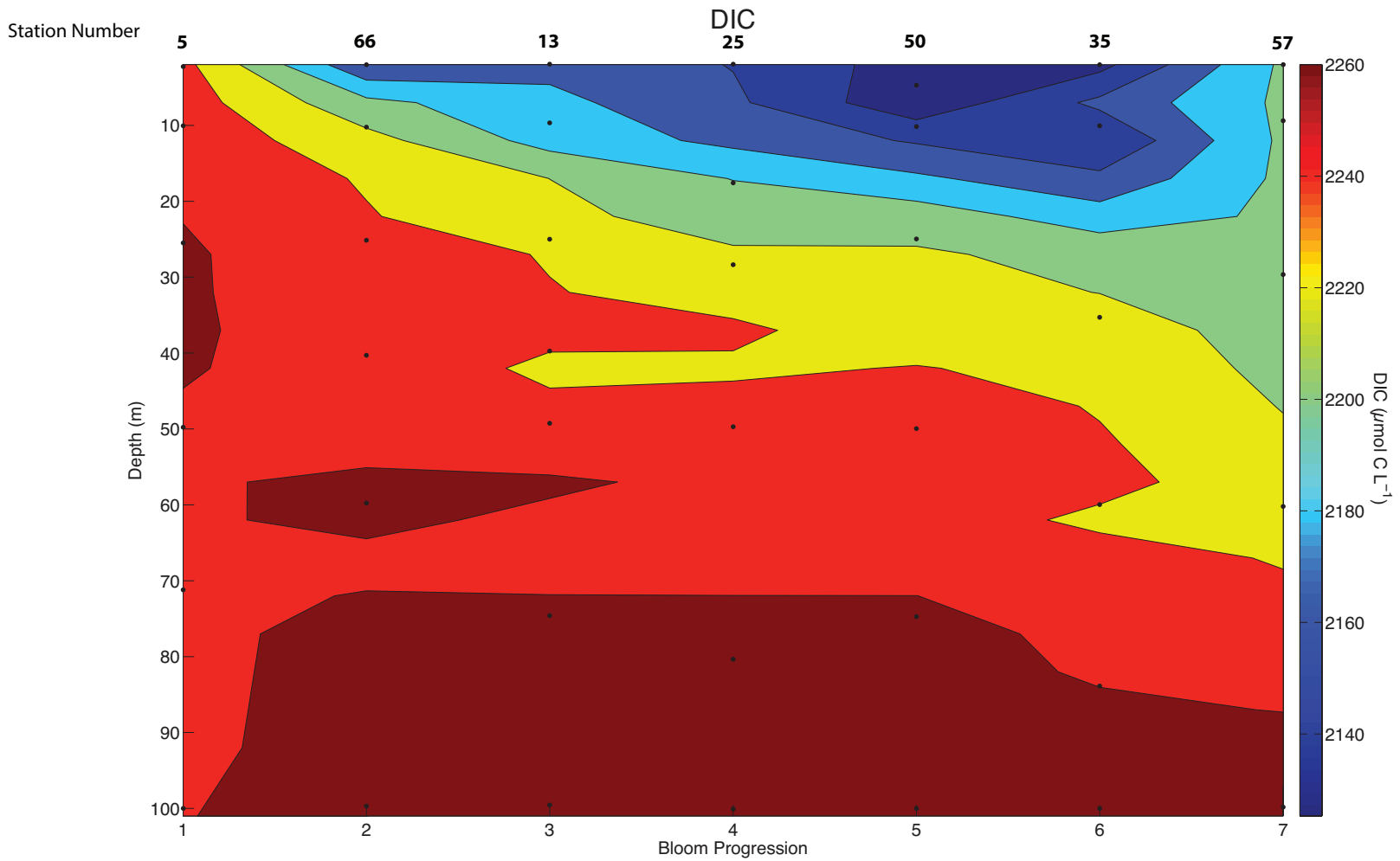

Figure S.3: (DIC within the ASP arranged by bloom progression)

References

Alderkamp, A.C., G. Kulk, A.G.J. Buma, R.J.W. Visser, G.L. van Dijken, M.M. Mills, and K.R. Arrigo (2012), The effect of iron limitation on the photophysiology of *Phaeocystis antarctica* (Prymnesiophyceae) and *Fragilariopsis cylindrus* (Bacillariophyceae) under dynamic irradiance. *J. Phycol.* 48: 45-59. doi: 10.1111/j.1529-8817.2011.01098.

Alonso-Sáez, L., J.M. Gasol, J. Aristegui, J.C. Vilas, D. Vaqué, C.M. Duarte, and S. Agusti (2007), Large-scale variability in surface bacterial carbon demand and growth efficiency in the subtropical northeast Atlantic Ocean. *Limnol and Oceanogr.* 52.2: 533-546.

Arrigo, K.R., D.H. Robinson, D.L. Worthen, R.B. Dunbar, G.R. DiTullio, M. VanWoert, and M.P. Lizotte (1999), Phytoplankton Community Structure and the Drawdown of Nutrients and CO_2 in the Southern Ocean. *Science*. 283: 365-367. doi: 10.1126/science.283.5400.365

Arrigo, K.R., and G.L. van Dijken (2003), Phytoplankton dynamics within 37 Antarctic coastal polynya systems. *Journal of Geophysical Research*. 108.C8.

Arrigo, K.R., G.L. van Dijken, and S. Bushinsky (2008), Primary Production in the Southern Ocean. *J. Geophys. Res.* 113: C08004,doi: 10.1029/2007JC004551

Arrigo, K.R., K.E. Lowry, and G.L. van Dijken (2012), Annual changes in sea ice and phytoplankton in polynyas of the Amundsen Sea, Antarctica. *Deep Sea Research Part II*. Vol. 71-76: 5-15.

Asper, V.L., and W.O. Smith Jr. (2012), Particle fluxes during austral spring and summer in the southern Ross Sea, Antarctica. *Journal of Geophysical Research*. 104: 5345-5359. doi: 10.1029/1998JC900067

Azam, F., J.G. Field, J.S. Gray, L.A. Meyer-Reil, and F. Thingstad (1983), The Ecological Role of Water-Column Microbes in the Sea. *Mar. Ecol. Prog. Ser.* 10: 257-263.

Azam, F., D.C. Smith, and J.T. Hollibaugh (1991), The role of the microbial loop in Antarctic pelagic ecosystems. *Polar Research.* 10(1): 239-244.

Azam, F. (1998), Microbial Control of Oceanic Carbon Flux: The Plot Thickens. *Science.* 280: 694-696.

Billen, G. (1984), Heterotrophic utilization and regeneration of nitrogen. In: Hobbie, J.E., LeB Williams, P.J. (Eds.), *Heterotrophic Activity in the Sea*. Plenum Press, New York, pp. 313–355.

Billen, G., and S. Becquevort (1990), Phytoplankton – bacteria relationship in the Antarctic marine ecosystem. *Polar Research.* 10(1): 245-253.

Bjørnsen, P.K., and J. Kuparinen (1991), Determination of bacterioplankton biomass, net production and growth efficiency in the Southern Ocean. *Mar. Ecol. Prog. Ser.* 71: 185-194.

Bowman, J.P., S.A. McCammon, M.V. Brown, D.S. Nichols, and T.A. McMeekin (1997), Diversity and Association of Psychrophilic Bacteria in Antarctic Sea Ice. *Applied and Environmental Microbiology.* 63(8): 3068-3078.

Boyce, D.G., M.R. Lewis, and B. Worm (2010), Global Phytoplankton Decline Over the Past Century. *Nature*. 466: 591-596. doi: 10.1038/nature09268

Brussaard, C.P.D., G. Bratbak, A.C. Baudoux, and P. Ruardij (2007), *Phaeocystis* and its interaction with viruses. *Biogeochemistry*. 83: 201-215.

Cai, W.J. (2011), Estuarine and Coastal Ocean Carbon Paradox: CO_2 Sinks or Sites of Terrestrial Carbon Incineration? *Annu. Rev. Mar. Sci.* 3: 123-145. doi: 10.1146/annurev-marine-120709-142723

Calbet, A., and M.R. Landry (2004), Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. *Limnol. Oceanogr.* 49(1): 51-57.

Carlson, C.A., H.W. Ducklow, D.A. Hansell, and W.O. Smith Jr. (1998), Organic carbon partitioning during spring phytoplankton blooms in the Ross Sea polynya and the Sargasso Sea. *Limnol. Oceanogr.* 43(3): 375-386.

Carlson, C.A., N.R. Bates, H.W. Ducklow, and D.A. Hansell (1999), Estimation of bacterial respiration and growth efficiency in the Ross Sea, Antarctica. *Aquat Microb Ecol.* 19: 229-244.

Carlson, C.A., D.A. Hansell, E.T. Peltzer, and W.O. Smith Jr. (2000), Stocks and dynamics of dissolved and particulate organic matter in the southern Ross Sea, Antarctica. *DSR II.* 47: 3201-3225.

Caron, D.A., E.L. Lim, R.W. Sanders, M.R. Dennett, and U.G. Berninger (2000), Responses of bacterioplankton and phytoplankton to organic carbon and inorganic nutrient additions in contrasting oceanic ecosystems. *Aquat. Microb. Ecol.* 22: 175-184.

Church, M.J., E.F. DeLong, H.W. Ducklow, M.B. Karner, C.M. Preston, D.M. Karl (2003), Abundance and distribution of planktonic *Archaea* and *Bacteria* in the waters west of the Antarctic Peninsula. *Limnol. Oceanogr.* 48(5): 1893-1902.

Cloern, J.E. (1999), The Relative Importance of Light and Nutrient Limitation of Phytoplankton Growth: A Simple Index of Coastal Ecosystem Sensitivity to Nutrient Enrichment. *Aquatic Ecology*. 33: 3-16. doi: 10.1023/A:1009952125558

Cole, J.J., S. Findlay, and M.L. Pace (1988), Bacterial production in fresh and saltwater ecosystems: a cross-system overview. *Mar Ecol Prog Ser*. 43: 1-10.

Cooley, S.R., and P.L. Yager (2006), Physical and biological contributions to the western tropical North Atlantic Ocean carbon sink formed by the Amazon River plume. *Journal of Geophysical Research.* 111: C08018. doi: 10.1029/2005JC002954

Cullen, J.J. (1991), Hypotheses to Explain High-Nutrient Conditions in the Open Sea. *Limnol. Oceanogr.* 36(8): 1578-1599.

del Giorgio, P.A., J.J. Cole, and A. Cimbleris (1997), Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. *Nature.* 385: 148-151.

del Giorgio, P.A., and J.J. Cole (1998), Bacterial growth efficiency in natural aquatic systems. *Annual Review of Ecology and Systematics.* 29: 503-541.

del Giorgio, P.A., and C.M. Duarte (2002), Respiration in the open ocean. *Nature*. 420: 379-384.

del Giorgio, P.A., and J. Davis (2003), Patterns in dissolved organic matter lability and consumption across aquatic ecosystems. *Aquatic ecosystems: Interactivity of dissolved organic matter.* Edited by: S.E.G. Findlay, and R.L. Sinsabaugh. pp. 399-424. Academic Press.

Deming, J.W. (2002), Psychrophiles and polar regions. *Current Opinion in Microbiology.* 5: 301-309.

Dickson, A.G., C.L. Sabine, and J.R. Christian (2007), Guide to best practices for ocean CO_2 measurements. Sidney, British Columbia, North Pacific Marine Science Organization, 176pp. (PICES Special Publication, 3)

DiTullio, G.R., and W.O. Smith (1996), Spatial patterns in phytoplankton biomass and pigment distributions in the Ross Sea. *J. Geophys. Res.* 101: 18467-18477.

Dolan, J.R., E.J. Yang, S.H. Lee, and S.Y. Kim (2013), Tintinnid ciliates of Amundsen Sea (Antarctica) plankton communities. *Polar Research.* 32: 19784.

Dubnick, A., J. Barker, M. Sharp, J. Wadham, L. Grzegorz, J. Telling, S. Fitzsimons and M. Jackson (2010), Characterization of dissolved organic matter (DOM) from glacial environments using total fluorescence spectroscopy and parallel factor analysis. *Annals of Glaciology* 51(56): 111-122.

Ducklow, H.W., D.L. Kirchman, and H.L. Quinby (1992), Bacterioplankton cell growth and macromolecular synthesis in seawater cultures during the North Atlantic Spring Phytoplankton Bloom, May 1989. *Microbial Ecology*. 24(2): 125-144. doi: 10.1007/BF00174450

Ducklow, H.W. (1995), Ocean biogeochemical fluxes: New production and export of organic matter from the upper ocean. *Rev. Geophys.* 33: 1271-1276.

Ducklow, H.W., C.A. Carlson, and W. Smith (1999), Bacterial growth in experimental plankton assemblages and seawater cultures from the *Phaeocystis antarctica* bloom in the Ross Sea, Antarctica. *Aquat Microb Ecol.* 19: 215-227.

Ducklow, H.W., M.L. Dickson, D.L. Kirchman, G. Steward, J. Orchardo, J. Marra, and F. Azam (2000), Constraining bacterial production, conversion efficiency and respiration in the Ross Sea, Antarctica, January-February, 1997. *Deep Sea Research II*. 47: 3227-3247.

Ducklow, H.W., C. Carlson, M. Church, D. Kirchman, D. Smith, and G. Steward (2001), The seasonal development of the bacterioplankton bloom in the Ross Sea, Antarctica, 1994-1997. *Deep Sea Research Part II.* 48: Issues 19-20: 4199-4221.

Ducklow, H.W., D.L. Kirchman, and T.R. Anderson (2002), The magnitude of spring bacterial production in the North Atlantic Ocean. *Limnol. Oceanogr.* 47(6): 1684-1693.

Ducklow, H.W., and P.L. Yager (2007), Polynyas: Windows to the World, Ch. 10: Pelagic Bacterial Processes in Polynyas. *Elsevier Oceanography Series*. pp 323-361.

Ducklow, H.W., K. Baker, D.G. Martinson, L.B. Quetin, R.M. Ross, R.C. Smith, S.E. Stammerjohn, M. Vernet, and W. Fraser (2007), Marine pelagic ecosystems: the West Antarctic Peninsula. *Phil. Trans. R. Soc. B.* 362: 67-94 doi:10.1098/rstb.2006.1955

Ducklow, H.W. (2008), Bacterial Production and Biomass in the Oceans. *Microbial Ecology of the Oceans*. 2nd ed. Edited by D.L. Kirchman. Ch. 5, pp. 1-47. Wiley Press, New York, NY. ISBN: 978-0-470-04344-8

Ducklow, H.W., W.R. Fraser, M.P. Meredith, S.E. Stammerjohn, S.C. Doney, D.G. Martinson, S.F. Sailey, O.M. Schofield, D.K. Steinberg, H.J. Venables, and C.D. Amsler (2013), West Antarctic Peninsula: An Ice-Dependent Coastal Marine Ecosystem in Transition. *Oceanography* 26(3): 190-203. doi: , http://dx.doi.org/10.5670/oceanog.2013.62.

Dunbar, R.B., A.R. Leventer, and D.A. Mucciarone (1998), Water column sediment fluxes in the Ross Sea, Antarctica: Atmospheric and sea ice forcing. *Journal of Geophysical Research.* 103(C13): 30,741-30,759.

Falkowski, P.G. (1997), Evolution of the nitrogen cycle and its influence on the biological sequestration of CO_2 in the ocean. *Nature*. 387: 272-275.

Falkowski, P.G., R.J. Scholes, E. Boyle, J. Canadell, D. Canfield, J. Elser, N. Gruber, K. Hibbard, P. Högberg, S. Linder, F.T. Mackenzie, B. Moore III, T. Pedersen, Y. Rosenthal, S. Seitzinger, V. Smetacek, and W. Steffen (2000), The Global Carbon Cycle: A Test of Our Knowledge of Earth as a System. *Science.* 290: 291-296.

Feller, G., and C. Gerday (2003), Psychrophilic enzymes: Hot topics in cold adaptation. *Nature Reviews: Microbiology.* 1: 200-208. doi:10.1038/nrmicro773

Fenchel, T. (2008), The microbial loop – 25 years later. *Journal of Experimental Marine Biology and Ecology.* 366: 99-103.

Feng, X., J.E. Vonk, B.E. van Dongen, O. Gustafsson, I.P. Semiletov, O.V. Dudarev, Z. Wang, D.B. Montluçon, L. Wacker, and T.I. Eglinton (2013), Differential mobilization of terrestrial carbon pools in Eurasian Arctic river basins. *PNAS.* 110(35): 14,168-14,173.

Field, C.B., M.J. Behrenfeld, J.T. Randerson, and P. Falkowski (1998), Primary production of the biosphere: Integrating terrestrial and oceanic components. *Science.* 281: 237-240.

Fransson, A., M. Chierici, P.L. Yager, and W.O. Smith Jr. (2011), Antarctic sea ice carbon dioxide system and controls. *Journal of Geophysical Research.* 116: C12035. doi: 10.1029/2010JC006844,

Fuhrman, J.A., and F. Azam (1980), Bacterioplankton secondary production estimates for coastal waters of British Columbia, Antarctica, and California. *Applied Environmental Microbiology.* 39: 1085-1095.

Fuhrman, J.A. (1992), Bacterioplankton Roles in Cycling of Organic Matter: The Microbial Food Web. *Primary Productivity and Biogeochemical Cycles in the Sea.*vol. 43, edited by: P.G. Falkowski, A.D. Woodhead, and K. Vivirito, pp 361-383, Springer US, doi: 10.1007/978-1-4899-0762-2_20

Fuhrman, J.A. (1999), Marine viruses and their biogeochemical and ecological effects. *Nature*. 399: 541-548. doi: 10.1038/21119

Fuhrman, J.A., I. Hewson, M.S. Schwalbach, J.A. Steele, M.V. Brown, and S. Naeem (2006), Annually reoccurring bacterial communities are predictable from ocean conditions. *PNAS*. 103(35): 13104-13109. doi: 10.1073/pnas.0602399103

Garzio, L.M., D.K. Steinberg, M. Erickson, and H.W. Ducklow (2013), Microzooplankton grazing along the Western Antarctic Peninsula. *Aquat. Microb. Ecol.* 70: 215-232. doi: 10.3354/ame01655

Glibert, P.M., and D.A. Bronk (1994), Release of Dissolved Organic Nitrogen by Marine Diazotrophic Cyanobacteria, *Trichodesmium spp. Applied and Environmental Microbiology.* 60(11): 3996-4000.

Gobler, C.J., D.A. Hutchins, N.S. Fisher, E.M. Cosper, and S.A. Sañudo-Wilhelmy (1997), Release and bioavailability of C, N, P, Se, and Fe following viral lysis of a marine chrysophyte. *Limnol. Oceanogr.* 42(7): 1492-1504.

González, J.M., J.S. Covert, W.B. Whitman, J.R. Henriksen, F. Mayer, B. Scharf, R. Schmitt, A. Buchan, J.A. Fuhrman, R.P. Kiene, and M.A. Moran (2003), *Silicibacter pomeroyi* sp. nov. and *Roseovarius nubinhibens* sp. nov., dimethylsulfoniopropionate – demethylating bacteria from marine environments. *International Journal of Systematic and Evolutionary Microbiology.* 53: 1261-1269. doi: 10.1099/ijs.0.02491-0

Hansell, D.A., and C.A. Carlson (1998), Net community production of dissolved organic carbon. *Global Biogeochemical Cycles.* 12(3): 443-453.

Hedges, J.I., and J.H. Stern (1984), Carbon and Nitrogen Determinations of Carbonate Containing Solids. *Limnol. Oceanogr.* 29: 657-663.

Henley, S.F., A.L. Annett, R.S. Ganeshram, D.S. Carson, K. Weston, X. Crosta, A. Tait, J. Douglas, A.E. Fallick, and A. Clarke (2012), Factors influencing the stable carbon isotopic composition of suspended and sinking organic matter in the coastal Antarctic sea ice environment. *Biogeosciences.* 9: 1137-1157. doi: 10.5194/bg-9-1137-2012

Herndl, G.J., T. Reinthaler, E. Teira, H. van Aken, C. Veth, A. Pernthaler, and J. Pernthaler (2005), Contribution of *Archaea* to Total Prokaryotic Production in the Deep Atlantic Ocean. *Applied and Environmental Microbiology.* 71(5): 2303-2309. doi: 10.1128/AEM.71.5.2303-2309.2005

Holm-Hansen, O. (1985), Nutrient Cycles in Antarctic Marine Ecosystems. *Antarctic Nutrient Cycles and Food Webs*. Edited by: W.R. Siegfried, P.R. Condy, and R.M. Laws. pp 6-10, Springer-Verlag Berlin Heidelberg GmbH. doi: 10.1007/978-3-642-82275-9

Hong, Y., and W.O. Smith Jr. (1997), Studies on Transport Exopolymer Particles (TEP) Prodced in the Ross Sea (Antarctica) and by *Phaeocystis antarctica* (Prymnesiophyceae). *J. of Phycology.* 33(3): 368-376.

Howard, E.C., J.R. Henriksen, A. Buchan, C.R. Reisch, H. Bürgmann, R. Welsh, W. Ye, J.M. González, K. Mace, S.B. Joye, R.P. Kiene, W.B. Whitman, and M.A. Moran (2006), Bacterial Taxa That Limit Sulfur Flux from the Ocean. *Science*. 314: 649-652. doi: 10.1126/science.1130657

Huston, A.L., and J.W. Deming (2002), Relationships between Microbial Extracellular Enzymatic Activity and Suspended and Sinking Particulate Organic Matter: Seasonal Transformations in the North Water. *Deep Sea Research Part II*. 49(22-23): 5211-5225.

Irigoien, I., K.J. Flynn, and R.P. Harris (2005), Phytoplankton blooms: a 'loophole' in microzooplankton grazing impact? *Journal of Plankton Research*. 27(4): 313-321. doi: 10.1093/plankt/fbi011

Johnson, K.M., K.D. Wills, D.B. Butler, W.K. Johnson, and C.S. Wong (1993), Coulometric total carbon dioxide analysis for marine studies: Maximizing the performance of an automated gas extraction system and coulometric detector. *Mar. Chem.* 44: 167-187.

Jumars, P.A., D.L. Penry, J.A. Baross, M.J. Perry, and B.W. Frost (1989), Closing the microbial loop: dissolved carbon pathway to heterotrophic bacteria from incomplete digestion, digestion, and absorption in animals. *DSR I.* 36(4): 483-495.

Jumars, P.A., J.W. Deming, P.S. Hill, L. Karp-Boss, P.L. Yager, and W.B. Dade (1993), Physical Constraints on Marine Osmotrophy in an Optimal Foraging Context. *Marine Microbial Food Webs.* 7(2): 121-159.

Karl, D.M., J.R. Christian, and J.E. Dore (1996), Microbiological oceanography in the region west of the Antarctic Peninsula: Microbial dynamics, Nitrogen cycle, and Carbon flux. *Antarctic Research Series*. AGU. 70: 303-332.

Karl, D.M., J.R. Christian, J.E. Dore, D.V. Hebel, R.M. Letelier, L.M. Tupas, and C.D. Winn (1996), Seasonal and interannual variability in primary production and particle flux at station ALOHA. *Deep-Sea Research.* 43: 539-568.

Karl, D.M., D.V. Hebel, K. Björkman, and R.M. Letelier (1998), The role of dissolved organic matter release in the productivity of the oligotrophic North Pacific Ocean. *Limnol. Oceanogr.* 43(6): 1270-1286.

Kennedy, F., A. McMinn, and A. Martin (2012), Effect of temperature on the photosynthetic efficiency and morphotype of *Phaeocystis antarctica. Experimental Marine Biology and Ecology.* 429: 7-14. doi:http://dx.doi.org/10.1016/j.jembe.2012.06.016

Kiene, R.P., L.J. Linn, J. González, M.A. Moran, and J.A. Bruton (1999), Dimethylsulfoniopropionate and Methanethiol Are Important Precursors of Methionine and Protein-Sulfur in Marine Bacterioplankton. *Applied and Environmental Microbiology.* 65(10): 4549-4558.

Kiene, R.P., and L.J. Linn (2000), Distribution and turnover of dissolved DMSP and its relationship with bacterial production and dimethylsulfide in the Gulf of Mexico. *Limnol. Oceanogr.* 45(4): 849-861.

Kiene, R.P., L.J. Linn, and J.A. Bruton (2000), New and important roles for DMSP in marine microbial communities. *J. Sea Res.* 43: 209-224.

Kim, J.G., S.J. Park, Z.X. Quan, M.Y. Jung, I.T. Cha, S.J. Kim, K.H. Kim, E.J. Yang, Y.N. Kim, S.H. Lee, and S.K. Rhee (2013), Unveiling abundance and distribution of planktonic *Bacteria* and *Archaea* in a polynya in Amundsen Sea, Antarctica. *Environmental Microbiology*. doi: 10.1111/1462-2920.12287

Kirchman, D.L., E. K'nees, and R. Hodson (1985), Leucine Incorporation and Its Potential as a Measure of Protein Synthesis by Bacteria in Natural Aquatic Systems. *Applied and Environmental Microbiology.* 49.3: 599-607.

Kirchman, D.L. (2001), Measuring Bacterial Biomass Production and Growth Rates from Leucine Incorporation in Natural Aquatic Environments. Chapter 12: *Methods in Microbiology*, vol. 30. Academic Press Ltd. 227-236.

Kirchman, D.L., X.A.G. Morán, and H. Ducklow (2009), Microbial growth in the polar oceans – role of temperature and potential impact of climate change. *Nature Reviews Microbiology*. 7: 451-459.

Knap, A., A. Michaels, A. Close, H.W. Ducklow, and A. Dickson (1996), Protocols for the Joint Global Ocean Flux Study (JGOFS) Core Measurements. *JGOFS Report No. 19*. Reprint of the IOC Manuals and Guides No. 29. UNESCO.

Lancelot, C., G. Billen, C. Veth, S. Becquevort, and S. Mathot (1991), Modeling carbon cycling through phytoplankton and microbes in the Scotia-Weddell Sea area during sea ice retreat. *Mar. Chem.* 35: 305-324.

Landry, M.R. and R.P. Hassett (1982), Estimating the Grazing Impact of Marine Micro-zooplankton. *Marine Biology.* 67: 283-288.

Landry, M.R. and A. Calbet (2004), Microzooplankton production in the oceans. *ICES Journal of Marine Science.* 61: 501-507. doi: 10.1016/j.icesjms.2004.03.011

Larsson, U., and Å. Hagström (1982), Fractionated Phytoplankton Primary Production, Exudate Release and Bacterial Production in a Baltic Eutrophication Gradient. *Marine Biology.* 67: 57-70.

Laws, E.A., and T.T. Bannister (1980), Nutrient and Light-Limited Growth of *Thalassiosira fluviatilis* in continuous culture, with implications for phytoplankton growth in the ocean. *Limnol. Oceanogr.* 25(3): 457-473.

Leakey, R.J.G., S.D. Archer, and J. Grey (1996), Microbial dynamics in coastal waters of East Antarctica: bacterial production and nanoflagellate bacterivory. *Mar. Ecol. Prog. Ser.* 142: 3-17.

Liss, P.S., G. Malin, S.M. Turner, and P.M. Holligan (1994), Dimethylsulphide and *Phaeocystis*: a review. *J. Mar. Syst.* 5: 1-4.

Long, R.A., and F. Azam (2001), Antagonistic Interactions among Marine Pelagic Bacteria. *Applied and Environmental Microbiology.* 67(11): 4975-4983. doi: 10.1128/AEM.67.11.4975–4983.2001

Luecker, T.J., A.G. Dickson, and C.D. Keeling (2000), Ocean pCO_2 Calculated from Dissolved Inorganic Carbon, Alkalinity, and Equations for K_1 and K_2: Validation Based on Laboratory Measurements of CO_2 in Gas and Seawater at Equilibrium. *Marine Chemistry.* 70: 105-119.

Malmstrom, R.R., M.T. Cottrell, H. Elifantz, and D.L. Kirchman (2005), Biomass Production and Assimilation of Dissolved Organic Matter by SAR11 Bacteria in the Northwest Atlantic Ocean. *Applied and Environmental Microbiology.* 71(6): 2979-2986. doi: 10.1128/AEM.71.6.2979-2986.2005

Marie, D., F. Partensky, S. Jacquet, and D. Vaulot (1997), Enumeration and cell cycle analysis of natural populations of marine picoplankton by flow cytometry using the nucleic acid stain SYBR Green I. *Applied and Environmental Microbiology.* 63.1: 186-193.

Martin, J.H., S.E. Fitzwater, and R.M. Gordon (1990), Iron deficiency limits phytoplankton growth in Antarctic waters. *Global Biogeochemical Cycles.* 4(1): 5-12. doi: 10.1029/GB004i001p00005

Martinez, J., D.C. Smith, G.F. Steward, and F. Azam (1996), Variability in ectohydrolytic enzyme activities of pelagic marine bacteria and its significance for substrate processing in the sea. *Aquat. Microb. Ecol.* 10: 223-230.

McDonnell, A.M.P., and K.O. Buesseler (2010), Variability in the average sinking velocity of marine particles. *Limnol. Oceanogr.* 55(5): 2085-2096. doi: 10.4319/lo.2010.55.5.2085

Middelboe, M., N.O.G. Jørgensen, and N. Kroer (1996), Effects of Viruses on Nutrient Turnover and Growth Efficiency of Noninfected Marine Bacterioplankton. *Applied and Environmental Microbiology.* 62.6: 1991-1997.

Middelboe, M., and P.G. Lyck (2002), Regeneration of dissolved organic matter by viral lysis in marine microbial communities. *Aquat. Microb. Ecol.* 27: 187-194.

Middelboe, M., L. Riemann, G.F. Steward, V. Hansen, O. Nybroe (2003), Virus-induced transfer of organic carbon between marine bacteria in a model community. *Aquat. Microb. Ecol.* 33: 1-10.

Middelboe, M., and N.O.G. Jørgensen (2006), Viral lysis of bacteria: an important source of dissolved amino acids and cell wall compounds. *J. Mar. Biol. Ass. U.K.* 86: 605-612.

Monier, A., R.M. Welsh, C. Gentemann, G. Weinstock, E. Sodergren, E.V. Armbrust, J.A. Eisen, and A.Z. Worden (2011), Phosphate transporters in marine phytoplankton and their viruses: cross-domain commonalities in viral-host gene exchanges. *Environmental Microbiology.* 14(1): 162-176. doi:10.1111/j.1462-2920.2011.02576.x.

Montes-Hugo, M., S.C. Doney, H.W. Ducklow, W. Fraser, D. Martinson, S.E. Stammerjohn, O. Schofield (2009), Recent Changes in Phytoplankton Communities Associated with Rapid Regional Climate Change Along the Western Antarctic Peninsula. *Science*. 323:5920 : 1470-1473

Moore, C.M., M.M. Mills, K.R. Arrigo, I. Berman-Frank, L. Bopp, P.W. Boyd, E.D. Galbraith, R.J. Geider, C. Guieu, S.L. Jaccard, T.D. Jickells, J. LaRoche, T.M. Lenton, N.M. Mahowald, E. Marañón, I. Marinov, J.K. Moore, T. Nakatsuka, A. Oschlies, M.A. Saito, T.F. Thingstad, A. Tsuda, and O. Ulloa (2013), Processes and Patterns of Oceanic Nutrient Limitation. *Nature Geoscience.* 6: 701-710. doi:10.1038/ngeo1765

Morris, R.M., M.S. Rappé, S.A. Connon, K.L. Vergin, W.A. Slebold, C.A. Carlson, and S.J. Giovannoni. SAR11 clade dominates ocean surface bacterioplankton communities. *Nature.* 420: 806-810.

Mou, X., S. Sun, R.A. Edwards, R.E. Hodson, and M.A. Moran (2008), Bacterial carbon processing by generalist species in the coastal ocean. *Nature.* 451: 708-713. doi: 10.1038/nature06513

Myklestad, S.M. (2000), Dissolved Organic Carbon from Phytoplankton. *The Handbook of Environmental Chemistry.* Vol. 5, Part D: Marine Chemistry. edited by P. Wangersky. Chapter 5: pp 112-148. Springer – Verlag Berlin Heidelberg.

Nitsche, F.O., Jacobs, S., Larter, R.D. and Gohl, K., 2007 Bathymetry of the Amundsen Sea Continental Shelf: Implications for Geology, Oceanography, and Glaciology. *Geochemistry, Geophysics, Geosystems*,8: Q10009, doi:10.1029/2007GC001694.

Ortega-Retuerta, E., F. Joux, W.H. Jeffrey, and J.F. Ghiglione (2013), Spatial variability of particle-attached and free-living bacterial diversity in surface waters from the Mackenzie River to the Beaufort Sea (Canadian Arctic). *Biogeosciences.* 10: 2747-2759. doi: 10.5194/bg-10-2747-2013

Payet, J.P., and C.A. Suttle (2008), Physical and biological correlates of virus dynamics in the southern Beaufort Sea and Amundsen Gulf. *J. Mar. Syst.* 74: 933-945.

Philosof, A., N. Battchikova, E.M. Aro, and O. Béjá (2011), Marine cyanophages: tinkering with the electron transport chain. *The ISME Journal.* 5(10): 1568-1570. doi: 10.1038/ismej.2011.43

Pomeroy, L.R. (1974), The Ocean's Food Web, A Changing Paradigm. *Bioscience.* 24: 499-504.

Pomeroy, L.R., and W.J. Wiebe (2001), Temperature and substrates as interactive limiting factors for marine heterotrophic bacteria. *Aquat. Microb. Ecol.* 23: 187-204.

Pomeroy, L.R., P.J. Williams, F. Azam, and J.E. Hobbie (2007), The Microbial Loop. *Oceanography*. 20(2): 28-33.

Porter, K.G., and Y.S. Feig (1980), The use of DAPI for identification and enumeration of bacteria and blue-green algae. *Limnol Oceanogr*. 25: 943-948.

Prézelin, B.B., E.E. Hofmann, C. Mengelt, and J.M. Klinck (2000), The Linkage between Upper Circumpolar Deep Water (UCDW) and Phytoplankton Assemblages on the West Antarctic Peninsula Continental Shelf. *Journal of Marine Research.* 58: 165-202. doi: http://dx.doi.org/10.1357/002224000321511133

Raimbault, P., N. Garcia, and F. Cerutti (2008), Distribution of Inorganic and Organic Nutrients in the South Pacific Ocean – Evidence for Long-Term Accumulation of Organic Matter in Nitrogen-Depleted Waters. *Biogeosciences.* 5: 281-298.

Redfield, A.C., B.H. Ketchum, and F.A. Richards (1963), The Influence of Organisms on the Composition of Sea-water. *The Sea*, vol. 2, edited by: M.N. Hill, pp. 26-77, Interscience, New York, NY.

Riemann, L., G.F. Steward, and F. Azam (2000), Dynamics of Bacterial Community Composition and Activity during a Mesocosm Diatom Bloom. *Applied and Environmental Microbiology.* 66(2): 578-587. doi: 10.1128/AEM.66.2.578-587.2000

Rivkin, R.B., and L. Legendre (2001), Biogenic Carbon Cycling in the Upper Ocean: Effects of Microbial Respiration. *Science.* 291: 2398-2400.

Robinson, C., S.D. Archer, and P.J. le B. Williams (1999), Microbial dynamics in coastal waters of East Antarctica: plankton production and respiration. *Mar. Ecol. Prog. Ser.* 180: 23-36.

Rohwer, F., and R.V. Thurber (2009), Viruses manipulate the marine environment. *Nature.* 459: 207-212. doi: 10.1038/nature08060

Rose, J.M., and D.A. Caron (2007), Does low temperature constrain the growth rates of heterotrophic protists? Evidence and implications for algal blooms in cold waters. *Limnol Oceanogr.* 52.2: 886-895.

Rich, J., M. Gosselin, E. Sherr, B. Sherr, and D.L. Kirchman (1997), High bacterial production, uptake and concentrations of dissolved organic matter in the Central Arctic Ocean. *Deep Sea Research Part II.* 44: 1645-1663.

Ruiz-González, C., M. Galí, J.M. Gasol, and R. Simó (2012), Sunglight effects on the DMSP-sulfur and leucine assimilation activities of polar heterotrophic bacterioplankton. *Biogeochemistry.* 110: 57-74.

Schoemann, V., S. Becquevort, J. Stefels, V. Rousseau, and C. Lancelot (2005), *Phaeocystis* blooms in the global ocean and their controlling mechanisms: a review. *Journal of Sea Research.* 53: 43-66. doi: 10.1016/j.seares.2004.01.008

Schofield, O., H.W. Ducklow, D.G. Martinson, M.P. Meredith, M.A. Moline, and W.R. Fraser (2010), How Do Polar Marine Ecosystems Respond to Rapid Climate Change? *Science*. 328:5985 : 1520-1523

Sheik, A.R., C.P.D. Brussard, G. Lavik, P. Lam, N. Musat, A. Krupke, S. Littmann, M. Strous, and M.M.M. Kuypers (2013), Responses of the coastal bacterial community to viral infection of the algae *Phaeocystis globosa. The ISME Journal.* 8: 212-225. doi: 10.1038/ismej.2013.135

Sherr, E.B., and B.F. Sherr (2002), Significance of predation by protists in aquatic microbial food webs. *Antoine van Leeuwenhoek*. 81: 293-308.

Sherr, E.B., and B.F. Sherr (2007), Heterotrophic dinoflagellates: a significant component of microzooplankton biomass and major grazers of diatoms in the sea. *Mar. Ecol. Prog. Ser.* 352: 187-197. doi: 10.3354/meps07161

Shields, A.R., and W.O. Smith Jr. (2009), Size-fractionated photosynthesis/irradiance relationships during *Phaeocystis antarctica*- dominated blooms in the Ross Sea, Antarctica. *J. Plankton Res.* 31(7): 701-712. doi: 10.1093/plankt/fbp022

Simon, M., and F. Azam (1989), Protein content and protein synthesis rates of planktonic marine bacteria. *Mar. Ecol. Prog. Ser.* 51: 201-213.

Simon, M. (1991), Isotope dilution of intracellular amino acids as a tracer of carbon and nitrogen sources of marine planktonic bacteria. *Mar. Ecol. Prog. Ser.* 74: 295-301.

Smith, D.C. and F. Azam (1992), A Simple, Economical Method for Measuring Bacterial Protein Synthesis Rates in Seawater Using ^{3}H-leucine. *Marine Microbial Food Webs.* 6(2): 107-114.

Smith, D.C., M. Simon, A.L. Alldredge, and F. Azam (1992), Intense hydrolytic enzyme activity on marine aggregates and implications for rapid particle dissolution. *Nature.* 359: 139-142.

Smith, V.H., G.D. Tilman, and J.C. Nekola (1999), Eutrophication: Impacts of Excess Nutrient Inputs on Freshwater, Marine, and Terrestrial Ecosystems. *Environmental Pollution.* 100: 179-196.

Smith Jr., W.O., A.R. Shields, J.C. Dreyer, J.A. Peloquin, and V. Asper (2011), Interannual variability in vertical export in the Ross Sea: Magnitude, composition, and environmental correlates. *Deep Sea Research Part I.* 58(2): 147-159.

Smith Jr., W.O., and L.I. Gordon (2012), Hyperproductivity of the Ross Sea (Antarctica) polynya during austral spring. *Geophysical Research Letters.* 24(3): 233-236. doi: 10.1029/96GL03926

Smith Jr., W.O., S. Tozzi, M.C. Long, P.N. Sedwick, J.A. Peloquin, R.B. Dunbar, D.A. Hutchins, Z. Kolber, and G.R. DiTullio (2013), Spatial and temporal variations in variable fluorescence in the Ross Sea (Antarctica): Oceanographic correlates and bloom dynamics. *Deep Sea Research Part I.* 79: 141-155.

Stammerjohn, S.E., D.G. Martinson, R.C. Smith, and R.A. Iannuzzi (2008), Sea ice in the western Antarctic Peninsula region: Spatio-temporal variability from ecological and climate change perspectives. *Deep Sea Research Part II*. 55(18-19): 2041-2058. doi: http://dx.doi.org/10.1016/j.dsr2.2008.04.026

Stefels, J., and M.A. van Leeuwe (1998), Effects of iron and light stress on the biochemical composition of Antarctic *Phaeocystis sp.* (Prymnesiophyceae). I. Intracellular DMSP concentrations. *J. Phycol.* 34: 486-495.

Steinberg, D.K., C.A. Carlson, N.R. Bates, S.A. Goldthwait, L.P. Madin, and A.F. Michaels (2000), Zooplankton vertical migration and the active transport of dissolved organic and inorganic carbon in the Sargasso Sea. *Deep Sea Research I*. 47: 137-158.

Steinberg, D.K., C.A. Carlson, N.R. Bates, R.J. Johnson, A.F. Michaels, and A.H. Knap (2001), Overview of the US JGOFS Vermuda Atlantic Time-series Study (BATS): a decade-scale look at ocean biology and biogeochemistry. *Deep Sea Research II.* 48: 1405-1447.

Steinberg, D.K., N.B. Nelson, C.A. Carlson, and A.C. Prusak (2004), Production of Chromophoric Dissolved Organic Matter (CDOM) in the Opean Ocean by Zooplankton and the Colonial Cyanobacterium *Trichodesmium* spp. *Mar. Ecol. Prog. Ser.* 267: 45-56.

Steinberg, D.K., B.A.S. Van Mooy, K.O. Buesseler, P.W. Boyd, T. Kobari, and D.M. Karl (2008), Bacterial vs. zooplankton control of sinking particle flux in the ocean's twilight zone. *Limnol. Oceanogr.* 53(4): 1327-1338.

Stuart, R.K., C.L. Dupont, D.A. Johnson, I.T. Paulsen, and B. Palenik (2009), Coastal Strains of Marine *Synechococcus* Species Exhibit Increased Tolerance to Copper Shock and a Distinctive Trancriptional Response Relative to Those of Open-Ocean Strains. *Applied Environmental Microbiology.* 75(15): 5047-5057. doi: 10.1128/AEM.00271-09

Suttle, C.A., and F. Chen (1992), Mechanisms and Rates of Decay of Marine Viruses in Seawater. *Applied and Environmental Microbiology.* 58(11): 3721-3729.

Suttle, C.A. (2007), Marine viruses – major players in the global ecosystem. *Nature Reviews: Microbiology.* 5: 801-812. doi: 10.1038/nrmicro1750

Swanson, M.M., B. Reavy, K.S. Makarova, P.J. Cock, D.W. Hopkins, L. Torrance, E.V. Koonin, and M. Taliansky (2012), Novel Bacteriophages Containing a Genome of Another Bacteriophage within Their Genomes. *PLoS One.* 7(7): 1-12. doi: 10.1371/journal.pone.0040683

Sweeny, C., W.O. Smith Jr., B. Hales, R.R. Bidigare, C.A. Carlson, L.A. Codispoti, L.I. Gordon, D.A. Hansell, F.J. Millero, M.O. Park, and T. Takahashi (2000), Nutrient and carbon removal ratios and fluxes in the Ross Sea, Antarctica. *Deep Sea Research: Part II.* 47(15-16): 3395-3421

Tagliabue, A., and K.R. Arrigo (2003), Anomalously low zooplankton abundance in the Ross Sea: An alternative explanation. *Limnol Oceanogr.* 48.2: 686-699.

Tang, K.W., H.H. Jakobsen, and A.W. Visser (2001), *Phaeocystis globosa* (Prymnesiophycae) and the planktonic food web: Feeding, growth, and trophic interactions among grazers. *Limnol. Oceanogr.* 46(8): 1860-1870.

Teeling, H., B.M. Fuchs, D. Becher, C. Klockow, A. Gardebrecht, C.M. Bennke, M. Kassabgy, S. Huang, A.J. Mann, J. Waldmann, M. Weber, A. Klindworth, A. Otto, J. Lange, J. Bernhardt, C. Reinsch, M. Hecker, J. Peplies, F.D. Bockelmann, U. Callies, G. Gerdts, A. Wichels, K.H. Wiltshire, F.O. Glöckner, T. Schweder, and R. Amann (2012), Substrate-Controlled Succession of Marine Bacterioplankton Populations Induced by a Phytoplankton Bloom. *Science.* 336: 608-611.

Thompson, G.A., V.A. Alder, D. Boltovskoy, and F. Brandini (1999), Abundance and biogeography of tintinnids (Ciliophora) and associated microzooplankton in the Southwesters Atlantic Ocean. *Journal of Olankton Research.* 21(7): 1265-1298.

Thurman, E.M. (1985), Organic Geochemistry of Natural Waters. Martinus Nijhoff/Dr. W. Junk Publishers, Dordrecht.

Trull, T.W., S.G. Bray, S.J. Manganini, S. Honjo, and R. François (2001), Moored sediment trap measurements of carbon export in the Subantarctic and Polar Frontal Zones of the Southern Ocean, south of Australia. *Journal of Geophysical Research.* 106(C12): 31,489-31,509.

Turner, J.T. (2002), Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. *Aquat. Microb. Ecol.* 27: 57-102.

Turner, J.T. (2004), The Importance of Small Planktonic Copepods an Their Roles in Pelagic Marine Food Webs. *Zoological Studies.* 43(2): 255-266.

Tynan, C.T. (1998), Ecological Importance of the Southern Boundary of the Antarctic Circumpolar Current. *Nature*. 392: 708-710.

Valliéres, C., L. Retamal, P. Ramlal, C.L. Osburn, and W.F. Vincent (2008), Bacterial production and microbial food web structure in a large arctic river and the coastal Arctic Ocean. *J. Mar. Syst.* 74: 756-773. doi: :10.1016/j.jmarsys.2007.12.002

Vance, T.R., A.T. Davidson, P.G. Thomson, M. Levasseur, M. Lizotte, M.A.J. Curran, and G.B. Jones (2013), Rapid DMSP production by and Antarctic phytoplankton community exposed to natural surface irradiances in late spring. *Aquat. Microb. Ecol.* 71: 117-129. doi:10.3354/ame01670

Veit-Köhler, G., K. Guilini, O. Sachs, E.J. Sauter, and L. Würzberg (2011), Antarctic deep-sea meiofauna and bacteria react to the deposition of particulate organic matter after a phytoplankton bloom. *Deep Sea Research Part II.* 58(19-20): 1983-1995. doi: 10.1016/j.dsr2.2011.05.008

Volkman, J.K., and E. Tanoue (2002), Chemical and Biological Studies of Particulate Organic Matter in the Ocean. *Journal of Oceanography.* 58: 265-279.

Wiebe, W.J., W.M. Sheldon Jr., and L.R. Pomeroy (1992), Bacterial growth in the cold: evidence for an enhanced substrate requirement. *Applied Environmental Microbiology.* 58: 359-364.

Wiebe, W.J., W.M. Sheldon Jr., and L.R. Pomeroy (1993), Evidence for an enhanced substrate requirement by marine mesophilic bacterial isolates at minimal growth temperatures. *Microb. Ecol.* 25: 151-159.

Wilhelm, S.W., and C.A. Suttle (1999), Viruses and nutrient cycles in the sea. *Bioscience.* 49: 781-788.

Wright, S.W., S.W. Jeffrey, R.F.C. Mantoura, C.A. Llewellyn, T. Bjørnland, D. Repeta, and N. Welschmeyer (1991), Improved HPLC method for the analysis of chlorophylls and carotenoids from marine phytoplankton. *Mar. Ecol. Prog. Ser.* 77: 183-196.

Yager, P.L., T.L. Connelly, B. Mortazavi, K.E. Womack, N. Bano, J.E. Bauer, S. Opsahl, and J.T. Hollibaugh (2001), Dynamic bacterial and viral response to an algal bloom at sub-zero temperatures. *Limnol. Oceanogr.* 46: 790-801.

Yager, P.L., R.M. Sherrell, S.E. Stammerjohn, A.C. Alderkamp, O. Schofield, E.P. Abrahamsen, K.R. Arrigo, S. Bertilsson, D. Garay, R. Guerrero, K.E. Lowry, P.O. Mosknes, K. Ndungu, A.F. Post, E. Randall-Goodwin, L. Riemann, S. Severmann, S. Thatje, G.L. van Dijken, and S. Wilson (2012), ASPIRE: The Amundsen Sea Polynya International Research Expidition. *Oceanography.* 25(3): 40-53. doi: 10.5670/oceanog.2012.73

Yoch, D.C. (2002), Dimethylsulfoniopropionate: It's Sources, Role in the Marine Food Web, and Biological Degradation to Dimethylsulfide. *Applied and Environmental Microbiology*. 68(12): 5804-5815. doi: 10.1128/AEM.68.12.5804–5815.2002

Zehr, J.P., and R.M. Kudela (2011), Nitrogen Cycle of the Open Ocean: From Genes to Ecosystems. *Annu. Rev. Mar. Sci.* 3: 197-225. doi:10.1146/annurev-marine-120709-14