Microbial Dynamics In Polar Oceans: A Bipolar Comparison

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ABSTRACT

Despite the relevance of high latitude oceans to models and budgets of global biogenic carbon and the central role of heterotrophic microbes in biogeochemical cycles, the patterns of energy flow through the lower food web in polar oceans are poorly understood. Differences in geomorphology, circulation patterns and riverine inputs lead to generally higher concentrations of dissolved organic carbon, bacterial abundances and standing stock, and bacterial production in the Arctic than the Southern Ocean. Despite these differences, the average rates of bacterial growth in these two polar regions are not significantly different from one another or from the global average. Bacterial abundances in polar regions are relatively constant and are typically 5 to 10 fold lower than in warm temperate and tropical oceans. The condition of relatively high growth rate and low and constant bacterial abundance implies that essentially all bacterial production is channelled to protistan grazers. Since primary production in polar regions is highly seasonal and is often limited to only a few months of the year, whereas bacterial production can occur even during the aphotic polar winter and under heavy ice cover, bacterivory or omnivory, rather than herbivory may be the dominant feeding mode of both protistan and metazoan grazers.

Introduction

Heterotrophic microbial metabolism is a dominant pathway of organic matter transformation in the sea [3,15]. Although net photosynthesis sets the upper limit for the biological pump that transfers atmospheric CO_2 into the ocean interior, sinking or mixing of dissolved and particulate inorganic and biogenic carbon below the pycnocline are the principal factors controlling this flux [26]. Decomposition, recycling and remineralization of particulate material by bacteria, and other heterotrophic plankton, influence the magnitude and composition of sinking fluxes by altering both the size of sinking particles and the equilibrium between the particulate and dissolved phases. The activity of bacterioplankton, and the ingestion rates of protistan and metazoan grazers influence the production of dissolved organic carbon, the flow of carbon between dissolved pools and metazoan food-webs, the magnitude and composition of sinking fluxes [7,9,10; and references cited therein] and ultimately the CO_2 exchange between atmosphere and ocean. Hence, the processes that occur within the microbial trophic level as well as the coupling between microbes and metazoans influence both the recycling of carbon within the surface layer and the export of biogenic carbon to depth or to higher trophic levels.

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The Arctic and Southern Oceans account for ~20% (~ 9.3 Gt C yr^{-1}) of global primary production [17], are sites of active deep convective mixing and are potentially significant for carbon sequestration [28]. Despite the relevance of the high latitude oceans to models and budgets of biogenic carbon, and the central role of heterotrophic microbes in global biogeochemical cycles, the patterns of energy flow through the lower food web in polar regions are poorly understood. Several recent studies reporting that microbial populations are active in both polar oceans [6,13,16,19,27] were typically limited in temporal scope, hence it is uncertain if active microbial populations are a local or general characteristic of polar systems. In this study, we report on the seasonal patterns of bacterial growth rates at high latitude sites in the Arctic and Antarctic and speculate on the role of bacterial based food webs and microbial trophic pathways in overall energy and material cycling in high latitude oceans.

Materials and Methods

Field Sites

In the Canadian Arctic, water was collected at 5 to 10 m in Resolute Passage (74° 38.5' N, 94° 51.5' W) by repeated sampling through a permanent sample hole in sea ice (March through June, November through December) or by boat during the open water period (July through October) [2,23]. Water samples were returned within one hour of collection to the Resolute Bay Marine Laboratory for analysis and processing. In McMurdo Sound, Antarctica, samples were collected at 10 to 15 m through a permanent sample hole in sea ice at our seasonal camp (78° 25' S, 166° 30' W) [20,22]. Samples were either processed immediately at our field laboratory (September through mid-November) or returned within two hours of collection to the Eckland Biological Laboratory for analysis and processing (late November through mid-January).

Biomass and Bacterial Growth Rates

Samples (preserved with gluteraldehyde, 1.5% final concentration) were filtered onto black 0.2 µm Poretics or Nuclepore filters, stained with acridine orange (usually within two weeks of collection) and bacterioplankton were counted by epifluorescence microscopy [11]. Bacterial growth rate was computed from the incorporation of [methyl- ^{3}H] thymidine (^{3}H-TdR; ICN, 60-90 Ci $mmol^{-1}$; 5 nmol TdR final concentration) [25]. Samples were incubated in replicate 100 ml polycarbonate bottles in the dark at -1.5°C ± 0.2°C. Triplicate 15 ml aliquots were removed immediately after adding the isotope (t_0), and at the end of a ~6 h incubation (t_f). Particulate material was collected onto 0.2 µm membrane filters, rinsed with filtered seawater, and ice cold 5% trichloracetic acid (TCA), and filters were counted in a liquid scintillation spectrometer [20,24]. All counts were corrected for quench and for background radiation, and incorporation was computed as net (t_f - t_o) uptake of TdR.

Conversion factors relating cell production to TdR uptake were empirically determined [5,14,25] using seawater dilution cultures. Briefly, < 1.0 µm filtrate was diluted 1:5 with 0.2 µm membrane filtered seawater, ^{3}H-TdR (5 nmol TdR final concentration) was added to 1-liter polycarbonate bottles containing the 900 ml of the dilution culture, and the time course of change of cell abundances and the incorporation of TdR was determined at ~12 h intervals for ~48 h. All incubations were carried out in the dark at ~ -1.5°C ± 0.2°C.

Conversion factors were determined from regression analysis using the cumulative method [5,25].

Nutrient Enrichment Experiments

At both the Arctic and Antarctic sites, the influence of nutrients on bacterial growth rates was examined as previously described [25] for samples collected in the upper mixed layer (5 to 10 m). Triplicate bottles containing bacterivore-free seawater cultures, prepared as described in [25], were enriched in with 5 µmol glucose or 5 µmol glutamic acid [22,25] and incubated in the dark at the temperature from the depth of collection (± 0.2°C), and bacterial abundances were estimated at ~24 h intervals for ~96 h.

Results and Discussion

North and South Polar seas share a number of similar characteristics: The pattern of solar irradiance is highly seasonal and seawater temperatures are persistently low. However there are a number of differences: The Arctic Ocean its and adjacent seas (17×10^6 km^2) receive the outflow (~3,500 km^3 yr^{-1}) of several major rivers from the North American and Eurasian continents, are ice covered for most of the year and are circumscribed by land masses and have an extensive system of shallow continental shelves. Although the Arctic Ocean represents ~5% of the World Ocean, it accounts for ~25% of all continental shelves. In contrast, the Southern Ocean (38×10^6 km^2) has negligible riverine and freshwater ($\leq$ 675 km^3 yr^{-1}) input, mainly from glacial melt, is seasonally ice covered and has a very

Table 1. General distribution of dissolved organic carbon (DOC), bacterial abundance, production and growth rates in the upper water column of the Arctic Ocean and Ross Sea, Antarctic. For DOC and bacterial biomass, means and ranges (in parentheses) are presented and for bacterial production and growth rates, ranges only are presented.

	Arctic Ocean			Ross Sea	
	Shelf	Slope	Basin	Pre-Bloom	Bloom
DOC (µmol)	*34.8* (32.1 - 37.5)	*72.5* (59.8 - 80.6)	*82.9* (60.4 - 101.3)	*43.5* (43.2 - 43.8)	*44.3* (42.6 - 54.6)
Bacterial Biomass (µg C l^{-1})	6.5 (5.6 - 7.1)	11.5 (7.6 - 15.4)	9.1 (7 - 13)	0.44 (0.29 - 0.77)	1.31 (0.78 - 2.2)
Bacterial Production (ng C l^{-1} d^{-1})	870 - 2150 (3.2 - 54.4)	580 - 800 (304 - 368)	1070 - 2500	32	344
Bacterial Growth Rates (d^{-1})	0.13 - 0.33	0.05 - 0.07	0.11 - 0.27	0.07	0.26

Ross Sea data: [6]
Arctic Ocean data: [19,27,30]

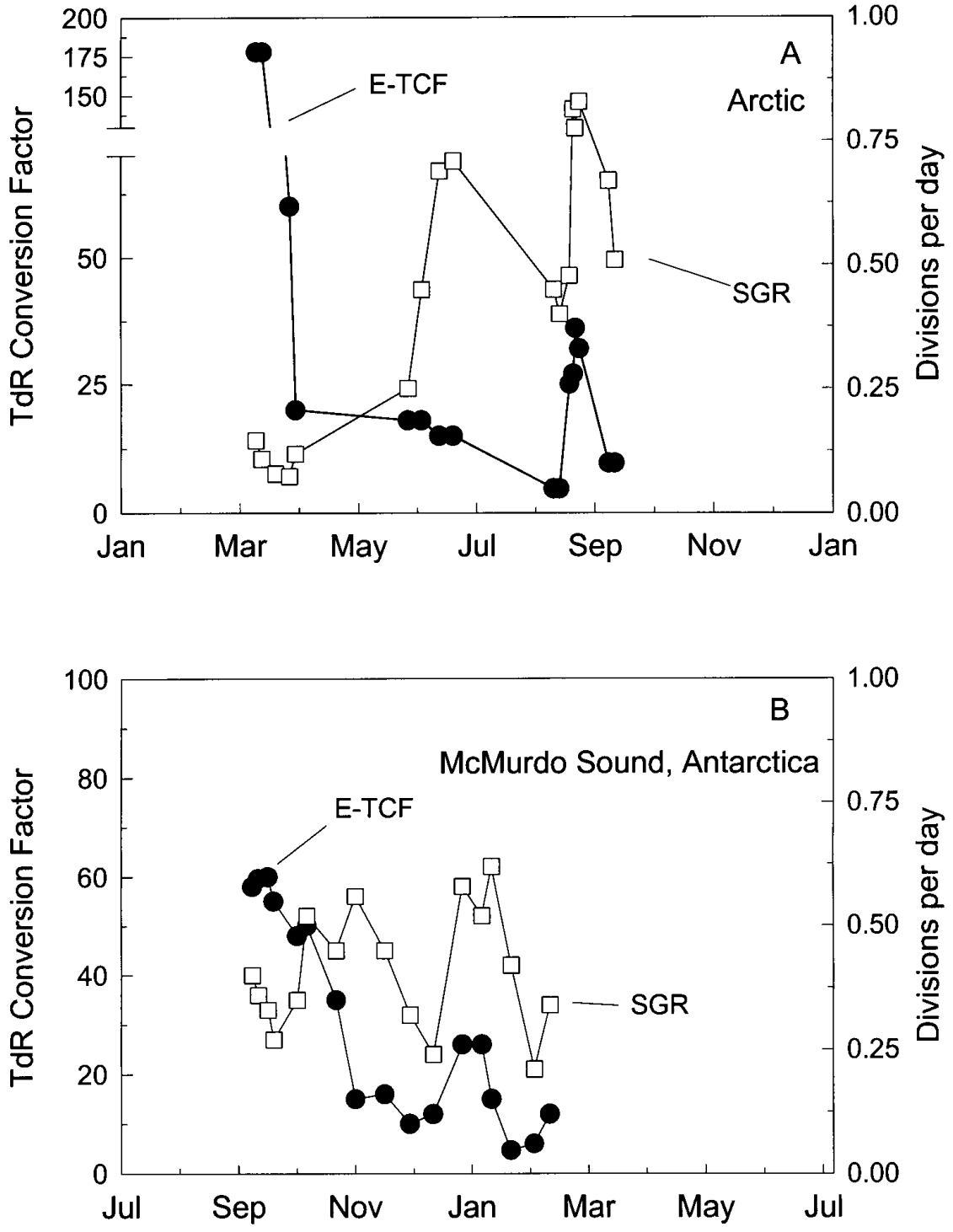

Figure 1. Temporal patterns in empirical thymidine conversion factors (● -10^6 cells produced pmol TdR^{-1} incorporated; E-TCF) and cell division rates (- divisions per day; SGR) of bacterioplankton in (A) Resolute Bay, NWT and (B) McMurdo Sound, Antarctica. Average Coefficient of Variation for E-TCF = 15-20% and for SGR = 20%.

limited deep continental shelf (i.e. Ross and Weddell Seas) and essentially no shallow continental shelf system. These differences have major consequences for the microbial ecology of these regions. The concentration of dissolved organic carbon (DOC), bacterial abundances and standing stock, and bacterial production are generally higher in the Arctic than the Ross Sea (Table 1). In contrast, the rates of bacterial growth are not significantly different. This pattern is consistent with previous reports of higher bacterial biomass and production in Resolute Bay, NWT, than in McMurdo Sound, Antarctic [2,20,23].

The annual average rates of bacterial growth were similar in both Resolute Bay (0.44 ± 0.27 d^{-1}) and McMurdo Sound (0.40 ± 0.13 d^{-1}), however the seasonal patterns differed (Fig. 1). At the Arctic site (Fig. 1A), growth rates ranged from ~0.1 to 0.85 d^{-1} with minima in late winter, an increase through the spring, a decrease prior to the phytoplankton bloom and a seasonal maximum during the bloom before declining in the early autumn. In contrast, at the Antarctic site (Fig. 1B), bacterial growth rates were relatively constant over the season (~0.25 to 0.65 d^{-1}) with minima in the late winter and prior to the phytoplankton bloom in early December and maxima in late spring and during the phytoplankton bloom in late December to early January. Bacterial growth rate varied by only 5 to 8 fold (Fig. 1) despite a 300 to 1000 fold variation in the volume specific ^{3}H-TdR uptake rates in the Arctic and Antarctic, respectively. Cell production is related to TdR uptake by a thymidine conversion factor (TCF), and since we empirically determined these conversion factors (E-TCF) at frequent intervals (Fig. 1), we were able to convert rates of ^{3}H-TdR incorporation to cell division. In the Arctic, the E-TCF declined from a maximum of ~175 x 10^{6} cells pmol TdR^{-1} incorporated in late winter (when TdR incorporation rates are at their seasonal minimum) to ~7 x 10^{6} cells pmol TdR^{-1} in summer (Fig. 1A). In the Antarctic (Fig. 1B), the E-TCF range was smaller (~5 to 60 x 10^{6} cells pmol TdR^{-1}), however the trend (maximum E-TCF in late winter with a general decrease through the season) was similar to the Arctic. Although the early season E-TCF was high and the seasonal range in the E-TCF was large (12 to 25 fold in the Antarctic and Arctic, respectively), similar values and ranges in the TCF have been previously reported (43 fold range [23] and ~600 fold range [8,14] respectively).

Table 2. Bacterial growth rate response to the amending of bacterivore-free seawater cultures with organic nutrients (5 µmol glucose plus 5 µmol glutamic acid). Experiments were carried out during the transition from late winter to late summer in the Arctic (Resolute Bay, NWT) and the Antarctic (McMurdo Sound).

	Late Winter	Early Spring	Pre-Bloom	Bloom	Post-Bloom
Arctic	-	+	++	+	++
Antarctic	-	-	+++	+	++

"-" No enhancement of growth rate upon the addition of organic nutrients (% control response $\leq$ 125%).

"+" Marginal enhancement of growth rate upon the addition of organic nutrients (% control response = 125 to 200%).

"++" Moderate enhancement of growth upon the addition of organic nutrients (% control response = 200 to 350%).

"+++" Profound enhancement of growth upon the addition of organic nutrients (% control response $\geq$ 350%).

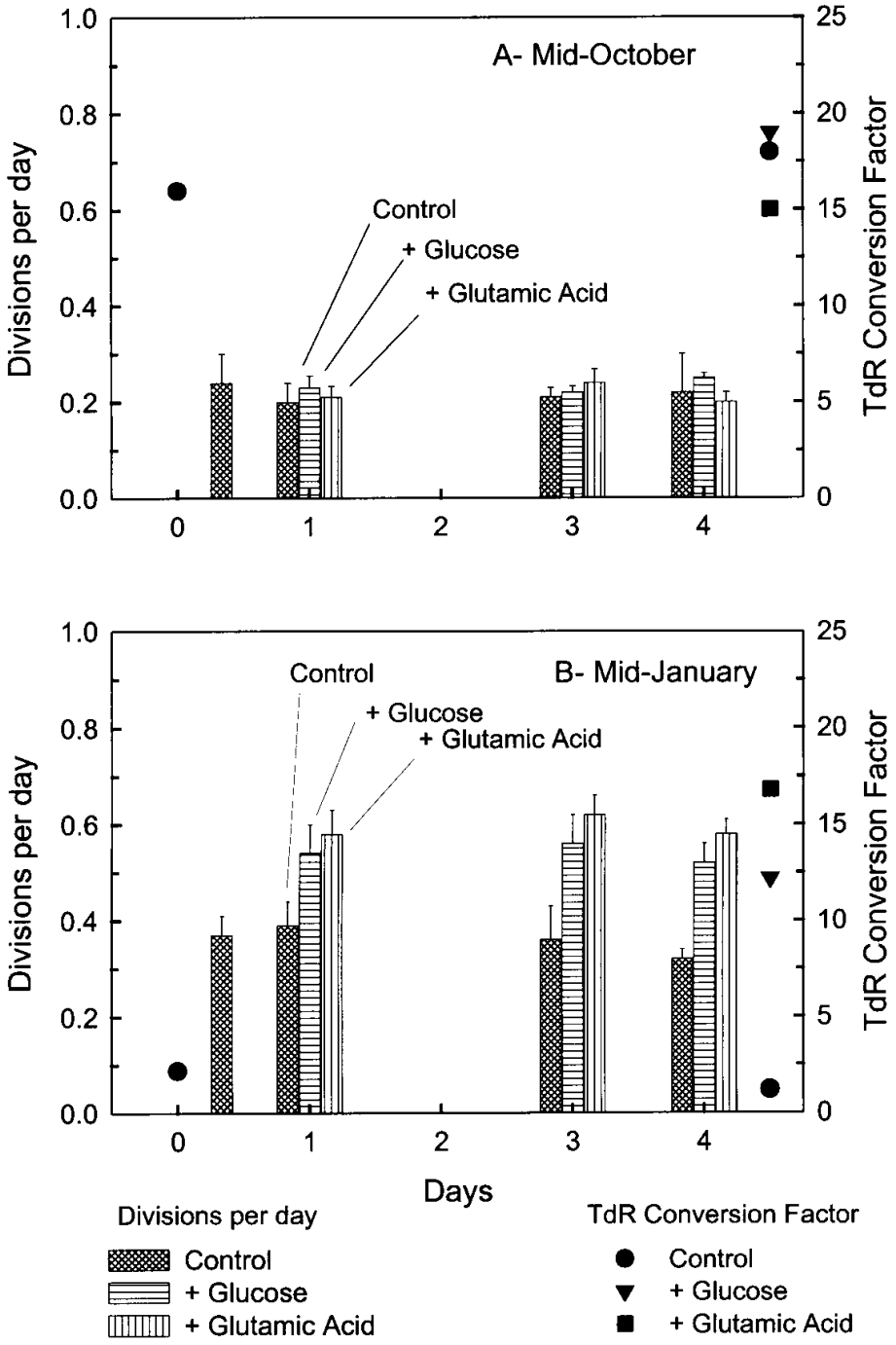

Figure 2. Effect of the addition of 5 µmol glucose or glutamic acid on cell division rate (divisions per day; vertical bars) and the empirical thymidine conversion factor (E-TCF- 10^6 cells produced pmol TdR^{-1} incorporated; symbols ● , ▼ , ■) of bacterioplankton in McMurdo Sound, Antarctic during (A) mid-October (i.e. early spring) and (B) mid-January (i.e. post-bloom). Control is the nutrient-free condition. The thymidine conversion factors were measured before adding nutrients (i.e. day 0) and at the end of the nutrient enrichment experiment (i.e. day 4) for each nutrient treatment. Error bars for growth rates are the standard error of triplicate incubation bottles and the average Coefficient of Variation for E-TCF = 15-20%.

What controls the rates of growth and the E-TCF in polar regions where temperatures are constant and low? To address this, we examined the influence of organic nutrients (glucose or glutamic acid) on the growth and E-TCF of bacterioplankton during different seasons in both the Arctic and Antarctic. These results are summarized in Table 2 and Fig. 2. The trends in both systems are similar, with minimal or marginal effects of nutrients on growth during late winter, early spring, and during the phytoplankton bloom and moderate to profound enhancement during the pre-bloom and post-bloom periods (Table 2). Since the E-TCF was higher during the late winter and early spring, than at other times of year, we proposed that there was an interaction between substrate availability, the nutrient status of the bacterioplankton and the E-TCF [24]. This was tested by measuring the effect of nutrient enrichment on concurrent estimates of bacterial growth rates and the E-TCF (Fig. 2). During early spring (mid-October) in McMurdo Sound, growth was not enhanced by substrate amendments and the E-TCF was similar (~15 to 19 x 10^6 cells pmol TdR^{-1}) both before (day 0) and after (day 4) the addition of nutrients. In contrast, during the post-bloom period (mid-January) the growth rate doubled after enrichment with glucose and glutamic acid (Fig. 2B) and the E-TCF increased from ~2 x 10^6 cells pmol TdR^{-1} incorporated before (day 0) the addition of nutrients to ~12 to 16 x 10^6 cells pmol TdR^{-1} afterwards (Fig. 2). Similar nutrient dependence of the E-TCF was observed in Resolute Bay, and Conception Bay, Newfoundland (Rivkin, in prep.). It is known that bacteria can catabolize TdR [8,12; and references cited therein] and although the relative patterns of catabolism and incorporation into DNA have been characterized in a variety of habitats, consistent relationships with environmental variables have not been found [reviewed by 12]. The results presented here suggest that nutrient-limited bacteria may catabolize TdR as a carbon or nitrogen source (C:N = 4.3 by weight), and this could result in a lower E-TCF than would be expected if TdR were used primarily for DNA synthesis. This relationship is currently being elucidated.

A recent review of the literature [24] showed that average growth rate of bacterio-plankton from cold ($\leq$ 4 ^oC) and temperate (> 4 ^oC) oceans are similar (0.41 ± 0.42 d^{-1} and 0.39 ± 0.41 d^{-1}, respectively) at their respective ambient temperatures. We have extended this literature review to assess the growth rates of bacterioplankton from polar. Average rates of bacterial growth in the Arctic (0.30 ± 0.27 d^{-1}) and Antarctic (0.34 ± 0.23 d^{-1}) are not significantly different from one another (t-test, $P < 0.05$) or from the global average of 0.40 ± 0.43 d^{-1} (Student-Neuman-Kuels, $P < 0.05$). The growth rates (0.90 ± 0.35 d^{-1}) of bacteria from sea ice communities at a temperature of ~-1.8 ^oC are significantly greater than the global average as well as that of bacteria in the underlying water column (SNK, P = 0.05) [21]. Bacteria appear to be very sensitive to small changes in temperature between -1.8 and 0^o C [24], and both the lowest growth rate and greatest range (ca. 10^4) in growth rates occur within this temperature range. The high variability of growth rates in this temperature range may reflect heterogeneity in the distribution of labile organic substrates and the stimulation of cell division by elevated substrate concentrations at low ambient temperatures [18].

Bacterial biomass and rates of bacterial production in polar regions are 5 to 15 fold lower than in temperate oceans [4,6,8,19,20,29; and references cited therein]. Although it has been generally accepted that bacterial growth rates are low in polar regions [18], the

results reported above and in [24] suggest that bacterial growth rates are similar in polar and temperate oceans. Is this a reasonable assumption? We can indirectly evaluate this by back-calculating bacterial abundances using the average growth rates for global warm oceans (0.39 d^{-1}), the Antarctic (0.34 d^{-1}) and the Arctic (0.30 d^{-1}), and the average rates of bacterial production for Coastal/Shelf (12 to 34 mg C m^{-3} d^{-1}), Ocean (4 to 11 mg C m^{-3} d^{-1}) and Southern Ocean (2 to 4 mg C m^{-3} d^{-1}) reported in Table 6 of [8]. The calculated abundances (Coastal/Shelf = 6 to 12 x 10^8 cells l^{-1}; Ocean = 2 to 6 x 10^8 cells l^{-1}; Southern Ocean = 1 to 3 x 10^8 cells l^{-1}; assuming 20 fg carbon bacteria^{-1}) fall within the ranges reported for these regions. It therefore follows that the bacterial growth rates are indeed similar across cold and warm ocean regimes and the differences in bacterial production across oceanic provinces reflect spatial variations in biomass rather than rates of growth.

Bacterial abundances in polar seas are relatively low and constant. Since the steady-state abundance is the balance between growth and mortality, the magnitude of losses (due to bacterivory and viral lysis), must be similar to that of growth. Based upon the observed seasonal pattern in bacterial growth rates (Fig. 1, and [1,20,23]) and cell abundances [20,23], we predict that ~ 95 to 98% of *in situ* bacterial production is channeled into bacterivores (or viruses). This suggests that bacterial based food webs and microbial trophic pathways are important in overall energy and material cycling in high latitude oceans. Moreover, since primary production in polar regions is highly seasonal and is often limited to only a few months of the year, whereas bacterial production can occur even during the aphotic polar winter and under heavy ice cover, bacterivory or omnivory, rather than herbivory may be the dominant feeding mode of both protistan and metazoan grazers.

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