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Pelagic bacterial processes in polynyas

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ABSTRACT

Polynyas are considered model ecosystems for understanding high-latitude carbon cycling, especially with regards to climate-sensitivity of the biological pump. Explanations for highly efficient carbon export from polynyas and other marginal ice zones often focus on the balance of autotrophy and heterotrophy in these perennially cold ecosystems. The remineralization of algal production is controlled, at least in part, by the activities of pelagic heterotrophic bacteria. Here, we review these activities in both Arctic and Antarctic polynya ecosystems and include a discussion of commonly used methods. Recent research findings from the Northeast Water (NEW), North Water (NOW), and Ross Sea Polynya (RSP) programs are summarized and compared. Overall the pelagic bacteria of these ecosystems respond quickly to spring and summertime algal blooms, similar to their temperate counterparts. We find little evidence for growth rate limitation by low temperature, at least during the phytoplankton growing season. Despite sometimes significant rates of bacterivory and viral lysis, bacterial growth is fast enough for stocks to accumulate to levels similar to observed in temperate oceans. Despite apparent differences in DOM cycling and availability, Arctic and Antarctic polynya bacteria are more similar than dissimilar in their seasonal activities. High-latitude food web structure, leading bacteria to a focus on hydrolysis and solubilization of particulate matter may partly explain this finding. We speculate about the impacts of global warming on these ecosystems and envision a scenario in which hemispheric differences in polynya microbial ecology and biogeochemical function will be amplified.

1. INTRODUCTION.

One of the regions where global climate changes are expected to have the greatest impact is the high latitudes (Hansen et al. 1984, Cubasch et al. 2001). Both the Arctic as a whole,

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and the Antarctic Peninsula are experiencing the most rapid rates of regional warming on the planet (R. Smith et al. 1996, Shindell et al. 1999). Significant reductions have occurred during the past 30 years in both the areal extent (Johanessen et al. 1999, Parkinson and Cavalieri, 2002) and thickness (Yu et al., 2004) of arctic sea ice cover. High-latitude oceans are also unique and critical to the global carbon cycle for several reasons, including strongly seasonal, short-term but high rates of biological productivity and the formation of deep water (Sarmiento and Toggweiler 1984). The geochemical models outlined in these papers show how the "efficiency of the biological pump" (which depends inversely on the extent of remineralization) in high-latitude seas significantly determines the degree to which carbon is sequestered in the global deep sea, therefore influencing the long-term atmospheric CO_2 concentration.

Coastal polar ecosystems are among the most productive in the world, with spatial and temporal heterogeneity as common characteristics. Seasonally ice-covered regions such as marginal ice zones (Treguer and Jacques 1992) and polynyas are sites where the strong influences of light, nutrients, and temperature merge to create short-term but dramatic blooms which can occur rapidly (Sullivan et al. 1988, W. Smith and Gordon 1997). In an environment characterized by strong localized pulses of primary production, the response of microorganisms within the euphotic zone may determine the rate of carbon, nitrogen, and phosphate remineralization and also the fraction of total production that is exported from that zone (Wiebe and Pomeroy 1991).

High latitude oceans account for approximately 10-20% of the global oceanic carbon production (Behrenfeld and Falkowski 1997) and 4-11% of the global carbon export to the deep (Laws et al., 2000). They are sites where the f-ratio (new/total production) or e-ratio (export/total production) is found to be quite high relative to temperate and tropical latitudes, this effect is thought to be due to the combination of low temperature and high production (Laws et al. 2000). While this outcome has often been attributed to the disabling of bacteria by low temperatures, we now know that high rates of bacterial growth can be observed in polar waters (Rivkin et al. 1996; Rich et al. 1997, Carlson et al. 1998) and that both bacterial and viral communities have been observed to respond dynamically to small increases in

Table 1.

Biological carbon pump efficiency and particle export in marginal ice zones (after Sarmiento et al. 2004).

	Northern Hemisphere (NH) Marginal Ice Zones	**Southern Hemisphere (SH) Marginal Ice Zones**
Biological Pump Efficiency	0.45-50 (low end for NH)	0.14 - 0.17 (lowest for SH)
Particle Export Rate	22 μmol C m-2 d-1 (highest)	3 – 5 μmol C m-2 d-1
Particle Export Ratio	0.4 (highest for NH)	0.3 (highest for SH)

Data pulled from figures in Sarmiento et al. (2004); NH includes data from the Northeast Water Polynya; SH includes data from the Ross, Weddell, and Bellinghausen Seas (J. Dunne, personal communication).

available substrate; i.e. they exhibit pulse-responsiveness to patchy resource supply (Yager and Deming 1999) and springtime algal blooms (Yager et al. 2001). Microbial communities in the polar oceans are therefore dynamic and appear not to be perpetually limited by temperature (Pomeroy and Wiebe 2001).

The explanation for high export ratios remains focused on the strongly seasonal and sometimes extremely high rates of biological production that occur at high latitudes. Interestingly, the efficiencies of the northern and southern high-latitude biological pumps (**Table 1**; defined as the effectiveness of reducing surface nutrients relative to subsurface values, Sarmiento et al., 2004) seem to differ significantly, with the northern marginal ice zones showing greater efficiencies, greater particle export, and somewhat higher particle export ratios, on average. The structure of high-latitude food webs and the role of cold-adapted bacteria may be a critical part of understanding what determines the different high export fractions. Significant insights to these processes have come from recent microbiological studies in Arctic and Antarctic polynyas, which we review here.

Polynyas are considered model environments for seasonally ice-covered continental shelves with potentially climate sensitive shelf-slope-basin interactions (NEWater Investigators 1993). The proposed biological pump for the Northeast Water Polynya (NEW) region (Cochran 1995, Bauerfeind et al. 1997, Daly et al. 1999), for example, identifies carbon shunts to both the local shelf benthos and the nearby slope and Greenland Sea basin. The timing of biological activity with respect to sea-ice coverage is quite important, however, in controlling the magnitude and direction of carbon flux in seasonally ice-covered oceans like a polynya (Yager et al. 1995, Miller et al. 2002). Biological and biogeochemical processes in polynyas are therefore coupled to climate through their dependence on sea ice distribution and timing.

The high-latitude pump efficiency most likely depends on the fate of the particulate organic matter produced. High particulate organic matter (POM) concentrations are associated with high primary production in the Antarctic, where there are no terrestrial POM inputs. The Arctic receives significant inputs of terrestrial organic matter (Opsahl et al. 1999, Benner et al. 2005), but most of the material is dissolved and the particulate material is mostly deposited in the delta or on the shelf (Macdonald et al. 1998). Thus, POM in the Arctic is also often strongly correlated to chlorophyll (e.g., Guo et al. 2004), even on the shelves (Hodges et al. in press). In contrast, DOM concentrations in the Arctic tend to be high (see Benner et al. 2005 and references therein), but do not correlate well with other bloom indices (Wheeler et al. 1997, Hodges et al., in press), perhaps because terrestrial inputs of DOM are so large, production mechanisms (e.g., Jumars et al. 1989) are slow, or bacterial uptake is rapid (e.g., Yager and Deming 1999). DOM appears not to accumulate beyond the seasonal scale in the Antarctic, and is not an important part of the export production (Carlson et al. 1998, 2000).

In addition to being an effective link between high-latitude pelagic and benthic food webs (Petersen and Curtis 1980), particles are an important source of organic matter to bacterioplankton in arctic seas during summertime production (Ritzrau 1997, Yager et al. 2001). Increased particle-associated bacterial activity, depletion of nitrogen in POM, and increased extracellular protease activity observed in the summertime NEW and North Water (NOW) polynyas suggest that particle-associated bacteria respond to POM (Vetter and

Deming 1994, Huston and Deming 2002). Particle-associated bacteria may therefore be responsible for observable changes in bacterial abundance and community structure during times of high particle production in summertime Arctic and Antarctic seas (Putt et al. 1994, Yager et al., 2001, Hodges et al., in press).

In coastal polar regions, where carbon export may not follow typical steady-state assumptions, the efficiency of the biological pump may also depend on the role of the microbial loop (Legendre and Fèvre 1995); i.e., whether microbes operate as a carbon link between dissolved organic matter (DOM) and higher trophic levels or simply respire the available organic carbon, returning primary production to the inorganic pool, and allowing little carbon transfer to higher trophic levels or direct export. The behavior of the microbial loop in high-latitude regions is of particular interest (Karl 1993, Pomeroy and Wiebe 1993) because sub-zero in situ temperatures may constrain some marine bacteria to utilizing organic matter only when it is available in high concentrations (Pomeroy and Deibel 1986, Pomeroy et al. 1990).

Seasonally ice-covered seas at high latitudes may be potential one-way sinks for atmospheric carbon, driven by a unique linkage between strongly seasonal biological productivity and sea-ice formation (Yager et al. 1995). This scenario is sensitive to climate change because of the predicted increase in the areal extent of these regions due to global warming (Ingram et al. 1989) and provides a negative feedback to increasing anthropogenic CO_2. The rectification scenario, however, also depends on low pelagic respiration rates during summer, which allow primary production to draw down inorganic carbon in the surface waters, and the exact phasing of biological activity and the cycle of sea ice formation and ablation (Carrillo et al. 2004). The scenario further assumes that biological activity would remain the same if high-latitude oceans warm. This is not a reasonable expectation since many of the marine biota in these regions have adapted to a narrow range in temperature and may show especially strong sensitivity to warming (Baross and Morita 1978). Warming of a few degrees would likely increase overall rates of activity, but the relative rates of increase in production, respiration, and hydrolytic activity, as well as any resulting changes in community structure, are largely unknown.

2. OVERVIEW: MICROBIAL FOOD WEBS IN POLAR SEAS.

2.1 Methods and terminology.

The methods and terminology used to describe microbial ecology may not be familiar to all readers so we provide a brief summary here. Interested readers can consult Kirchman (2000) for further details. The generic term “microbial” refers to any organism so small a microscope is needed to see it. In practical terms, most all plankton organisms except krill and the larger copepods are included in this grouping. Nonetheless the term is often used as a synonym for “bacteria”. Here we try to restrict its use to the more inclusive meaning that refers to the total plankton assemblage that can be caught in a Niskin bottle, including viruses, bacteria, phytoplankton, protozoan and microzooplankton grazers. “Bacteria” is incorrectly used as a catchall term (e.g., Ducklow 2001) for members of two of the three principal Domains of Life, the *Archaea* and the *Bacteria*. Both groups are very small (usually < 1 μm long in seawater), unicellular prokaryotes that look superficially alike but are distinct groups,

differing fundamentally at the most basic levels of genomic and molecular structure. Domain *Bacteria* includes both heterotrophic and autotrophic groups, and very likely mixotrophic organisms as well. The autotrophic bacteria are members of the cyanobacteria, but they are rare in cold waters and probably absent in any significant functional way from the Arctic and Antarctic marine ecosystems (Azam et al. 1991, Robineau et al. 1999). *Archaea* are genetically about as distant from *Bacteria* as each group is from *H. sapiens*. Both groups are well represented in Antarctic (Murray et al. 1999, Church et al. 2003) and Arctic (Bano and Hollibaugh 2002, Bano et al. 2004) seas. Before the recognition of the *Archaea* as a Domain by Woese and colleagues in the 1980s (Woese 1990) microbiologists considered "archaebacteria" as primitive true bacteria. Since they are indistinguishable under light microscopes, most reports of "bacterial" standing stocks still contain an unrecognized fraction of *Archaea*. Here, when we use the term bacteria without italics it should be understood that it may include members of both groups. Most *Archaea* (and even most *Bacteria*) still cannot be cultured in the lab; hence our understanding of their roles in nature is very limited, save for a few special groups like the Methanogens.

The standing stocks of "bacteria" are estimated using epifluorescence microscopy (Hobbie et al. 1977) or more recently, flow cytometry (Brown and Landry 2001). These methods utilize fluorochrome dyes that bind to nucleic acids in cells and enhance detection of particles with the same dimensions as the wavelength of visible light. There are generally 10^8 – 10^9 cells per liter in seawater, with higher numbers near the surface and much lower numbers below a few 100 meters. These methods do not by themselves distinguish individual bacterial species (or Domains) unless coupled with molecular probes specific for individual groups such as fluorescent *in situ* (meaning inside intact cells) hybridization or FISH (DeLong 1993). FISH investigation of bacterial community composition is just beginning and it is not yet well known if there are blooms of individual bacterial species mirroring diatom and other phytoplankton blooms.

Bacteria utilize organic matter but are not able to incorporate particles or dissolved molecular forms greater than about 500 Da directly. Water samples are incubated with individual, radioisotopically-labelled organic compounds like glucose or acetate or mixtures of compounds (e.g., amino acids; see discussion in Yager and Deming 1999) to determine uptake rates. When coupled with chemical analysis of the ambient concentrations, the turnover times can be calculated for these same compounds in the original sample. When multiple incubations are run with a range of substrate concentrations, uptake kinetic parameters (e.g., maximum specific utilization rates and specific affinity; Button 2004) can be assessed. These kinetic parameters give an indication of the capabilities of the microbial community (including permease abundance and properties), independent of potentially dynamic substrate concentrations. Unfortunately, there is a myriad of potentially usable compounds dissolved in seawater and the exact composition is still very poorly known. This makes very difficult the detection of the individual substances bacteria are really using at any given time. An alternative approach is to look instead at the bacterial production (BP) rate, which is the metabolic result of uptake of whatever substances were used over some previous time interval. Bacterial (secondary) production is the synthesis of biomass from preformed organic precursors, in contrast to primary production, at the expense of sunlight and inorganic nutrients. It is estimated most often from incorporation of ^{3}H-labelled thymidine or ^{3}H-

leucine, biosynthetic precursors of DNA and protein respectively (Ducklow 2000). The approach is based on the fundamental argument that actively growing cells are necessarily making protein and DNA, thus the rates of cell production can be extrapolated from these processes. In practice extrapolation is uncertain because the relationship between precursor incorporation, macromolecular synthesis and production varies as a largely unknown function of environmental conditions and physiological state of the cells. Bacterial production rates tend to mirror the distributions of bacterial stocks in space and time, and average 5-20% of the simultaneous rates of primary production (PP). Below, we review several extensive studies of bacterial stocks and production in Arctic and Antarctic polynyas.

An important concept linking bacterial utilization of organic substances or bacterial carbon demand (BCD) and bacterial production (BP) rates is the conversion or growth efficiency (BGE = BP/BCD) of the cells (del Giorgio and Cole 1998). Various metabolic costs and requirements impose a tax on utilization of resources such that the rate of biomass production is somewhat less than the original rate of uptake. The difference is the respiration, which can be measured independently but the techniques are painstaking and so respiration estimates are much less common than production estimates. For convenience, if not accuracy, the total consumption rates are often back-calculated from production estimates and some assumed value of the conversion efficiency. BGE averages 10-30% in most ocean systems. Thus, if BP/PP is ~10% and BGE 20%, bacteria are using an amount of carbon equivalent to about half the primary production (0.1/0.2 = 0.5). In other words, over some appropriate time and space scales trophodynamic processes in plankton food webs route about half the primary production through bacterial metabolism. The rest accumulates, sinks or is metabolized by animals. An alternative approach, if radioisotopically-labelled substrates are used to measure cell uptake, determines the fraction respired to CO_2 by capturing the $^{14}CO_2$ or $^{3}H_2O$ produced by the cells after incubation long enough to assume steady state. Adding this respiration component (R) together with the substrate incorporated into biomass (I) gives total utilization (U). Respiration efficiency (RE = R/U) or incorporation efficiency (IE = I/U) can then be calculated for a specific substrate or known mix of substrates (see for example Griffiths et al. 1978). Incorporation efficiencies measured in this way are usually higher than BGE, which is usually based on the incorporation of bulk DOM rather than a specific (and usually highly labile) model substrate. The effect of cold temperature on the partitioning of primary production through particulate and dissolved pools is a major research topic in polar microbiology (see below).

2.2 Food web structure and function.

Microbial food webs consist of autotrophic primary producers and protozoan grazers in addition to bacteria. Together these microscopic (<20 μm) plankton form food webs functionally and structurally analogous to, and integrated with, the food web of larger plankton (Miller 2004). Bacterioplankton are important in marine food webs and biogeochemical cycles because they are the principal agents of dissolved organic matter (DOM) utilization and oxidation in the sea (Ducklow 2001, Carlson 2002). All organisms liberate DOM through a variety of physiological processes, and additional DOM is released when zooplankton fecal pellets and other forms of organic detritus dissolve and decay (Nagata 2000). By recovering the released DOM, which would otherwise accumulate,

bacterioplankton initiate the *microbial loop*, a complicated suite of organisms and processes based on the flow of detrital-based energy through the food web. The flows of energy and materials through the microbial loop can rival or surpass those flows passing through traditional phytoplankton-grazer-based food webs. Bacteria also play a role in decomposition and mineralization of particulate matter through production of extracellular hydrolytic enzymes (DC Smith et al. 1992, Christian and Karl 1995, Vetter et al. 1998). Although attached and particle-associated bacteria are usually much less abundant than free-living cells, they are important members of the plankton community during the terminal stages of blooms (Putt et al. 1994), in marine snow (Azam and Long 2001) and in the vertical flux of sinking particles (Karl et al. 1988). Marine planktonic *Archaea* are abundant but play as-yet unknown ecological roles in microbial food webs (Karner et al. 2001).

Whether or not the structure and functioning of microbial food webs in polar seas are the same as in lower latitudes remains controversial. After it was recognized that energy and material flows through plankton food webs in the temperate, tropical and even subpolar seas (Miller 1993) were often dominated by microbial processes, Antarctic food webs were thought to be the last bastion the "classic" diatom-krill-predator food chain. This idea was attractive because of the well-known high productivity at upper levels of Antarctic food webs (whales, seals, birds, etc) presumably sustained by short food chains of larger plankton (El-Sayed 1988, Azam et al. 1991). But even Antarctic coastal regions under the pervasive influence of sea ice were often found to be dominated by nanoplankton, <20 μm diatoms and microzooplankton grazers (Hewes 1985, Weber and El-Sayed 1987), leaving open the question of how long food webs built of nanoplankton, protozoans and bacteria could support the whales. The importance and role of bacteria in polar oceans remains a contentious issue.

A major question concerns not the roles but rather the controls and dynamics of bacterial growth in polar seas and how the total bacterial assemblage or individual groups are "coupled" to the ultimate source of their nutrition, primary production by phytoplankton. In a widely cited paper Cole et al. (1988) showed in an early synthesis of data from lakes and oceans that bacterial production (BP) and abundance were correlated with both primary production (PP) and chlorophyll, with a mean BP:PP ratio of about 30%. This global scale conclusion demonstrated the ultimate dependence of bacterioplankton on phytoplanktonic primary producers. 30% now appears to be too high a proportion of the PP, at least for habitats not receiving subsidies of allochthonous organic matter, with about 10% suggested as a more realistic value for the open sea (Ducklow 1999). Characteristic levels of BP:PP may be a fundamental distinction between the Arctic, which receives terrigenous inputs of organic matter (Hansell et al. 2004) and has high levels of BP:PP (Rich et al. 1997) and the Antarctic, which doesn't have either.

The coupling problem is complicated by lack of agreement on the meaning of the term coupling, which can be thought of as having two components: phase and intensity. Bacteria can be considered well- or tightly-coupled to phytoplankton if relevant properties (biomass, production) in various samples in a time series of measurements are correlated with phytoplankton (phasing) and if the bacterial production is a significant fraction of the primary production (intensity); or as Bird and Karl (1999) put it, "…it should be shown that bacterial community production is not just correlated with primary production, but is a substantial fraction of it…" In the RACER (Research on Coastal Antarctic Ecosystem Rates) Project

Karl and colleagues carried out intensive seasonal (summer, Dec. – March 1987; spring, Nov. 1989) investigations of microbial processes in the West Antarctic Peninsula and Drake Passage. During the spring bloom in the Gerlache Strait, bacteria were not correlated with chlorophyll levels, with no apparent response of increased abundance at Chl > 2.5 $\mu g\ l^{-1}$ (Bird and Karl 1999). Bacterial biomass was <2% of the total plankton biomass and BP was ~3% of the co-occurring primary production. They ascribed the lack of response to intense bacterivory by heterotrophic nanoplankton (HNAN) populations that suppressed the bacterial response as the phytoplankton bloomed, and kept BP:PP low (see below), i.e., to top-down control. Bird and Karl concluded that at least in their study area and during the spring bloom period, the microbial loop was uncoupled from primary producers, but they added that the uncoupling was not necessarily more widespread in space and time, and could be expressed more strongly in other seasons.

Moran et al. (2002) defined phytoplankton-bacterial coupling by focusing specifically on the release of recently synthesized DOC from active phytoplankton (14% of total PP). They showed that the released DOC met the metabolic requirement of bacteria in the Austral summer in the Bransfield Strait region of the West Antarctic Peninsula and concluded that bacteria and phytoplankton were strongly coupled. They also concluded that BP was a very low fraction (mean 1.5 ± 0.4%) of the total particulate plus dissolved production but termed the coupling "strong" nonetheless.

Judging the degree of coupling is complicated by lags in response of bacterial consumers to phytoplankton production. In the RACER summer study, bacterial abundance, glutamate and thymidine incorporation rates peaked in January following the phytoplankton peak in December, though a careful analysis of spatial statistics failed to reveal strong correlations between the bacterial and phytoplankton properties within either month (Bird and Karl 1991). A regression model incorporating lags showed that glutamate incorporation was best predicted by total plankton biomass and total phytoplankton pigment, indicating a direct flow of resources from the producers to microheterotroph consumers, expressed over a longer period than a single cruise. But Karl et al. explained the lack of direct coupling by concluding that either the glutamate and thymidine activity were due to phytoplankton uptake or that a large portion of the bacterial assemblage was inactive.

Polynyas often experience reduced ice cover or ice-free conditions earlier in the growing season, and under lower irradiance conditions than other marginal ice zone habitats. Therefore growth conditions for phytoplankton and bacterioplankton in these habitats may differ significantly from the surrounding marginal ice zones. The related issues of controls and coupling of plankton populations in polynyas are considered below.

2.3 Bacterial growth in cold water.

Polar microbiology dates almost from the beginning of modern marine microbiology. Levin (1899) reported almost no bacterial cells in water samples from Spitsbergen, but his methods were suspected to be faulty since he also failed to detect any microorganisms in bird feces. Ekelöf (1907) first noted the presence of viable bacteria in waters near Ross Island, Antarctica. More modern studies date from the early work of John Sieburth at McMurdo Station in the late 1950s (Sieburth 1963) and from the Soviet expeditions throughout the

world oceans in the 1960s (Kriss et al. 1967), before more intensive investigations flowered in the 1980s (Fuhrman and Azam 1980). The key factor facing polar bacteria is, of course, persistent cold temperature near the freezing point of seawater at –1.8ºC. Unlike in the temperate or tropical surface ocean, pulse-responsive bacteria in polar oceans must also be cold-adapted (i.e. able to respond quickly to a food source while living at sub-zero temperatures). Prevailing wisdom suggests that most organisms operate very slowly when they are cold. Yet, slow organisms, designed for a steady food supply, seem ill-suited for the dynamic polar environment. This apparent contradiction has been one of the underlying themes of recent research, directing the focus toward those organisms that seem to do best, by some measure, at low temperature. Psychrophilic (cold-loving) bacteria have been studied in the laboratory for decades and, while we do not review that literature here (see for example reviews by Russell 1990, Karl 1993 and references therein, especially earlier reviews of Baross and Morita (1978) and Morita (1966), there are indications that strategies for survival and definitions of optimality may be fundamentally different from those we consider standard in the temperate environment. The same case can be made for organisms living in especially low-nutrient environments, or oligotrophs (see reviews by Morgan and Dow 1986). These two types of "extreme" environments, and the constraints on organisms associated with them, probably come together in polar areas, much like they do in the deep sea (Deming 1986, who suggested a link between oligotrophy and barophily). While there are times in the polar spring and summer when phytoplankton bloom and dissolved organics may become readily available (either directly or via grazing), the most common condition in these permanently cold environments is probably low concentrations of organic nutrients. As a consequence, the most competitive organism might have a rapid response to high nutrient pulses, but overall a greater tendency for storage (Amy et al. 1983) and low endogenous metabolism (e.g., more active and/or efficient respiratory chain, lower energy of maintenance, and lower minimal growth rate; Morgan and Dow 1986). Transport systems that capture the ephemeral food supply must be constitutive, i.e., always ready (Koch 1979), but catabolic enzymes that utilize specific substrates should be sensitive to available substrate concentrations (Novitsky and Morita 1977, Harder and Dijkhuizen 1983). There also appear to be advantages in being a generalist (Button 1994).

The link between temperature and substrate concentration lies at the center of the polar microbial activity debate. At issue is whether bacteria in permanently cold (<5°C) waters respond differently to pulses of substrates than do bacteria in permanently or seasonally warm water. The initial results of Pomeroy and co-workers (Pomeroy and Deibel 1986, Pomeroy et al. 1990) suggested that the microbial community in northern seas require relatively high concentrations of organic matter at low temperatures. These greater food requirements might result in an under-utilization of primary production and thus provide a greater chance for carbon export (Pomeroy and Wiebe 1988). Yager and Deming (1999) examined temperature and substrate effects on bacterial utilization and incorporation efficiency, directly testing the Pomeroy hypothesis for its application in the NEW Polynya, and found that only some stations fit the Pomeroy prediction (see below). In their recent review, Pomeroy and Wiebe (2001) concluded, “inhibitory effects are not sufficient to alter overall ecosystem function.”

Bacteria in low-nutrient or pulsed-nutrient environments can increase their potential uptake of substrate in two ways: by increasing the number of binding proteins on the cell surface

(thereby increasing their maximum specific uptake rate, V_{max}), or by synthesizing a binding protein with a greater affinity for substrate (thereby lowering the half-saturation constant, K_m; Matin and Veldkamp 1978). ANT-300, a psychrophilic marine *Vibrio* from Antarctic waters, has at least two transport systems with different affinities for arginine (Geesey and Morita 1979). Some bacteria from low nutrient environments have more affine amino acid transport systems than their copiotrophic counterparts from nutrient-rich habitats (Ishida et al. 1982). Whether these organisms studied in lab culture are typical of the vast majority of non-cultured organisms is not yet known. New genomic studies linking gene sequences to gene expression in situ may answer this key question (Peck et al. 2005)

In an environment where the food supply is often scarce, it also makes sense for organisms to use the energy wisely. Deming and Yager (1992) suggested that polar deep-sea sediment bacteria show uniquely high incorporation efficiencies on certain organic substrates. The metabolic pathway of dissolved organic carbon taken up by heterotrophic bacteria can vary according to the quantity and type of compounds available. Griffiths *et al.* (1978) report respiration efficiencies for the Beaufort Sea that depend on substrate type, temperature, and also on the season. Growth efficiency in protozoa (e.g., bacteriovores) can depend on the physiological state of the cell (Fenchel and Finlay 1983) and increases with lower temperature in some psychrophilic organisms (Choi and Peters 1992), perhaps providing a means for surviving dark polar winters with low food availability (Levinson et al., 2000). The fate of bacterial carbon may therefore differ fundamentally in low temperature environments and be sensitive to warming. The adaptations of bacteria for utilization of naturally-occurring substrates in persistent cold are illustrated by the observation that semilabile DOC produced during phytoplankton blooms is entirely consumed within the growth season (Carlson et al. 1998) in contrast to subtropical habitats (Carlson et al. 2002).

Polynyas are ideal sites for studying bacterial processes in persistently cold water because they afford access to high-latitude, ice-free areas during periods when the surrounding ocean is ice-covered, and because they exhibit high productivity, making possible tests of the substrate-temperature relationship that governs bacterial growth in perpetually cold waters. Here we examine bacterial processes in the three best-studied polynya systems, the Ross Sea polynya (Antarctica) and the North and Northeast Water polynyas in the Arctic (Figure 1).

3. BACTERIAL PROCESSES IN THE ROSS SEA POLYNYA (RSP).

The Ross Sea polynya, the largest in the Antarctic at 400,000 km^2, is formed and maintained near the edge of the Ross Ice Shelf at 76-79ºS., 180ºW by sensible heat flux and katabatic winds blowing off the ice shelf and advecting the sea ice to the north. Remotely sensed ice images reveal an area of reduced to absent ice cover throughout the year (Gloersen et al. 1992). Early season access (October-November) to the southern Ross Sea was achieved in 1994 by the US Research Icebreaker Nathaniel B Palmer, allowing detailed studies of water column biogeochemistry, ecology and microbiology in the RSP (W. Smith and Gordon 1997, W. Smith et al. 2000b, Ducklow et al. 2001). There are no extensive, systematic observations of microbial processes in other principal Antarctic polynyas such as those in the Weddell Sea and Marguerite Bay. In contrast to other studies (e.g. RACER; Huntley et al. 1991), observations were carried out in the RSP above the Antarctic Circle over a wide range of

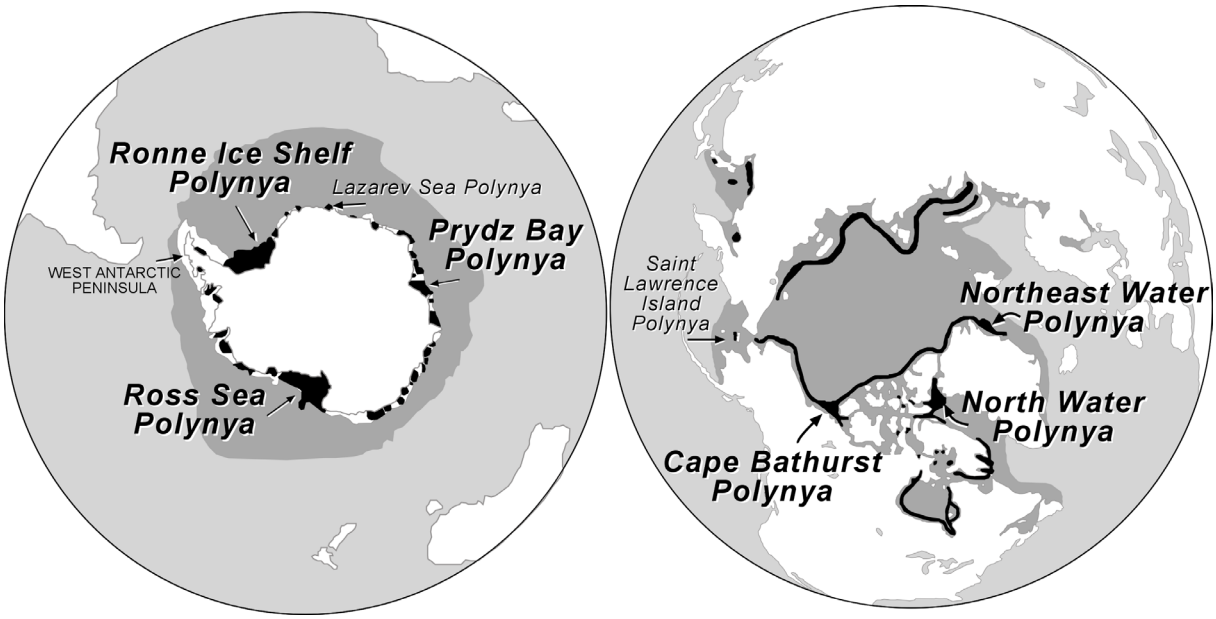

Figure 1. Polar projections of the southern (left) and northern (right) hemispheres showing the distribution of polynyas (in black). Typical wintertime sea ice coverage is also shown (dark gray). The Antarctic figure is based on Arrigo and van Dijken (2003) and the Arctic map is modified from an original figure prepared by Martin Fortier (available on the International Arctic Polynya Program website: http://www.aosb.org/IAPP.html) based on the distributions given in Smith and Rigby (1981).

irradiance and day length conditions and over a large segment of the annual cycle in a single year. Comprehensive studies of the plankton ecosystem in the RSP were carried out during the Ross Sea Polynya Project cruises in Nov-Dec 1994 and Dec. 1995 – Jan. 1996 (W. Smith and Gordon 1997, W. Smith et al. 1999); Research on Ocean-Atmosphere Variability and Ecosystem Response in the Ross Sea (ROAVERRS, 1996-98; (Arrigo et al. 1999)) and the US JGOFS Antarctic Environment and Southern Ocean Process Study (AESOPS, Oct. 1996 – Dec., 1997; (W. Smith et al. 2000a)). Much of the sampling in the latter two programs was carried out in the vicinity of the polynya along latitude 76º 30 South.

The most conspicuous and important feature of plankton ecology in the RSP is dominance of the phytoplankton bloom by the colonial haptophyte *Phaeocystis antarctica* (W. Smith et al. 2003), which exerts strong influence over the ecology and biogeochemistry of the region. In particular, the colonial morphology of *P. antarctica* may be an adaptation protecting the cells against grazing by micro- and macrozooplankton (W. Smith et al. 2003). Possibly as a consequence there is a paucity of krill in the central and southern Ross Sea (Atkinson et al. 2004). Zooplankton play an important role in releasing DOM from algal cells through sloppy feeding and their own metabolic processes (Nagata 2000, Carlson 2002); thus the presence or absence of *Phaeocystis* may indirectly influence bacterial stocks and dynamics by modulating the supply of grazer-induced DOM release.

The JGOFS program provided observations in the RSP during a single annual growth cycle, extending from 80-100% ice cover in October, 1996 through ice retreat in November and the *Phaeocystis* bloom to the end of the solar irradiated Austral daytime in April, 1997. The polynya was nearly 100% ice covered in October, 1996, with a physically homogeneous

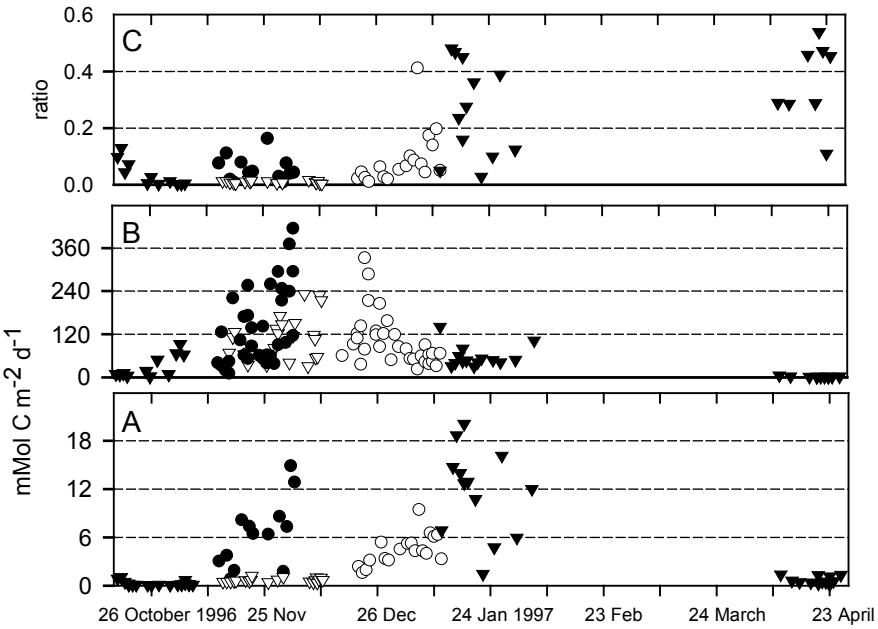

Figure 2. A: Bacteria in the upper 150 meters and B: primary production in the Ross Sea polynya in the 1996-97 Austral summer (closed triangles). C: ratio of 150 m bacterial production to primary production. Open symbols are cruises in 1994-95. Circle-dots are Nov. 1997.

(well-mixed, -1.85ºC) water column to ~ 100 m with 31 µMol NO_3 l^{-1} and low chlorophyll, indicating the bloom had not been initiated. Observations in Nov.-Dec. 1994 and 1996 show the physical oceanography of the water column was nearly the same. Ice cover still ~80% but it was thin, permitting an extensive under-ice bloom of *Phaeocystis* to commence. The extent of nitrate drawdown indicated the *Phaeocystis* bloom was also at the same stage although there was somewhat higher Chl *a* in 1994. Primary productivity was very high in both years, reaching to > 200 mmol C m^{-2} d^{-1} (W. Smith and Gordon 1997, W. Smith et al. 2000b) (Figure 2B). The bloom peaked in Dec. and was declining by January (W. Smith et al. 2000b) but showed the strongest nitrate depletion at that time. By late April, deep mixing had greatly diluted the remaining stock of phytoplankton in the water column and recharged the nitrate under conditions of intermittent ice formation. Primary production was very strongly light limited (PAR < 10 E m^{-2} d^{-1}) and was < 2 mmol C m^{-2} d^{-1} at that time (W. Smith et al. 2000b). In comparison to the diatom bloom in the Palmer LTER region of the marginal ice zone (not a polynya) offshore of the West Antarctic Peninsula (R. Smith et al. 1998a), the bloom in the RSP starts a month earlier, reaches higher levels of biomass and is dominated by *Phaeocystis*.

Bacterioplankton grew steadily and dramatically in the RSP between mid-October and mid-February (Figure 3). In October, prior to the *Phaeocystis* bloom, the bacterial cell abundance was low, about 1 x 10^8 cells $liter^{-1}$, equivalent to the lowest surface water levels observed in

the world oceans, while by February they reached 2 x 10^9 cells $liter^{-1}$ (Figure 3A), which is nearly the highest abundance observed in the open sea (Ducklow 1999). Thus the RSP

exhibits the full range of bacterioplankton variability observed in oceanic systems studied to

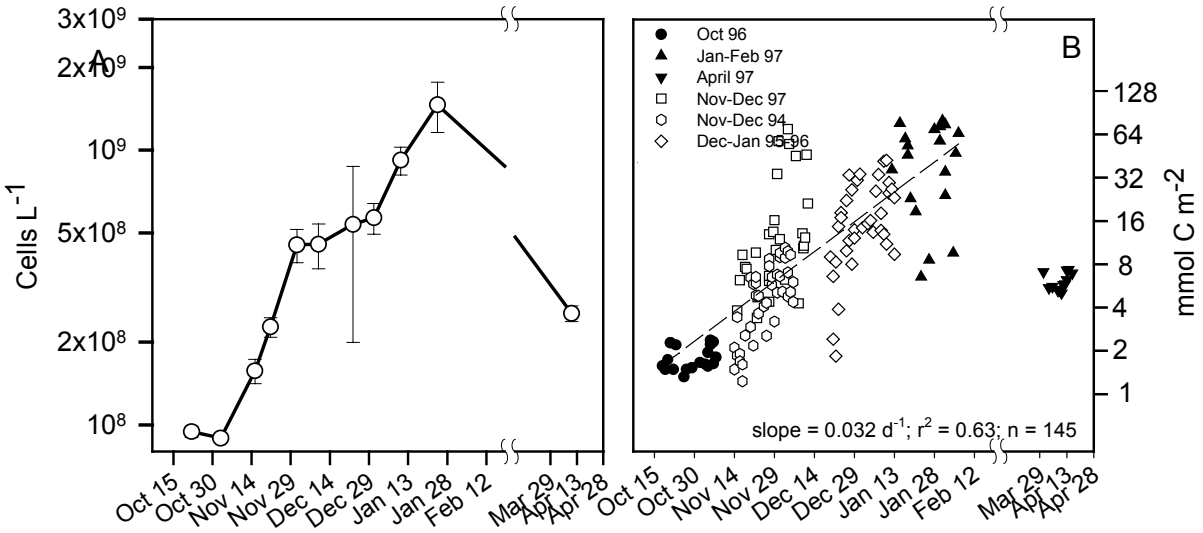

Figure 3. Growth of bacteria in the Ross Sea polynya. A: Abundance, averaged over the upper 50 m and over successive 10-day intervals. B: biomass over 0-50 meters. The regression line has a slope of 0.03 d-1 (r2 = 0.63, n = 145, not including the April cruise).

date. Bacterial biomass (some of which is probably *Archaeal*) ranges over two orders of magnitude, from 2 – 200 mmol C m^{-2} in the upper 50 m (Figure 3B), growing exponentially with a doubling time of about 20 d. This is the net rate of increase reflecting the slight excess of growth over removal by predation, adsorption on sinking particles, viral lysis and other processes. The mean intrinsic growth rate of the cells must be greater than the 0.03 d^{-1} net observed rate of increase of 0.03 d^{-1} suggested here (slope in Figure 3B). There is large spatial and interannual variability in the upper 100 m, but bacterial stocks were relatively uniform and constant between 100-200 m. By April, the bacterial abundance declines as a result of removal and deep mixing (Ducklow et al. 2001).

Bacterial production rates also increased dramatically, from 0.1 – 1 mmol C m^{-2} d^{-1} in October-November to over 10 mmol C m^{-2} d^{-1} in January (Ducklow et al. 2001). This bacterial production was equivalent to about 5-15% (mean 4%) of the simultaneous primary production (^{14}C estimates) in October-November, with substantial spatial and temporal variability (Figure 2A,C). The fraction then increased, at some stations, to 40-50% by January with a mean of 11%, as bacteria decomposed organic matter in the now declining *Phaeocystis* bloom, and as primary production rates declined from by a factor of 2-4 (W. Smith et al. 2000b). Specific growth rates derived from conservative bacterial production estimates (Ducklow et al. 1999, Ducklow et al. 2000) and abundance data (i.e., P/B ratios) were < 0.1 d^{-1} in October and increased to 0.25 – 0.5 d^{-1} in November-December 1994, but stayed < 0.25 d^{-1} in November-December, 1997. Rates up to 0.25 d^{-1}, suggesting potential doubling times of ~3 d, are common in the upper 50 m. These potential rates of increase were suppressed to a mean net rate of 0.03 d^{-1} by removal processes but still permitted doubling of the stock in ~20 days.

To understand further the bacterial role in the carbon cycle of the RSP, Carlson et al. (1999) conducted a series of incubation experiments in gas-tight plastic bags to monitor bacterial growth, DOC consumption and DIC production. In this way, complete carbon budgets were constructed for bacterial conversion of ambient DOC into biomass and respired CO_2, and conversion efficiencies (growth efficiencies, BGE) were evaluated. The BGE in the RSP had a mean value over the October - January period of 25% but it increased from 11% in October to 43% in late January. To some extent the increase in BGE offsets the lower BP:PP ratios (Figure 2C) observed early in the season. In October, when BGE was 11% and BP:PP averaged 0.04, the bacteria metabolized 0.04/0.11 or 36% of the contemporaneous primary production. In January, when BP:PP averaged 0.11 and BGE was 43%, the bacteria metabolized 26% of the primary production. In a closer analysis of the bacterial carbon budget Ducklow (2003) integrated the euphotic zone bacterial and primary production rates and followed the standing stock of DOC over two time intervals, Oct. 18 – Feb 02 and Feb 02 – April 28, which denoted the period of active phytoplankton growth until the peak of the bloom, and the period of decline from the peak of the bloom to the end of the sampling period, respectively. Over the full growth season, the ^{14}C-estimated particulate net primary production was 14 Mol C. DOC production was estimated by calculating the amount of labile carbon metabolized by the bacteria (the BCD) during the October-February period when semilabile, bulk DOC was accumulating, and adding the DOC accumulation. Gross DOC excretion rates were not measured and some, but probably not all of the DOC production could have been at the expense of the particulate biomass as it was consumed and metabolized by grazers. As a result it is not possible to calculate the true ratio of DOC production to total primary production. However, we note that nearly all (93%) the DOC produced over the course of the season was consumed by the bacteria, and this amounted to 20% of the total seasonal primary production.

Large-volume (20-liter) seawater cultures showed that bacterial growth in the RSP was not temperature- or substrate-limited. In control (whole-water) experiments incubated at ambient temperatures (-1.8 to 0° C) with no added substrates, bacteria grew at 0.15 - 0.3 d^{-1} in the presence of bacteriovores with brief lag periods following enclosure and setup (0-2 d; W. Smith et al. 1998). Bacterial abundance reached 1 – 2 x 10^9 cells L^{-1}, about the same as attained in the RSP a few weeks later in the growth season. Experimental treatments included temperature manipulations (+ 2-3° C above ambient; i.e., growth at 0 to 3° C) and substrate additions (60 µM carbon as glucose or 10-15 µM natural plankton lysates; Ducklow et al. 1999). Some samples were gently filtered through 0.8 µm membranes to reduce grazer abundance and increase growth yields. In these treatments, DOC was increased by 10-15 µM over the ambient concentration of 43 µM, due to breakage of *Phaeocystis* cells. In these samples with reduced grazing and enhanced organic matter, bacterial growth rates were no different from control treatments. Bacterial growth rates were also unaffected by increased temperature (which was limited to the seasonal range for the RSP). In general these results suggest that bacteria in the RSP were poised for rapid growth even early in the season (November) when temperatures were at the annual minimum. Growth was not inhibited by temperature, or alternatively, there was already sufficient organic matter present in the water to release the bacteria from any temperature limitation (see above). In addition, bacterial growth did not respond to increased substrate concentrations, indicating either that nutrient

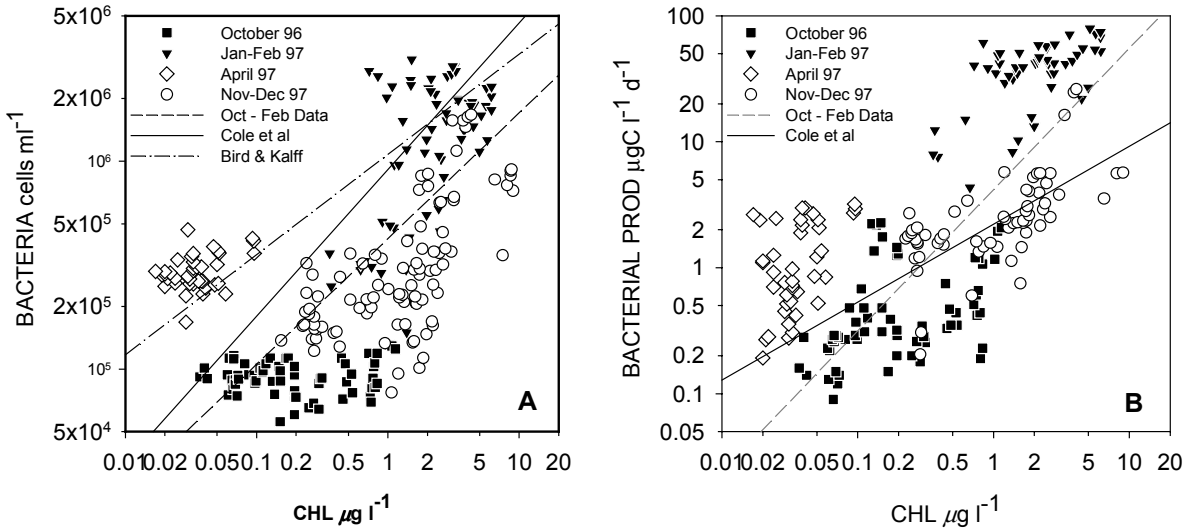

Figure 4. Bacteria - chlorophyll relationships in the Ross Sea polynya (upper 50 meters; after Cole et al. 1988). A: Abundance vs Chl. B: Bacterial production vs Chl. See text for explanation of lines.

limitation was imposed by other elements or compounds, or that bacteria were growing at near-maximum rates.

Finally, we ask, how does bacterial ecology inside the polynya differ from other regimes? The best-studied region outside the Ross Sea is the West Antarctic Peninsula (WAP; see Figure 1), previously studied by Karl and colleagues in the RACER Program and by the Palmer, Antarctica Long-Term Ecological Research Program (Ross et al. 1996a). The WAP differs from the Ross Sea principally in phytoplankton composition. Seasonal blooms are dominated by diatoms and start about a month later than in the RSP (R. Smith et al. 1998a,b). As described previously, Karl and colleagues concluded that bacterial production was poorly coupled to phytoplankton processes during the bloom. They ascribed the lack of coupling to efficient suppression of the bacterial response by intensive bacterivory. As we showed above, bacteria respond conspicuously to the *Phaeocystis* bloom in the RSP: the amplitude of the bacterial bloom is as large as any in the global ocean.

The response, or coupling between bacteria and phytoplankton can be demonstrated by plotting bacterial abundance or production against chlorophyll for a time series during the growth season (Figure 4). Bacterial abundance did not respond to increasing Chl within cruise periods, except for November-December, suggesting that bacteria were not sustained directly from DOM release from the phytoplankton in October and January-February. Rather, they consumed semilabile DOC during those periods (Ducklow 2003). However coupling is evident over the entire October to February period (Figure 4A). Bacteria in the RSP are lower in abundance for a given level of Chl than elsewhere in the oceans, as indicated by the position of the observations below the regression lines from the global syntheses of Cole et al. (1988) and Bird and Kalff (1984). This may be due to intensive grazing as in the WAP or just because the bacteria start at such a low abundance in October. By the peak of the bloom in January-February, the bacteria "catch up" to the global relationship, attaining the levels of

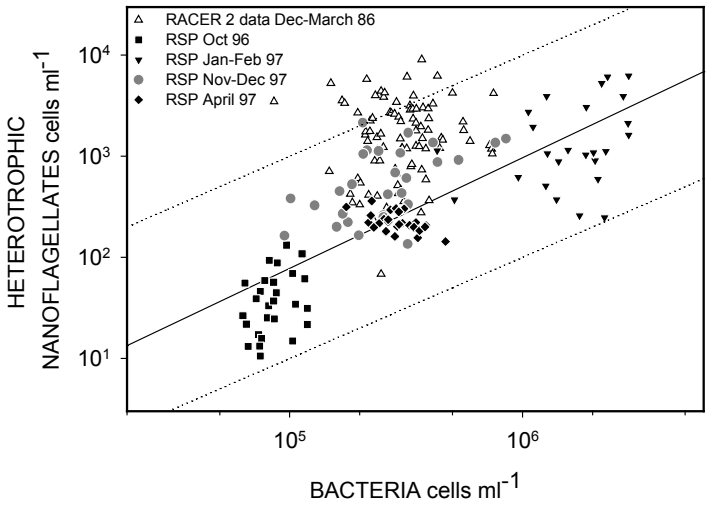

Figure 5. Bacteria - bacteriovore (heterotrophic nanoflagellate, HNAN) relationships in the Ross Sea polynya and Gerlache Strait (after Bird & Karl, 1999). The solid line is the Model II regression and the upper and lower dotted lines are the ratios 10,000:1 and 100:1 bacterial cells per HNAN cell, respectively.

abundance specified by the regressions. A slightly different pattern is manifested in bacterial production: it is somewhat low per unit chlorophyll in the early season, but an order of magnitude greater than the Cole et al. regression would predict in January-February (Figure 4B). Overall, bacteria are clearly coupled to phytoplankton processes during the *Phaeocystis* bloom in the RSP, in contrast to a lack of clear coupling during the diatom bloom in the WAP. Bacterial abundance and production rates are suppressed at low chlorophyll levels but attain high levels at peak chlorophyll concentrations during the peak of the bloom. The extent to which this behavior is a response to specific properties of the *Phaeocystis* cycle, or to other features of the Polynya, is not known.

Bird and Karl (1999) ascribed the lack of coupling in the Gerlache Strait (WAP) to intensive removal by heterotrophic nanoplankton bacteriovores (HNAN). They diagnosed this condition by computing the ratio of bacterial cells per individual HNAN for samples taken at various times of the bloom cycle. Figure 5 reproduces the observations of Bird and Karl (1999) along with observations from the RSP. There were only about 100 bacteria per HNAN in the WAP, and an order magnitude more in the RSP over the full growth season. There were consistently fewer HNAN available to graze on bacterial cells in the RSP than in the WAP system studied by Bird and Karl (1999). The Bacteria:HNAN ratio approached 10,000 in some samples in the RSP. The reasons for the disparity are not known but may reflect differing degrees of top-down control by krill in the two systems. Krill are scarce in the interior Ross Sea (Atkinson et al. 2004) perhaps due to unpalatibility of *Phaeocystis* (W. Smith et al. 2003). In contrast krill are abundant and serve as the principal, dominant herbivores in the WAP (Ross et al. 1996b). If there is an intermediate trophic level between krill and bacteriovores, the resulting trophic cascade could explain the contrasting relationship

of bacteria and the predators in the two systems.

4. BACTERIAL PROCESSES IN GREENLAND POLYNYAS (NEW AND NOW)

4.1 The Northeast Water (NEW) Polynya.

The NEW Polynya is a seasonally recurrent opening in the permanent ice of the coastal Arctic situated over the continental shelf of northeastern Greenland (77-81°N, 6-17°W' Figure 1). It was the study area for an intensive, international, multi-disciplinary research project investigating biogeochemical cycling in high-latitude oceans in 1992 and 1993 (NEWater Investigators 1993, Hirche and Deming 1997). The summer polynya typically starts to open in May, and closes by late September to mid-October with a maximum areal extent that ranged from 59,000 (in 1992) to 120,000 km^2 in 1985 (observations from 1978 to 1994, Böhm *et al.* 1997). Its formation involves several seasonally dependent mechanisms (Minnett et al. 1997): 1) new ice formation is reduced during the spring with the increase in solar insolation; 2) ice is exported from the region by an anticyclonic surface current (5-20 cm s^{-1}) that follows the topographic contours around Belgica Bank (Johnson and Niebauer 1995); 3) the resupply of ice to the area was limited by the presence of two semi-permanent ice shelves (Norske Øer to the south, and Ob Bank to the northeast; Schneider and Budéus 1995; we note that these ice shelves have recently melted and the continued existence of the NEW is now a matter of debate); and 4) small areas of open water, once present, reduce the albedo of the surface water, allowing greater absorption of solar insolation, increasing the rate of ice melt and some surface water warming (up to 3°C in the top meter; Minnett 1995). Wind events can easily redistribute the remaining sea ice, however, leading to a great deal of temporal and spatial heterogeneity in ice cover throughout the region (Gudmandsen et al. 1995; see for example, the AVHRR image of the region provided by Minnett et al. 1997). As with most of the Arctic, surface water is colder (~ -1.8 °C in the upper 100 m) than the deeper Atlantic-source waters (~ +2°C) and there is a strong halocline between them.

Nutrient concentrations in the East Greenland Shelf Water flowing into the NEW region are characterized by low nitrate (<4 μM; with a low N:P) and high silicate (10-14 μM; Kattner and Budeus 1997) characteristic of Pacific-origin Arctic surface water. New nutrients are supplied to the polynya as a tongue of cold water flowing northward from under the Norske Øer ice shelf (Wallace et al. 1995c). These nutrients are depleted by phytoplankton as the anticyclonic current carries them through the open water region, setting up a kind of "chemostat" or bloom gradient along the arc of the gyre between Norske Ør and the Westwind Trough. These spatial gradients of inorganic carbon and nitrogen are consistent with biological processes following the Redfield ratio (Wallace et al. 1995c). Additional nutrients may be supplied by the East Greenland Current or the Upper Halocline Arctic Water that flows over Ob Bank, triggering local hotspots of primary production and additional export near the shelf break.

During the 24-h sunlight of the boreal summer days, reduced snow and ice cover allow deeper light penetration, enabling ice-algae and phytoplankton blooms. Ice algal blooms dominate primary production early in the season, while phytoplankton blooms (mostly diatoms) develop later. Because of the heterogeneity in the summertime ice coverage, however, all stages of this succession may be present in the polynya region at any one time.

The average euphotic zone (0.1% I_0) depth in 1992 was 46 ± 18 m. Primary production in the NEW is nitrogen and light limited and was therefore modest in 1992 (22.5 ± 23.3 mmol C m^{-2} d^{-1}, maximum at 95 mmol C m^{-2} d^{-1}, W. Smith 1995) and only about two-fold higher on average in 1993 (Pesant et al. 1996, W. Smith et al. 1997). New production was a large fraction of the total production, with f-ratios averaging 0.65 overall (W. Smith et al. 1997), and dropping to 0.39 when nitrate concentrations dropped below 0.5 μM.

The northern region of the polynya is dominated by copepod species of arctic origin, particularly the small omnivorous *Metridia longa* (Ashjian et al. 1995). The generally low abundance of large herbivorous *Calanus* species increases the potential for export of unconsumed primary production (Ashjian et al. 1995) while at the same time reducing one of the main pathways (Jumars et al. 1989) by which dissolved organic matter is generated from particulate primary production and made available to pelagic bacteria. Estimates for the grazing impact on primary production based on copepod egg production were less than 30% at 90% of the stations sampled in 1993 (Hirche and Kwasniewski 1997). Yet, potential estimates based on particulate carbon and nitrogen production suggest a greater impact (averaging 45%; Daly 1997), with the C:N ratio of fecal pellets reflecting nitrogen deficiency.

Copepod pellet export was not considered a major pathway for carbon loss from the system (Bauerfeind et al. 1997), with contents of sediment traps consisting primarily of diatoms (averaging 10%; but up to 81% ice algae in June) and the houses and feces of appendicularians (up to 40% in August). These findings concur with the result that particulate matter in the polynya was primarily diatomaceous, with unusually elevated C:N ratios (typically greater than 10) apparently reflecting nitrogen limitation (W. Smith et al. 1995) at the surface. Particulate organic carbon concentrations in the polynya were generally high overall (surface values for all stations measured between July 18 – August 18, 1992 averaged 211 ± 181 mg m^{-3}; W. Smith et al. 1995) and exhibited a great deal of heterogeneity among stations that showed no association with ice cover.

Dissolved organic carbon (DOC) concentrations in the NEW start the summer season relatively high (100μM for the sub-euphotic surface mixed layer; Daly et al. 1999; 110 μM for surface waters in June; Skoog et al., 2001), but the C:N ratio of the dissolved organic pool is also quite high (ca. 20) compared to nearby regions. Unlike other arctic regions, the NEW receives no local riverine inputs that could explain the high DOC. The East Greenland Current carries levels of 75.8 μM (±10.2; Amon et al., 2003). One explanation for the early season high could be DOC production by ice algae and ice melt prior to the opening of the polynya (Skoog et a., 2001). According to one analysis based on depth gradients, a small buildup (23 μM) of DOC was observed in the NEW polynya over the early summer of 1993 (Daly et al. 1999), with no coincident buildup of DON, despite potentially significant DON excretion by zooplankton (Daly et al. 1999). In a contradictory analysis based on water masses (Skoog et al., 2001), DOC decreased slightly (from 110 to 105 μM) while DON increased slightly (from 5.6 to 6.1 μM) in the polynya surface waters over the summer of 1993. A corresponding build up of DON in intermediate waters (from 4.83 to 5.97 μM; Skoog et al., 2001) requires solubilization of sinking particles as the explanation.

Bacterial abundance in the surface waters of the NEW was generally low with an average of 0.7 (± 0.45; n = 28 stations) x 10^8 cells per liter for the upper 50 m in 1992 (with individual

samples ranging from 0.12 to 5.3 x 10^8 L^{-1}; n = 281) and 1.6 (± 1.1; n = 37 stations) x 10^8 cells per liter in 1993 (with individual samples ranging from 0.20 to 7.9 x 10^8 L-1; n = 353).

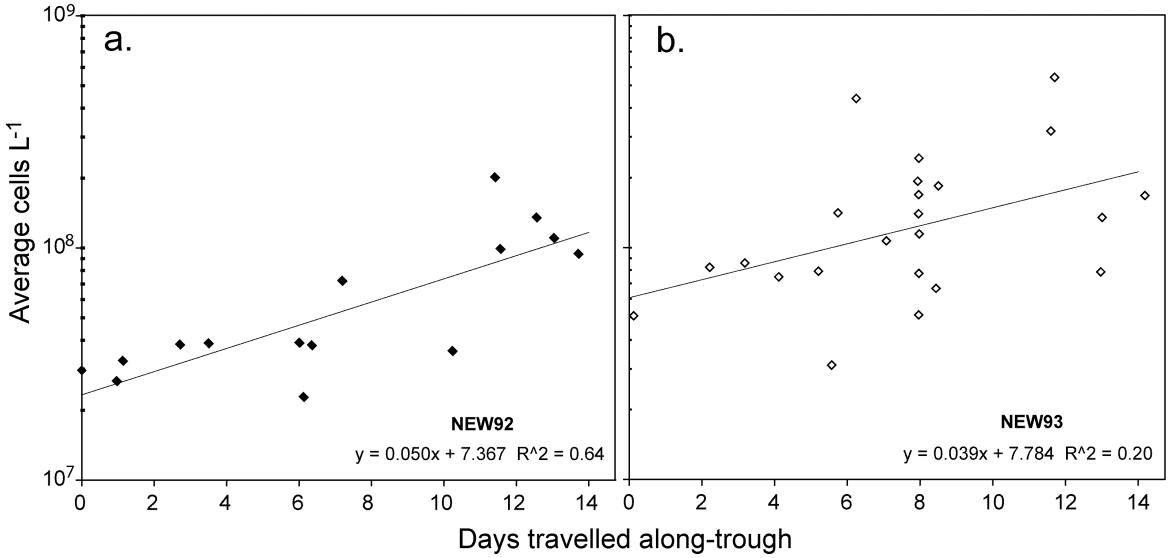

Figure 6. Average bacterial cell abundance (calculated by integrating over the top 50 m) in the Northeast Water during a) 1992 and b) 1993, plotted against the time each parcel of surface water has traveled through the open waters of the polynya. The time calculation was based on the distance from NEW 92 Station 42 (80°N, 16°W) and a current velocity of 10 cm s^{-1}. Net population growth rates of 0.05 (± 0.02; 95% ci) d^{-1} for 1992 and 0.039 (± 0.035) d-1 for 1993 are calculated from the slope of a Model 1 regression of the log(abundance) data against the time traveled.

Abundance generally increased toward the subsurface near 25 m and then decreased into deeper waters. While attempts were made during both field seasons to collect time series data by returning multiple times to the same geographic position, variability at the "time series station" (80.4°N, 13.3°W) was extremely high and no consistent temporal changes were observed. Instead, several authors have used spatial variation along the principal axis of circulation in the NEW as a proxy for time (e.g. Wallace et al. 1995c, Touratier et al., 2000). If we apply those same assumptions (Figure 6), an increase in average bacterial abundance (based on integrating through the upper 50 m) by about an order of magnitude can be seen to occur during the approximately two weeks that it takes water to move out from under the Norske Ør ice shelf, along the Norske Trough and into the Westwind Trough region. Net accumulation rates of 0.05 and 0.04 per day can be calculated for 1992 (Figure 6A) and 1993 (Figure 6B), respectively. These growth rates are as high or higher than those measured in the RSP. The peak biomass (>10^9 L^{-1}) observed in the RSP during January is not attained in the NEW, however, perhaps because of the much shorter time available for the bloom to progress or because of nitrogen limitation of the entire system.

Bacterial abundance correlated significantly with particulate organic carbon in 1992 (W. Smith et al. 1995). Bacterial abundance also correlated with chlorophyll concentrations (Figure 7). Using the appropriate Model II geometric mean regression with correction factors (see Cole et al. 1988), the two years of data from the polynya have the same slope (0.47) but initial bacterial abundances are higher by about a factor of 5 (y-intercept increases from 4.85

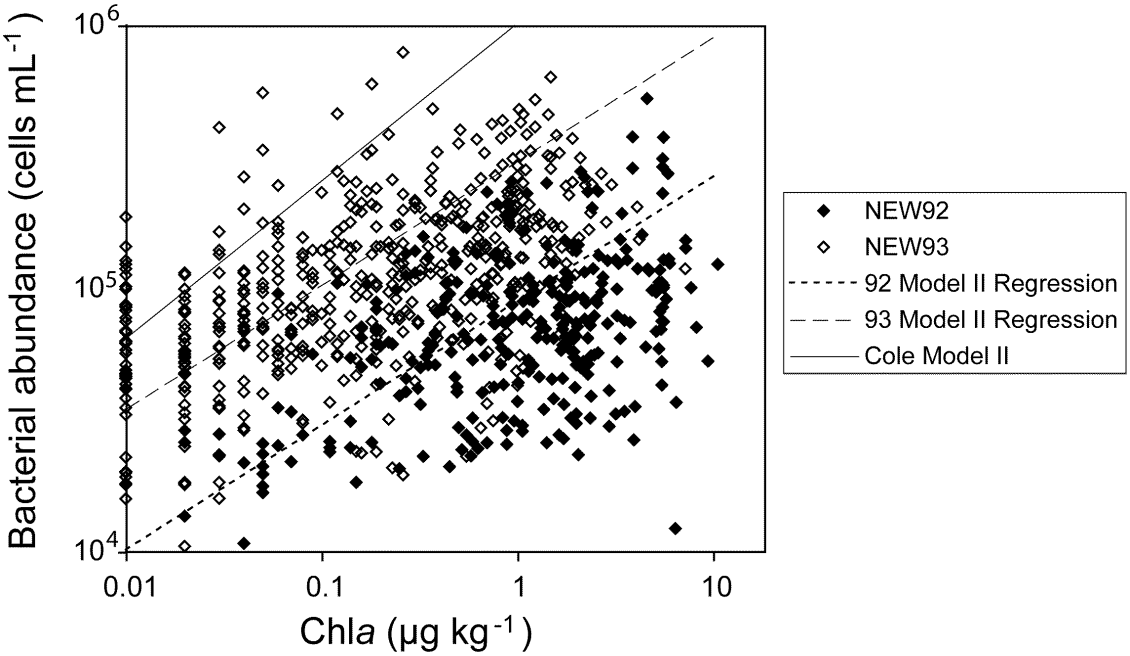

Figure 7. Bacterial abundance (cells per ml) plotted against chlorophyll a concentration (µg kg□1; data courtesy of Walker O. Smith Jr.) for all samples collected from the Northeast Water region in 1992 (closed diamonds) and 1993 (open diamonds). Samples were analyzed using standard methods (Smith et al., 1995). Regression lines (short dashed for 1992 and long dashed for 1993) are calculated using Model II regression. The solid line uses the Model II regression slope (but Model I intercept and correction factor) from Cole et al. (1988).

to 5.38). The significantly different intercept suggests that interannual variability, perhaps the timing of snow and ice melt and the extent of the ice algal bloom, may influence the initial conditions and thus the potential response of what is very likely to be a complex polynya ecosystem. Both years fall significantly below both the slope and intercept of the published relationship for all oceans (Cole et al. 1988) and significantly below the relationship observed in the RSP. The NEWP relationship is positive and significant, though, so the bacteria seem to be "coupled" to the algal bloom (unlike the lack of coupling observed in the Gerlache Strait; Bird and Karl 1999). Yet, their response does not result in as great an increase in abundance as seen elsewhere. In the absence of any other data, one might interpret the shallower slope as temperature limitation, but the growth rates described above (along with other data discussed below) would suggest otherwise. As mentioned above for the RSP, the reduced slope may indicate that the bacteria are under significant grazing pressure. This and other alternative hypotheses will be discussed below.

Bacterial biovolumes tended to be large, averaging 0.126 (± 0.003; n = 3500 cells measured) μm^3 per cell throughout the euphotic zone of the time series station during the two *Polar Sea* expeditions (Yager and Deming 1999). Cell size tended to increase with depth to 25 m. These biovolumes are larger than those observed in the RSP, although they are based on a much less extensive data set and do not include deeper samples. If we use 26.6 fgC $cell^{-1}$, appropriate for cells of 0.126 μm^3 (Simon and Azam 1989), across all the euphotic zone

samples, total integrated biomass in the upper 50 m ranged from 3 to 60 mmol C m^{-2} (average 17.6 ± 11.9; n = 37 stations). So, despite their much lower abundance, the larger pelagic bacteria in NEW may constitute about the same amount of biomass as found in the RSP during all but the peak season (Jan-Feb).

Bacterial production was estimated from ^{3}H-leucine incorporation (Kirchman 1993) at selected depths at or near the fluorescence maximum for seventeen stations (Yager 1996). Values ranged from 0.08 to 23.4 mg C m^{-3} d^{-1} (with the median rate at 1.2 mg C m^{-3} d^{-1} for 1992 stations and 6.1 mg C m^{-3} d^{-1} for 1993). These rates are comparable (using the same conversion factors) to all but the late season rates seen in the RSP. If we group all the data from both years (Figure 8A), no significant correlation (r = 0.14; n = 20) exists between chlorophyll concentration and bacterial production. This result is very likely due to the nature of the data set (a small range in chlorophyll values). Nevertheless, the data scatter well around the Cole et al. (1988) regression, suggesting that even though bacterial numbers did not increase as expected with chlorophyll, bacterial production levels were generally as high as we might predict. Notably, the 1993 data, with overall greater abundance, matched the Cole et al. (1988) prediction better than the data from 1992.

Using that same small data set from Yager (1996) to compare bacterial production to primary production (^{14}C method; W. Smith 1995 1997), a significant relationship is observed (Figure 8B; r = 0.46; n = 19). The Model II slope (0.80 ± 0.36) is not significantly different from that of Cole et al. (1988). The ratio of bacterial to simultaneous primary production ranged greatly (from 1.07 to 954%) with a median value of 18%. The highest value was

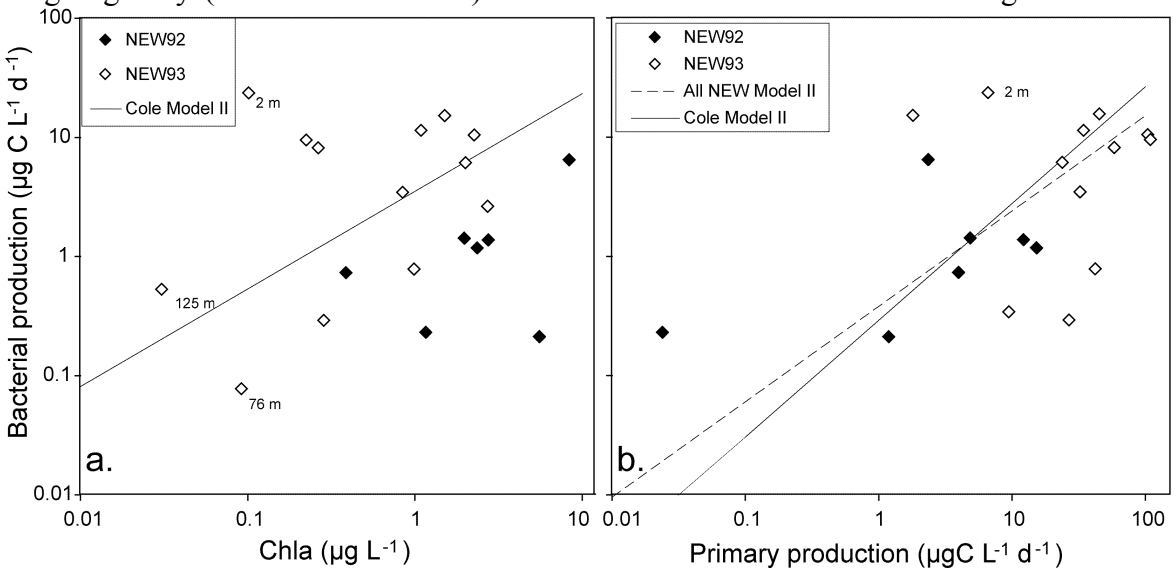

Figure 8. Bacterial production (BP; measured using 14C-leucine uptake, Kirchman 1993) plotted against a) chlorophyll a concentrations, and b) primary production (PP; measured using 14C-bicarbonate uptake; data courtesy of Walker O. Smith Jr.) for NEW 1992 (closed diamonds) and NEW 1993 (open diamonds). Except where labeled, these data are from fluorescence maximum depths (15 – 38 m) only. No significant correlation was found for BP versus chlorophyll, but the Cole et al. (1988) relationship is shown for reference (solid line). Combining the BP versus PP data from both years gives a significant correlation and regression line (dotted line) not significantly different from the Cole et al. (1988) relationship (solid line).

observed on Belgica Bank where primary production was very low, but measurable POM suggested advection from other regions. If we remove four values over 260% (three from the time series station about 8 days from Station 42), and plot the ratio along the axis of circulation (Figure 9; as with bacterial abundance above), there is a significant increase in BP:PP with time since entering the polynya ($r = 0.52$; $n = 15$). As with the bloom progression in biomass, the bacterial production in the NEW ramps up similarly to that in the RSP, except for the late season peak. Notably, the greatest variability (including three of the highest values >260%, but also the three lowest values <5%) was observed at the time series station with no apparent temporal trend, illustrating just how heterogeneous the system is.

One experiment at the time series station in mid-August 1993 (Yager 1996) compared BP at in situ temperature (-1°C) and at 0°C, observing a 39% *reduction* in the rate with warming. While a single experiment does not provide enough evidence to generalize confidently, it at least supports the possibility that psychrophilic bacterial populations sometimes dominate the polynya ecosystem (further supported by kinetic experiments discussed below) or suggests that conversion factors are sensitive to temperature.

Bacterial utilization of mixed amino acids throughout the water column (^{14}C-labeled, using a single substrate concentration, 18 nM; Ritzrau 1997) was highly correlated to POC concentration, pigment concentrations, and bacteria abundance. Rates were highest in the cold surface waters, compared to the warmer deep waters, with estimated amino acid turnover times ranging from 7 to 500 days. Bacterial utilization of dissolved substrate increased

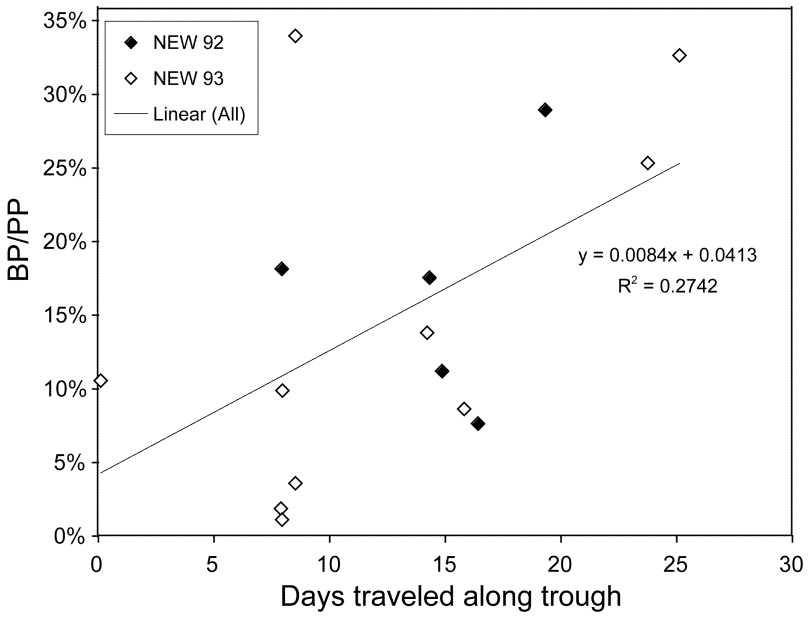

Figure 9. The ratio of bacterial production (BP; measured using 14C-leucine uptake, Kirchman 1993) to primary production (PP; measured using 14C-bicarbonate uptake; data courtesy of Walker O. Smith Jr.) for NEW 1992 (closed diamonds) and NEW 1993 (open diamonds) plotted against the time each parcel of surface water has traveled through the open waters of the polynya (as in Fig. 6). Three data points with ratios greater than 270% (from the time series station, about 8 days from Station 42) are

not included in the plot. A significant linear increase (R2 = 0.27) over time (solid line) was observed.

dramatically just above the seafloor where sedimenting bloom events combine with resuspension to create bottom boundary (or nepheloid) layers with very high rates of microbial activity (Ritzrau 1996, Ritzrau and Thomsen 1997). While the boundary-layer activity is clearly particle-associated, utilization rates there did not correlate with POC concentrations, suggesting that a great deal of solubilization had already occurred by the time the material reached the bottom.

A kinetic approach, where a range of mixed-amino acid concentrations were presented to bacteria at in situ temperatures (Yager and Deming 1999), revealed that NEW bacteria were always ready and able to respond to small increases in their available food supply, even at subzero temperatures. Specific affinities observed for mixed amino acids are among the highest ever reported. Maximum utilization rates (or the rate achieved at saturating levels of substrate, also called "heterotrophic potential" in the literature) are similar to other temperate and polar seas, confirming that rates are controlled by substrate availability and not some inherent characteristic of the bacterial population. Additional experiments incubating replicate samples at different temperatures (from -1 to +5C; a range reflecting NEW surface water variability) showed a great deal of heterogeneity in their response to short term warming (with Q_{10} for Vmax and specific affinity ranging from 0.25 to 13 and 0.23 to 5, respectively; Yager and Deming 1999), with the more psychrophilic responses (Q_{10} <1) coming from stations with greater amino acid concentrations or lower POC:PON ratios. Community structure, or the balance between psychrophilic and psychrotolerant bacteria, may therefore be controlled somewhat by nitrogen availability.

For 10 nM substrate additions incubated at in situ temperature over a total of eight stations in 1993, the uniformity of incorporation efficiency (IE) as a function of substrate type was remarkably high (Yager 1996). In general, leucine was used extremely efficiently, ranging from 90 to 100% (data not shown). Mixed amino acids were used slightly less efficiently, averaging 82 ± 5%. The efficiency on glucose averaged 68 ± 4%, while glutamic acid, which may go directly into the respiratory cycle, averaged 41 ± 5%. These incorporation efficiencies are greater than or equal to values typically reported for other marine systems (e.g. Williams 1970). Incorporation efficiencies in the NEW tended to drop with higher substrate concentrations (Yager 1996), perhaps indicating luxury consumption or lower tendency for storage. They also tended to be higher at low in situ temperatures, decreasing with short term warming. Under conditions of nitrogen limitation, bacteria store carbon energy in the form of long-side-chain polyhydroxyalkanoate (PHA; Ramsay *et al. 199*2). Lower temperature (Huijberts et al. 1992, Alvarez et al. 1997) and unsteady food supply (Pagni et al. 1992) can also increase PHA production. Carbon storage due to these or other factors may explain observations of high incorporation efficiency.

There is some discussion in the literature about the validity of using individual, specified radiolabeled substrates to measure growth efficiency (see for example, the review by Pomeroy and Wiebe 1993). Bacterial incorporation of ^{14}C-labeled substrates appears to be more efficient than that observed on a more "natural" mix of dissolved organic matter (e.g., Linley and Newell 1984) or than that determined by the ratio of net biomass production relative to the sum of respiration (CO_2) and net biomass production (e.g., Bjørnsen 1986,

Carlson et al. 1996 1999). Bacteria gain more benefit from taking up an amino acid than a less labile organic molecule, and may therefore utilize it differently (e.g., more efficiently). Since bacteria are known to be capable of diauxic growth (as originally proposed by Monod 1942), they can be expected to regulate their uptake processes so as to utilize the better substrate first when confronted with resources of diverse quality; i.e., as NEW polynya bacteria encounter amino acids, they will prefer them to other less labile material. By following a mixture of amino acids that mimics the composition of phytoplankton or zooplankton exudates, the NEW efficiencies may reflect "reality" better than a single substrate. Nevertheless, if the bacteria in the polynya are not regularly exposed to such a labile food supply, these efficiencies reflect their behavioral responses to high quality food pulses and not some "average" condition.

Bacteria use extracellular enzymes to hydrolyze particulate organic material to a dissolved form they can use directly (D. C. Smith et al. 1992). In the NEW polynya water column, potential hydrolysis rates scaled per bacterium are slower than reported for other more temperate pelagic environments, potentially favoring the export of POM (Vetter and Deming 1994; although rates may have been underestimated since saturating levels of substrate may not have been used; see discussion below). When scaled to sample dry weight, however, pelagic rates, especially those measured on live floating sediment trap samples, were greater than sediment hydrolysis rates, suggesting that water column processes are nevertheless important to the fate of carbon in the Arctic. This later result complements the high benthic boundary layer activity rates mentioned above. Hydrolysis rates generally increase with incubation temperature but peptidase activity in particular showed psychrophilic behavior (no increase in rate with short term warming) in several samples.

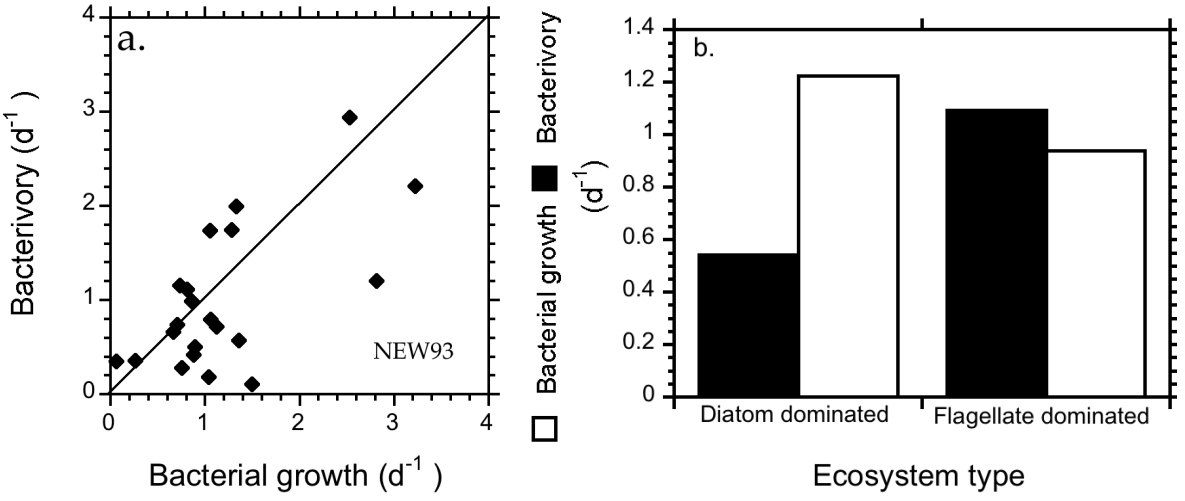

Figure 10. A) Grazing rate (d-1; estimated by the slope) by microzooplankton as a function of bacterial growth in the absence of grazers (μ, d-1; estimated by the y-intercept) determined from the dilution versus bacterial growth relationship (see Tremaine and Mills, 1987; data from Yager 1996). A solid line shows the 1:1 line where the two rates would be equal; B) Average bacterivory (black column) and bacterial growth (white column) for the Polarstern NEW 1993 stations

subdivided into Type I (diatom dominated; n = 5) and Type V (autotrophic flagellate dominated; n = 4) ecosystems (Pesant et al., 1996).

Bacterivory estimated using the dilution technique (Yager 1996) ranged from 0 to 2.9 d^{-1} and in general kept pace (Figure 10a) with bacterial specific growth rates. When *Polarstern* cruise stations are subdivided into the two ecosystem types suggested by Pesant *et al.,* (1996; using the size-fractionated phytoplankton biomass and production to divide the polynya stations into those ecosystems dominated by large diatoms, Type I, and those dominated by small autotrophic flagellates, Type V), bacterivory tends to equal or exceed bacterial growth at Type V stations (n=5) but fall short of growth at Type I stations (n = 4; Figure 10b). According to Legendre and LeFevre (1995), these ecosystem types indicate the local importance of the microbial loop, with Type I reflecting an herbivorous food web and Type V reflecting a microbial food web or loop. Our data confirm this idea in that a stronger link between bacterial growth and bacterivory occurs where autotrophic flagellates dominate. In an herbivorous food web, bacteria are thought to be active, but apparently not as strongly controlled by microzooplankton grazers.

Taken together, this suite of results points to the conclusion that bacteria in the NEW polynya were taking up dissolved organics as they became available, using them efficiently with minimal respiration, and passing the carbon and energy to higher trophic levels. Bacterial biomass does not accumulate as fast as it might, however, because the cells are living under intense grazing pressure. An obvious question arises: given that bacteria have minimized respiration in this and perhaps other polar environments, do the bacteriovores play a more dominant role than their prey in carbon and nitrogen remineralization? The only study of the growth efficiency of polar heterotrophic flagellates is that by Choi and Peters (1992). In this study using cultured organisms, IE was high at subzero temperatures (60-70%) and decreased with warming. If these flagellate results can be extrapolated to other grazers in polar waters, then highly efficient trophic links may continue up the food web, providing an ecosystem response that contributes as a whole to an efficient biological pump.

4.2. The North Water (NOW) Polynya

The NOW polynya (75-79°N, 68-80°W) is the largest (~80,000 km^2) and most biologically productive polynya in the Arctic (Deming et al. 2002; Figure 1). A historical debate concerns whether latent heat or sensible heat contributes most to the formation of the NOW, as the outcome will likely influence the mode of primary production. The most recent data from the region suggests that, in a fashion similar to the NEW, the NOW polynya forms because of wind and ocean advection of ice (latent heat) southward from Nares Strait, which is typically blocked by an ice bridge preventing the flow of ice from the Lincoln Sea into Baffin Bay (Ingram et al., 2002). Sensible heat comes into play later in the season, but is not enough to open the polynya alone (Melling et al., 2001). Two major currents move water through the area: the cold, fresher, silicate-rich Baffin Current from the north and the warmer, saltier West Greenland Current (WGC) from the south (Bacle et al. 2002).

The phytoplankton bloom starts in the southeast during April when nutrient rich WGC waters combine with moderate vertical stratification and partial ice cover; this bloom spreads north and westwards during May and June (Tremblay et al. 2002). In the northern reaches of the NOW, the bloom starts later in June once reduced ice cover allows sufficient light

penetration. The nutrient-rich Baffin Current creates a bloom gradient (or "chemostat") similar to that observed in the NEW. Maximum mean phytoplankton production (particulate plus dissolved; Klein et al., 2002) in the east occurs during May 1998 (5.3 g C m^{-2} d^{-1}), and in the north during June 1998 (3.3 g C m^{-2} d^{-1}). Nitrogen-limited new production (averaging 1.1 g C m^{-2} d^{-1}; Tremblay et al., 2002) is 3 to 8 times higher than in the NEW. One reason for this may be the intermittent spring and summer storm activity that helped mix nutrients up from below. The steep canyon walls around the NOW contribute to much greater wind speeds than were ever experienced in the NEW. Less than half of the measured new production was based on pre-season nitrogen inventories; the rest came from deep mixing (Tremblay et al., 2002).

Diatoms dominate the algal bloom (Lovejoy et al. 2002) and lead to high potential export of particulate organic carbon (up to 155 g C m^{-2} yr^{-1}; Klein et al., 2002) with f-ratios ranging from 0.4 to 0.7. Dinoflagellates bloom later in the season, particularly on the eastern side after nutrient levels decrease; ciliates also contributed significantly to the bloom in some areas (Lovejoy et al., 2002). Most notable is that the growing season is much longer (April thru September; Booth et al., 2002) than typically observed in high latitudes. This extended season is primarily due to the remarkable life history (including resting spores) and low-nutrient tolerance of the colonial diatom, *Chaetoceros socialis* (Booth et al., 2002).

Although they recruited earlier than their counterparts in nearby Barrow Strait (Ringuette et al. 2002), copepods never attained the biomass expected for such high levels of primary production (Saunders et al. 2003). Large appendicularian tunicates such as *Oikopleura vanhoeffini* were important, especially late in the season, and were large and abundant enough to graze on the relatively small *C. socialis*, consume about 10% of primary production, and account for 4% of biogenic carbon export (Acuña et al., 2002). The diet of these filter feeders also includes microflagellates and ciliates, as well as bacteria.

Dissolved organic carbon concentrations in the NOW (Miller et al., 2002) are generally high in the spring, decrease during June, and then increase again in the late summer. They reach maximum concentrations (182 µM; over twice as high as in the RSP) in the east during May. The lowest values (40-50 µM, reflecting deep ocean levels) are observed in the north and west during June. By contrast, particulate carbon shows a single peak (40-60 µM, up from 8-10 µM in April; Miller et al., 2002), usually in June. Dissolved organic carbon in the NOW is also made more available to bacteria by exposure to ultraviolet light (Pinette-Matthews 2003).

Annual fluxes of particulate matter from the NOW polynya (1-14 g C m^{-2} y^{-1}) are the highest ever reported for ice-covered arctic regions (Hargrave et al., 2002; measured by moored sediment traps at ~200m), underscoring the importance of understanding not only free-living but also particle-attached bacterial activity. Two peaks in export occurred, a small one in the spring and a larger second peak in late summer. During the late summer peak, mucous-rich mats of *C. socialis* dominated the trap contents. These carbon-rich mats may be the remains of directly deposited colonial diatoms (Booth et al., 2002) or the discarded houses of appendicularians (Acuña et al., 2002). Except during times of peak sedimentation, the POC:N ratio of trap contents increased with depth (Hargrave et al. 2002) and between April and June (Huston et al. 2002), providing evidence for bacterial solubilization of particulate

nitrogen.

Bacterial abundance in the North Water during July 1998 ranged from 0.4 - 1.6 x 10^9 cells L^{-1} (Middelboe et al., 2002), generally higher than in the NEW. A somewhat smaller range was observed during August 1997 (averaging 1.06 – 5.59 x 10^8 cells L^{-1} in the top 50 m. Corresponding chlorophyll data for the 1997 data set (0.32 - 3.7 µg Chl *a* L^{-1} averaged over the top 50 m) sets the NOW data squarely between the NEW92 and NEW93 regression lines in Figure 8, also falling below the Cole et al. (1988) regression. Integrated chlorophyll values for July 1998 were similar to August 1997 values (Klein et al., 2002), so the higher abundances in the July 1998 data may correspond better with the January RSP data and the Cole et al. (1988) prediction.

Bacterial growth rates during August 1997 (measured by time dependent changes in cell abundance in diluted incubations) ranged from 0.11 - 0.24 d^{-1}. These rates are on the low end of those measured in the NEW using a similar technique, but they are much faster than NEW or RSP estimates of net population growth *in situ*, as expected when removal processes are operating. Using bacterial abundance data and assuming 20 fg C $cell^{-1}$, integrated bacterial carbon production ranged from 17 - 123 mg C m^{-2} d^{-1} over the top 50 m (0.332 to 2.46 mg C m^{-3} d^{-1}). These values also fit squarely within the range observed in the NEW and fall just below the Cole regression (Figure 8a) when plotted versus their reported average chlorophyll concentrations.

Bacterial growth rates in July 1998 (based on bacterial production measurements using ^{3}H-thymidine and experimentally determined conversion factors of 1.8 x 10^{18} cells per mole thymidine incorporated; Middelboe et al., 2002) are about the same or faster (0.11 to 0.40 d^{-1}) than those reported for 1997. Using conversion factors from nearby regions for cell carbon (29 fg C $cell^{-1}$) and growth yield (0.25), Middelboe et al. (2002) report the bacterial carbon demand measured in the NOW surface waters ranging from 6-7 µg C l^{-1} d^{-1} in the far north to 15-63 µg C l^{-1} d^{-1} in the south. Depth integrated bacterial carbon production ranged from 0.10-0.15 g C m^{-2} d^{-1} in the north to 0.27 to 0.45 g C m^{-2} d^{-1} in the south. Using average primary production data for the same regions and dates (includes particulate and dissolved production; Klein et al., 2002), the calculated BP:PP ratio ranges from 11-16% in the north to 100-167% in the south. If BGE was 25%, we calculate that the bacteria metabolized 44 - 64% of the primary production in the north and between 400 and 600% of the coincident primary production in the south. Values greater than 100% indicate either that the two rate processes are uncoupled in time and space (so averages are therefore deceiving), or that the NOW receives allochthonous organic matter inputs that pelagic bacteria can use. That the system is net heterotrophic, however, seems unlikely given that, between June and July 1998 in the northern stations, DOC increased from 52 to 120 µmol kg^{-1} and DIC decreased from 2120 to 2000 µmol kg^{-1} (Miller et al., 2002). Interestingly, the DIC stayed about the same in the south between June and July of 1998 (unfortunately, there are no DOC data available) despite the modest primary production.

Bacterial growth rates during July 1998 were enhanced by additions of 5 µM glucose and warming by 5°C, but not by additions of inorganic nitrogen (10 µM NH_4Cl) or phosphate (3 µM Na_2HPO_4), suggesting that they were carbon limited (Middleboe et al., 2002). The effects were more pronounced in the north compared to the central polynya region.

Bacterial activity on the sinking particles, as measured by extracellular enzyme activity and the percent of actively respiring cells (CTC+; Huston and Deming, 2002), was higher than in the surrounding seawater. Cell-specific hydrolysis rates in the subzero temperatures of the NOW are as high as those measured in temperate environments. Interestingly, Huston and Deming (2002) comment that the much lower hydrolysis rates measured in the NEW polynya (Vetter and Deming 1994) may have been due to methodological problems rather than environmental differences; according to experiments done in the NOW, the single level of substrate added to the NEW experiments (10 μM versus 200 μM) was probably below saturation and would have therefore underestimated actual hydrolysis rates.

Rates of hydrolysis correlated well with seasonal changes in the C:N ratios of the sinking particles, suggesting that the bacteria were responding to food quality. The observed enhancement of leucine-aminopeptidase activity relative to other extracellular enzyme activities measured (chitobiase and beta-glucosidase) would have preferentially solubilized nitrogen, consistent with the observed seasonal increase in the C:N ratio of particles (Huston and Deming, 2002). These results further support the idea that arctic polynya bacteria are particularly focused on the availability of dissolved organic nitrogen.

Grazing by microzooplankton on bacteria was estimated in August 1997 using the dilution technique. Samples were from the subsurface chlorophyll maximum. The fraction of bacterial biomass ingested ranged from 18% in the east to 51% in the west. The fraction of bacterial production ingested ranged from 41% in the east to 77% in the west. Clearly, grazers were having a significant impact on bacteria in the NOW polynya.

In the first study of viral impacts on polynya bacteria, Middelboe et al. (2002) found another agent of mortality for bacterial production. They determined (using both the frequency of visibly infected cells and viral production rates in batch cultures) that 6 – 28% of bacterial production was lost to viruses (Middelboe et al. 2002). Viral abundance ($1.4 – 5.6 \times 10^9$ L^{-1}) correlated well with bacterial abundance and bacterial production rates.

5. OTHER POLYNYAS.

The Cape Bathurst (CAB) Polynya and the Saint Laurence Island (SLIP) polynyas are other Arctic polynyas (Figure 1) where particle rich pelagic systems have been identified. The SLIP is primarily a winter polynya, with potentially significant particle flux to the benthos during brine formation (Cooper et al. 2002). As far as we know, however, no pelagic bacterial activities have been monitored there. The Cape Bathurst polynya on the Canadian Beaufort Shelf is tightly coupled to the dynamics of the Mackenzie River (Arrigo and van Dijken 2004).

Arrigo and van Dijken (2003) identified 37 Antarctic polynyas ranging in size from the Lazarev Sea polynya (1000 km^2) to 400,000 km^2 for the RSP (Figure 1). Most of these have not been studied at all, and very few have been sampled for bacterial properties. Data from Prydz Bay suggest that the phasing of bacterial and phytoplankton blooms might vary interannually. Billen and Becquevort (1990) attributed a one-month lag between the diatom and bacterial blooms in 1986-87 to delayed production and utilization of macromolecular, polymeric DOC. Lancelot et al. (1991) hypothesized a similar scenario for a *Phaeocystis* bloom in Prydz Bay. In the Prydz Bay polynya, the maximum abundances of bacteria and bacteriovores were 8.6×10^8 cells L^{-1} and 4.5×10^6 cells L^{-1} with a prey:predator ratio

of 80-300 (Leakey et al. 1996). However the bacteriovores only removed 10-36% of the daily bacterial production, allowing a small bloom (from 2 to 8 x 10^8 cells L^{-1}). Simon et al. (1999), in one of the few studies focusing on species composition of Antarctic microbial communities, observed that the bacterial community was dominated by members of the *Cytophaga-Flavobacterium* group following a *Phaeocystis* bloom in the Lazarev Sea.

6. SUMMARY AND PROSPECTS.

One theme of this Chapter is that many of our recent insights about bacterial growth in cold, polar waters come from observations and experiments performed in both Arctic and Antarctic polynyas. Although few of the 37 Antarctic polynyas and just a few Arctic polynyas have been examined in much detail, we can make some important observations about bacterial growth in these systems:

- Bacteria grow at rates identical to warmer, temperate habitats. There is little evidence for growth rate limitation or inhibition by low temperature, at least during the phytoplankton growing season.
- Bacterial physiology responded quickly to additions of organic matter in the Arctic, whereas in the Antarctic, no growth response was seen because growth was apparently already at near-maximum rates. The experimental approaches are not strictly comparable, but we conclude that bacteria in both these environments are adapted to respond quickly to organic matter additions resulting from phytoplankton blooms.
- Bacterial growth is in excess of removal by bacteriovores and viruses during or directly following local phytoplankton blooms, enabling bacterial stocks to accumulate to levels similar to those observed in temperate oceans.
- Bacterial growth efficiencies and incorporation efficiencies are similar to or higher than lower latitudes and bacterial production reaches similar ratios of BP:PP as in temperate oceanic regimes (5-15%; with some higher exceptions, especially in the Arctic).

The question remains, are bacterial ecology and population dynamics different in polynyas, compared to the surrounding marginal ice zones? Somewhat surprisingly, we are unable to answer this question because similar comprehensive seasonal studies have not been accomplished outside of polynyas. Another question is, are bacteria different in the Arctic and Antarctic? From the work discussed here, the answer at this time is, *not very*. Yet, the Arctic receives large inputs of river runoff, containing terrestrial organic matter. These inputs are entirely lacking in the Antarctic. With global warming leading to melting permafrost and tundra, river input to the Arctic will increase – it has increased 7% since 1936 (Peterson et al. 2002). Currently both the Antarctic and Arctic are experiencing the most rapid rates of warming on the planet, but the warming is regionally variable (Doran et al. 2002). Polynyas themselves are climate sensitive environments, which may increase or decrease in size, or may disappear entirely (as would seem to be the case with the NEW) with future warming. Depending on their location in either polar region, polynyas may experience different rates of warming (or cooling). Polynyas in the arctic may experience different rates of terrestrial input for the same reasons. As noted above, polynyas currently behave as rectified (one-way) sinks for atmospheric CO_2, but this behavior is sensitive to the precise phasing of the seasonal cycles of ice formation and retreat, phytoplankton blooming, and microbial respiration. With

additional terrestrial DOC and warming, bacterial respiration in Arctic polynyas may increase, tipping the CO_2 balance in favor of respiration and outgassing. In the Antarctic, warming may lead to melting of ice shelves (Rignot and Jacobs 2002, Shepherd et al. 2003), increased glacial runoff and stratification. Phytoplankton blooms may decrease in frequency and amplitude with the change in mixing regime. Increased warming will likely lead to changes in bacterial communities and their performance. Thus we envision a scenario in which differential warming may lead to increased differentiation of biogeochemical function and microbial ecology in polynyas.

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