Microbial growth in the polar oceans — role of temperature and potential impact of climate change

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Abstract | Heterotrophic bacteria are the most abundant organisms on the planet and dominate oceanic biogeochemical cycles, including that of carbon. Their role in polar waters has been enigmatic, however, because of conflicting reports about how temperature and the supply of organic carbon control bacterial growth. In this Analysis article, we attempt to resolve this controversy by reviewing previous reports in light of new data on microbial processes in the western Arctic Ocean and by comparing polar waters with low-latitude oceans. Understanding the regulation of *in situ* microbial activity may help us understand the response of the Arctic Ocean and Antarctic coastal waters over the coming decades as they warm and ice coverage declines.

Heterotrophic bacteria are crucial components of marine food webs and have key roles in controlling carbon fluxes in the oceans. These bacteria are part of the microbial loop, which consists of the production of dissolved organic material (DOM) by phytoplankton and other organisms, uptake of DOM by heterotrophic bacteria and consumption of bacteria by protist grazers (FIG. 1). The material and energy consumed by protozoan grazers can be transferred to larger organisms or can be exported down to the deep ocean, but much of the organic carbon is respired by bacteria and grazers to carbon dioxide, whereas other organic components are mineralized back to become essential inorganic nutrients, such as ammonium and phosphate. In a simplified view of the complex flows, most of the carbon consumed by bacteria and the rest of the microbial loop is carbon diverted from large organisms and from export and storage in the deep ocean. Consequently, microbial loop activity determines, in part, the response of oceanic ecosystems and the carbon cycle to climate change.

Extensive analysis has shown that heterotrophic bacteria often process the equivalent of about 50% of primary production in coastal waters and low-latitude oceans, although this fraction varies[1]. At one extreme are data indicating high rates of bacterial production, and even cases in which total consumption of organic carbon exceeds contemporaneous primary production[2], although this finding is controversial[3–5]. At the other extreme, bacterial production can be low relative to primary production, such as during 'phytoplankton blooms' (large increases in phytoplankton biomass), when primary production exceeds community respiration[6]. Uncoupling the microbial loop from phytoplankton in time and space leads to variation in phytoplankton–bacteria relationships and in the processing of primary production by heterotrophic bacteria.

In part because of this high variability, it is not clear if there are systematic differences between oceanic regions in microbial loop dynamics and in the fraction of primary production processed by heterotrophic bacteria. The most likely difference is between polar systems and lower-latitude waters. More than 20 years ago, Pomeroy and Deibel[7] postulated that low bacterial growth in cold waters allows rapid growth of larger organisms and vigorous fisheries in subarctic waters. Consistent with this idea, the annual average for bacterial production is in fact low in the Ross Sea[8] and the ratio of bacterial production to primary production in this Antarctic sea is among the lowest of all marine systems[6]. Several other studies have cast doubt on the Pomeroy hypothesis, however, and on whether bacterial growth is actually lower in perennially cold waters[9,10].

New data on the role of temperature in the regulation of bacteria–phytoplankton interactions[11,12] and on production rates and other key ecosystem properties in the western Arctic Ocean[13,14] have recently been published. These new data once again raise questions

Heterotrophic
The use of organic material to supply energy and carbon for synthesis of cellular components.

Marine food web
A term used to refer to the complex suite of predator–prey interactions among organisms in the ocean.

Protist
A single-cell eukaryote, sometimes referred to as a protozoan.

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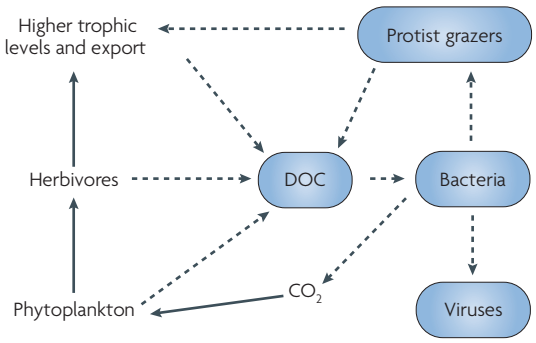

Figure 1 | **Schematic of the microbial loop.** All components of the microbial loop are shown in blue. 'Phytoplankton' includes cyanobacteria, which are major components of the phytoplankton community in some oceans. Protists are single-cell eukaryotes. All organisms, and not just bacteria, release CO_2 during respiration. The 'loop' refers to losses of dissolved organic carbon (DOC) from all organisms and its recovery into the food web by heterotrophic bacteria. Archaea are not abundant in the waters considered in this Analysis.

Primary production
The rate at which plant biomass is produced. The estimates discussed here were derived using the ^{14}C method, meaning that the rates are somewhere between gross primary production (without subtracting any loss owing to respiration) and net primary production (for which respiration is considered).

Bacterial production
Analogous to primary production, bacterial production is the rate at which bacterial biomass is produced in the absence of mortality.

Uncoupling
Bacteria are coupled to phytoplankton if their production or biomass levels co-vary over time and space and if correlations between the two are strong regardless of the magnitude of the production or biomass ratios.

Bacterial growth efficiency
The ratio of carbon used for biomass synthesis to total carbon use (synthesis and respiration). In addition to being a crucial parameter in bacterial energetics, bacterial growth efficiency is important in determining how much carbon taken up by bacteria is passed on to higher trophic levels versus that lost to respiration.

about what controls microbial growth in polar waters. In this Analysis article, we aim to integrate these new data with similar data from other oceans and to compare the western Arctic Ocean with the Ross Sea. We have used estimates of dissolved organic carbon (DOC) concentrations and other biogeochemical data to explore the differences in microbial properties, such as growth rates and biomass levels, between oceanic regions. The results described in this Analysis article will lead to a reassessment of old hypotheses about DOC–temperature interactions[15] in controlling microbial growth and provide some clues as to how the Arctic Ocean and Antarctic coastal waters might respond to the climate changes that are already impacting these fragile ecosystems.

Data sets and methodology

Supplementary information S1 (table) summarizes the data sets used for this Analysis article, including geographical locations, the number of sampling stations and important references. These data sets were used because of their size, the range of oceanic systems they covered and because virtually all of the projects discussed here used the same methodology, often by the same investigators. These similarities allow us to compare microbial and biogeochemical properties from diverse oceanic regions. The methods, which are described in Supplementary information S1 (table), Supplementary information S2 (box) and in more detail in the original publications referenced in Supplementary information S1 (table), are commonly used to study microbial oceanography.

Primary and bacterial production

We compared the western Arctic Ocean and the Ross Sea with four lower-latitude oceans: the Equatorial Pacific Ocean, the Arabian Sea, the North Atlantic Ocean and the subarctic Pacific Ocean (Supplementary information S1 (table)). Although principle component analysis of abiotic properties indicated that the six oceans are distinct (Supplementary information S3 (figure)), all microbial properties differed more between the polar environments and the other oceans than among the lower-latitude oceans. The microbial properties we considered in depth include bulk estimates of biomass (mass of cellular carbon per square metre), production (mass of cellular carbon produced per day per square metre) and growth rates (per capita daily change in abundance).

All of the properties examined here varied over time and space within the six oceanic regions, but the western Arctic Ocean and Ross Sea still differed significantly from the four lower-latitude oceans for two of the most basic properties of the plankton system: primary production and bacterial production rates (FIG. 2). Primary production estimates varied by nearly 100-fold, but the median rate varied less than fivefold, from about 20 mmol C m^{-2} d^{-1} in the western Arctic Ocean to about 90 mmol C m^{-2} d^{-1} in the Equatorial Pacific and Arabian Sea (FIG. 2a). Primary production in the western Arctic Ocean and Ross Sea was statistically the same, and primary production in both was significantly lower than in the other oceanic regions (based on analysis of variance (ANOVA); p <0.001–0.02, depending on which two regions were compared).

Bacterial production was also significantly lower in the western Arctic Ocean and Ross Sea than elsewhere (from ANOVA; p <0.001–0.01). Median rates in these two polar regions were <2 mmol C m^{-2} d^{-1}, which is approximately fivefold lower than in the Equatorial Pacific and Arabian Sea (FIG. 2b). Note, however, that the maximum rates of bacterial production in both polar regions overlapped with the minimum rates measured for the low-latitude oceans, including the Equatorial Pacific (FIG. 2b). Bacterial production was therefore lower on average in polar waters, but the high rates occasionally observed in perennially cold environments hint that factors other than temperature alone might control bacterial growth.

Microbial loop fluxes

We used the ratio of bacterial production to primary production to explore how the fraction of primary production processed by the microbial loop varies among the oceanic systems examined here. High bacterial production to primary production ratios would suggest that the microbial loop consumes a large fraction of primary production if bacterial growth efficiency (BGE) does not vary systematically over these gradients (an assumption discussed below in detail). Overall, we found that bacterial production correlated with primary production (r = 0.48; p <0.001; n = 223), but the bacterial production to primary production ratio varied substantially. This ratio was lowest in the Ross Sea and Arctic Ocean (medians less than 0.05), whereas it equalled or exceeded 0.1 in the other oceans (Supplementary information S4 (figure)).

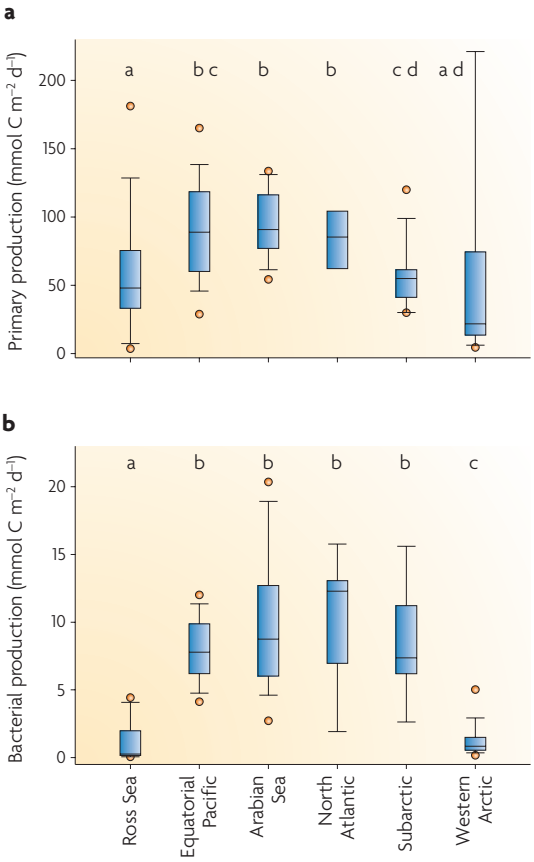

Figure 2 | **Box and whisker plot of biomass production integrated through the euphotic zone in six regions.** Primary production (**a**) and bacterial production (**b**). The ranges of the original data (not log transformed) are represented by points (5–95%), bars (10–90%) and boxes (25–75%). The line in the box represents the median. Values for regions with the same letter are not significantly different ($p > 0.05$) according to pair-wise, post hoc analysis of variance (ANOVA) analyses of log-transformed data.

Possible factors that affect the bacterial production to primary production ratio were explored with correlation analyses using data from all oceans. The two factors with the highest correlations were the euphotic zone depth ($r = 0.52$; $p < 0.0001$; $n = 212$) and temperature ($r = 0.42$; $p < 0.0001$; $n = 204$). If bacterial production decreases less with depth than primary production, as is often the case because of the dependence of primary production on light[16], there would be a high positive correlation between euphotic zone depth and the bacterial production to primary production ratio. The relationship between the bacterial production to primary production ratio and temperature is more complicated than implied by a simple linear correlation.

The bacterial production to primary production ratio increases with temperature, but only substantially for temperatures less than approximately 4 °C (FIG. 3a). In the low temperature range of –1.8–4 °C in the Arctic Ocean and the Ross Sea, bacterial production to primary production ratios vary greatly, from 0.01 to >0.2. These two cold systems have the lowest average bacterial production to primary production ratios, but several values are as high, or higher, than estimated for the warmer oceans. For waters warmer than approximately 4 °C, the bacterial production to primary production ratio does not vary systematically and remains at approximately 0.10. Although 0.10 seems small, in fact it implies that heterotrophic bacteria process a large percentage — over 50% — of primary production in the oceans, assuming that the BGE is approximately 0.15, which is the average for the oceans[17].

Regardless of the exact percentage, variation in the bacterial production to primary production ratio as a function of temperature has profound implications for the processing of organic carbon by heterotrophic bacteria and the rest of the microbial loop. The data imply that the fraction of organic carbon consumption by these microorganisms is insensitive to temperature, except for temperatures below approximately 4 °C. Variation in this fraction is mainly driven by changes in organic carbon consumption rates, not primary production, as the relationship between bacterial production and temperature (Supplementary information S5 (figure)) is similar to that depicted in FIG. 3a. We focus on the bacterial production to primary production ratio because it reveals more about the structure of marine food webs and carbon cycling than the bacterial production data alone. The data in FIG. 3a imply that a lower fraction of primary production is consumed by bacteria in cold polar waters than in warmer systems, pointing to fundamental differences in how carbon flows in these systems. However, these differences are not driven by temperature, as discussed below.

Our analysis uses a single BGE value because there is no clear evidence that BGE varies with temperature or systematically among oceanic regions. Some studies found a negative correlation between BGE and temperature[18–20], whereas others found no significant relationship[17,21–23]. Unfortunately, most of these studies did not examine the low temperatures (–1.8 to 4 °C) of the perennially cold environments considered here, where bacterial production to primary production ratios vary the most (FIG. 3a). A study in the western Arctic Ocean did not observe a significant temperature effect on BGE, which averaged 0.069 ± 0.090 ($n = 11$)[13]. Other estimates of BGE in polar waters include 0.24 ± 0.10 ($n = 3$) in the Arctic's Kara Sea[24] and 0.25 ± 0.13 ($n = 6$) in the Ross Sea[25]. These values are similar (bearing in mind experimental uncertainties) to those observed in warmer, lower-latitude systems[17].

Control by bottom-up factors

Why is bacterial production lower in the western Arctic Ocean and the Ross Sea than in the four lower-latitude oceans (FIG. 2b)? The answer seems to involve both bacterial biomass and, as suggested by the Pomeroy hypothesis[7], growth rates. To examine this hypothesis, growth rates of the total bacterial

Correlation analysis
A method for examining whether two factors co-occur ($r = 1$, if they do so perfectly, whereas $r = -1$, if they vary inversely to each other) that is often used in field studies to explore possible causal relationships that cannot be examined by direct experimentation.

Euphotic zone
The upper sunlit layer of the ocean, which extends down to a depth where light is 1% of the surface intensity.

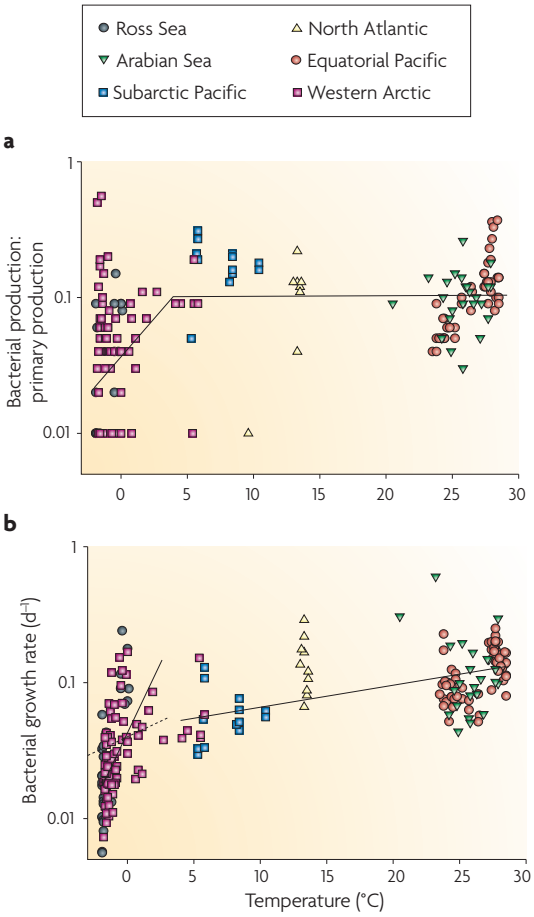

Figure 3 | **Effect of temperature on the bacterial production to primary production ratio and the bacterial growth rate. a** | Ratio of bacterial production to primary production as a function of temperature. Each point is the estimate for a sampling station in the indicated marine region. The lines are based on a segmented regression analysis that determined the break point to be 3.9 ± 2.8 °C (± the standard error). The slopes of log(bacterial production:primary production) versus temperature for temperatures below and above the break point are 0.111 ± 0.056 and 0.000679 ± 0.0065 per degree, respectively. **b** | Bacterial growth rate as a function of temperature. Each point is the average growth rate and temperature for the euphotic zone at a sampling station in the indicated marine region. The solid lines were derived from two linear regression analyses (–1.8 to 3.9 °C and >3.9 °C). Growth rates from –1.8 to 3.9 °C changed more than expected based on temperature alone; the actual change was 0.237 ± 0.037 per degree (solid line), whereas the change predicted from the temperature is 0.045 ± 0.011 per degree (dashed line). The predicted rates were calculated using the average activation energy estimated experimentally (TABLE 1). The slope of the log(growth rate) versus temperature was 0.016 ± 0.003 per degree for temperatures greater than 3.9 °C.

Q_{10}
The factor by which a rate increases after a 10 °C increase in temperature. Many biological reactions have a Q_{10} of 2, which is roughly equivalent to an activation energy of 50 kJ mol^{-1} at 20 °C.

community were estimated from integrated bacterial production divided by integrated bacterial biomass, yielding an average growth rate for the euphotic zone. Bacterial production in the Ross Sea and the western Arctic Ocean, which had virtually the same growth rates, was significantly lower than in the other oceanic systems (on the basis of ANOVA; p <0.03–<0.0001). Bacterial growth rates in the Arctic were 0.038 ± 0.047 d^{-1} (n = 94), which was threefold lower than in the Equatorial Pacific, for example, where rates averaged 0.12 ± 0.049 d^{-1} (n = 65).

We used correlation analyses and multivariable analyses to explore which microbial and biogeochemical properties might control growth rates of heterotrophic bacteria. The highest correlation was between growth rates and temperature (r = 0.71; p <0.001; n = 231). However, the relationship was not linear (FIG. 3b). Growth rates increased from –1.8 to approximately 4 °C, but increased tenfold less, based on the slopes of the regression lines, as temperatures continued to warm to 28 °C. The lowest rates were found in the coldest waters of the Ross Sea and the western Arctic. Yet a substantial number of the growth rate estimates for these two polar systems were as high as those observed in the warmer waters of the low-latitude oceans, such as the Equatorial Pacific (FIG. 3b). The nonlinear relationship between temperature and bacterial activity has been observed before in temperate estuaries[26,27], but growth rates levelled off at approximately 12 °C, or more than 10 degrees warmer than indicated in our global analysis. Another analysis of several marine systems[28] found a similar nonlinear relationship between growth and temperature, with rates reaching a maximum at approximately the same temperature (2 °C) as in our analysis.

The temperature effect implied by the field data for the lowest temperature range (<4 °C) is larger than that observed in short-term experiments, in which temperature is experimentally increased. The apparent activation energy calculated using the field data in FIG. 3 exceeds 125 kJ mol^{-1} for a temperature below 4 °C (TABLE 1), which is larger than the values of 44–96 kJ mol^{-1} estimated by controlled experiments of Arctic and Antarctic waters[11,29,30]. The implied activation energy for the North Atlantic was also high (249 ± 45 kJ mol^{-1}), whereas the value from the Equatorial Pacific for *in situ* communities (TABLE 1) was close to that estimated experimentally[31] and was roughly equivalent to a Q_{10} of 2. The experimentally determined activation energy suggests that growth rates vary less with temperature than is actually the case (FIG. 3b). It is conceivable that bacteria in regions estimated to have a high activation energy from *in situ* data, such as in polar waters, are more sensitive to temperature than those observed in experiments. However, it seems more likely that some other controlling factor co-varies with temperature.

We suggest that this other factor is the supply and concentration of labile DOM. Unfortunately, microbial ecologists do not have a good integrating measurement of DOM supply, and are forced to use a proxy, such as the rate of primary production, which is the ultimate source of most organic material in the sea. Bacterial growth rates were highly correlated with primary production for the six marine systems

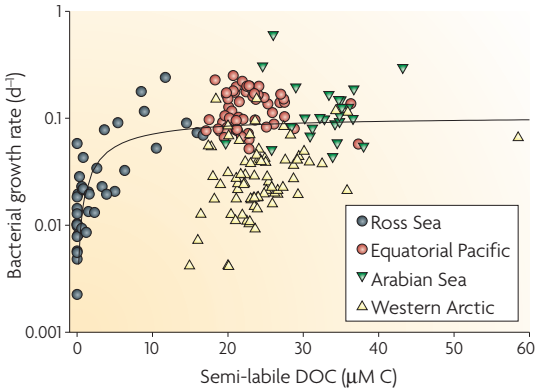

Figure 4 | **Bacterial growth rate as a function of semi-labile DOC concentrations.** Each point is the average growth rate and concentration for the euphotic zone at a sampling station in the indicated marine region. Dissolved organic carbon (DOC) data are not available for the North Atlantic and subarctic Pacific Ocean. The line was determined by fitting the bacterial growth rate data (μ) to the Monod equation: $\mu = \mu_{max} * S/(K_s+S)$, in which μ_{max} is the maximum growth rate and K_s is the concentration (S) at which the growth rate is half of μ_{max}. Nonlinear regression analysis yielded estimates of $\mu_{max} = 0.104 \pm 0.018\ d^{-1}$ and $K_s = 4.6 \pm 4.4\ \mu M\ C$ (± standard error).

examined here ($r = 0.55$; $p < 0.0001$; $n = 222$), which is consistent with the idea that DOM supply is important. Data on labile DOM concentrations are available only for a few of the oceans examined here[32,33], and may not be informative anyway because the concentrations were so low[34]. However, concentrations of one DOC component, semi-labile DOC, are high, and data are available from four of the six oceans examined here; data are not available for the subarctic Pacific and the North Atlantic oceans. In a three-pool model of DOC[35], semi-labile DOC is calculated from the difference between total DOC and refractory DOC because labile DOC concentrations are negligible. Concentrations of refractory DOC were assumed to be equal to concentrations of deep-water DOC[36], which is >1,000 years old[37] and is not used by bacteria on relevant timescales. We found that the correlation between semi-labile DOC and bacterial growth rates was 0.50 ($p < 0.001$; $n = 199$), which further supports the DOM hypothesis.

But the relationship was not linear. Growth rates increased with increasing semi-labile DOC in the Ross Sea, then reached an average for all regions of about 0.1 per day for semi-labile DOC concentrations that exceeded approximately 5 μM C (FIG. 4). The variability of semi-labile DOC in the Ross Sea reflects the seasonal cycle of its production and consumption[38]. Most interestingly, growth rates in the Arabian Sea and the Equatorial Pacific were slightly above the average, whereas growth rates from the western Arctic Ocean were below the average. Growth rates in the Arctic were about the same as in the Ross Sea, but were shifted by about 25 μM C in the growth rate versus semi-labile DOC graph (FIG. 4). This 25 μM C shift seems to be due to the input of refractory terrestrial DOC, which is high in the Arctic, but trivial in other oceans. The estimate of 25 μM C is similar to independent estimates of terrestrial DOC concentrations in basins of the Arctic Ocean[39,40].

The similarity in bacterial growth in the Ross Sea and the western Arctic becomes even more striking in light of the DOC data. The Ross Sea has lower DOC concentrations than the Arctic Ocean because there are no riverine inputs to Antarctic seas. The higher DOC concentrations in the Arctic do not lead to higher bacterial growth rates because terrestrial DOC does not support much microbial growth; the turnover time of terrestrial DOC is now approximately 7 years in the Arctic Ocean[39]. The slow degradation rates could be due to cold temperatures, and experiments have revealed that microbial activity increases after these waters are warmed[29,41]. However, given the long turnover times in the Arctic Ocean, terrestrial DOC is unlikely to support much bacterial growth even if Arctic waters were substantially warmed. High riverine inputs of particulate organic material[42] to the Arctic Ocean also do not seem to result in high growth rates, nor do they affect microbial communities far from coastal regions that are directly impacted by river discharge[43].

The standard explanation for the low growth in polar waters is that heterotrophic bacteria are limited by some combination of temperature and low DOM concentrations[15], a hypothesis that is supported by laboratory work[15,44] and experimental studies in the Arctic[41]. However, the data in FIG. 3 are not consistent with this explanation. By comparing rates predicted from temperature alone (dashed line in FIG. 3b) with actual data (solid line in FIG. 3b), we estimated that only 20% of the variation in bacterial growth rates below 4 °C could be due to temperature. Furthermore, the data are not consistent with a prediction by the temperature–DOM hypothesis that bacterial growth is more sensitive to temperature when DOM levels are low. By contrast, the relationship between bacterial growth rates and temperature was similar for low and high levels of semi-labile DOC and a proxy of the DOM supply (primary production) (data not shown). Finally, the activation energies and Q_{10} values measured experimentally are similar for both cold and warm ocean systems (TABLE 1). In summary, although temperature effects cannot be ignored, there seems to be no need to evoke any special effects to explain microbial dynamics in polar waters.

Control of bacterial biomass

In addition to growth rates, the difference in bacterial production between polar waters and elsewhere was also due to biomass levels. Bacterial biomass varies significantly among the six marine systems examined here (FIG. 5), whereas phytoplankton biomass did not (Supplementary information S6 (figure)), with the unsurprising exception that the North Atlantic, represented here by data from a spring bloom, had

Semi-labile DOC
One simple model of oceanic DOC divides it into three parts: the labile fraction used by bacteria on the day to week timescale; the refractory fraction that bacteria need from years to millennia to degrade; and the semi-labile fraction that is used on timescales between the extremes set by the other two DOC parts. Because labile DOC concentrations are trivial, the size of the semi-labile DOC pool in surface waters can be estimated from the difference between total DOC and deep-water DOC concentrations. DOC at depths below about 1,000 m is refractory and has turnover times that exceed 1,000 years.

Table 1 | **Summary of activation energies for bacterial growth rates (per day) as a function of temperature**

Regime	Temperature range (°C)	Activation energy (kJ mol^{-1})	Standard error for the activation energy	Refs
In situ *variation**				
Global: all	4 to 28.5	11	1.9	D.L.K., X.A.G.M. and H.D., unpublished observations
Equatorial Pacific	23.5 to 27.8	40	7.7	D.L.K., X.A.G.M. and H.D., unpublished observations
West Arctic	–1.8 to 9.4	47	12	13
West Arctic	–1.8 to 0	212	43	13
North Atlantic	9.6 to 13.6	249	45	D.L.K., X.A.G.M. and H.D., unpublished observations
Ross Sea	–1.9 to 0.6	316	44	D.L.K., X.A.G.M. and H.D., unpublished observations
Global: cold	–1.9 to 4	127	21	D.L.K., X.A.G.M. and H.D., unpublished observations
***Experimental*‡**				
Arctic	0 to 5	44	23	29
Antarctica	–2 to 8	96	77	64
Antarctica	–0.6 to 0.4	52	58	11

*There was no significant relationship between temperature and growth rates for the Arabian Sea (temperature range of 20.5 to 27.9 °C) and the subarctic Pacific Ocean (5.3 to 10.4 °C). ‡The activation energy was calculated from experiments in which temperature was experimentally increased (given as the 'temperature range'), whereas the other values were calculated from *in situ* variation in temperature. Ducklow *et al.*[65] did not observe any change in growth rates with a 2 °C increase in temperature in two Ross Sea experiments.

the highest average phytoplankton biomass of the six marine systems. Integrated bacterial biomass was significantly lower in the Ross Sea and western Arctic Ocean than in the other oceanic regions (FIG. 5), which contributed to the lower production rates observed in these two polar systems. The average bacterial biomass was 29 ± 23 mmol C m^{-2} (n = 54) and 35 ± 17 mmol C m^{-2} (n = 100) for the Ross Sea and western Arctic, respectively. This was substantially lower than, for example, in the Equatorial Pacific Ocean, which has a bacterial biomass of 67 ± 17 mmol C m^{-2} (n = 71).

The low levels of bacterial biomass in polar waters could be due to top-down control and exceptional rates of grazing and viral lysis. In support of this hypothesis, an experimental study in waters off Livingston Island (Antarctica) argued that fast growth by grazers prevents heterotrophic bacteria from responding to phytoplankton blooms[45]. Also, the number of potential bacteriovores was found to be high, relative to bacterial abundance, in West Antarctic Peninsula coastal waters[46]. However, other work indicates that grazing on bacteria is low during phytoplankton blooms in McMurdo Sound (Antarctica)[47], as is bacteriovore abundance in the Ross Sea[48], and Rose and Caron[49] argue that heterotrophic protists are sensitive to low temperatures, at least compared with phototrophs. Viral lysis probably accounts for the missing mortality in polar waters[50,51], although one study found that viral lysis was insignificant in the Chukchi Sea of the western Arctic[52].

The few relevant data gathered to date cannot be used to rule out the possibility that top-down control of bacteria is fundamentally different in polar waters. Still, we think it is unlikely that grazing and viral lysis are more effective in the Arctic Ocean and Ross Sea than elsewhere and that high mortality rates explain the low levels of bacterial abundance and biomass in these systems. What seems more likely is the most parsimonious explanation: low bacterial abundance is tied to the same factors, DOM supply and, to some extent, temperature, causing growth rates to be low in polar waters.

Implications for climate change

A rigorous understanding of how climate change affects material and energy flow in the oceans requires models that adequately represent the essential features of oceanic physics, biology and chemistry. Still, some speculation here may help the development of these models and the identification of crucial questions that need to be addressed. We focus on the Arctic Ocean, where climate change is already evident, but this discussion also applies to Antarctic seas that are also affected by global warming. The temperature of the Arctic system has been

Top-down
Top-down factors, such as grazing and viral lysis, affect biomass levels, whereas bottom-up factors, such as temperature and nutrient concentrations, control growth rates.

Bacteriovore
Any organism that eats bacteria. In lakes and the oceans, bacterivores are mostly protists.

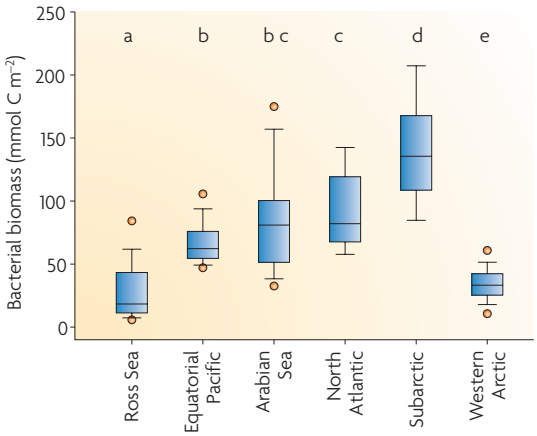

Figure 5 | **Box and whisker plot of bacterial biomass integrated through the euphotic zone in six regions.** The ranges of the original data (not log transformed) are represented by points (5–95%), bars (10–90%) and boxes (25–75%). The line in the box represents the median. Values for regions with the same letter are not significantly different ($p > 0.05$) according to pair-wise, post hoc analysis of variance (ANOVA) analyses of log-transformed data.

increasing over the past 100 years, and the sea surface of some regions was warmer by as much as 5 °C in 2007 compared with the previous 13 years[53]. That year also saw a record low for sea ice coverage[54] and is part of a trend that some models predict will end with an ice-free Arctic Ocean in summer by 2040 (REF. 55). Decreasing ice coverage lessens the contribution by sea ice algae and could affect the timing of spring phytoplankton blooms because of changes in mixing, but these and other processes are difficult to quantify. We know more about the potential impact of climate change on light and nutrient supplies, as summarized in FIG. 6.

The data presented in FIG. 3, if taken at face value, suggest that a warming of Arctic surface waters by even a few degrees could lead to substantially more carbon, and other elements, being processed by the microbial loop and potentially less going to higher trophic levels and export to the deep sea and the benthos. However, all of the experimental work conducted to date suggests that the direct effect of temperature would be minimal (TABLE 1). Even the direct temperature effect suggested by temperature-shift experiments may be an overestimate, because of adaptations by microbial communities to higher temperatures and limitations by other factors. The other factors that we suggest are more crucial than temperature include light for phytoplankton and inorganic and organic nutrients for phytoplankton and heterotrophic bacteria, respectively.

Both light levels and the inorganic nutrient supply are likely to change in the Arctic in the future, but possibly in opposite ways. Less ice means more light penetration into surface waters, whereas it is more difficult to predict how nutrient supply may change. In the western Arctic Ocean, most of the external or 'new' nutrients currently come from the North Pacific Ocean through the Bering Strait[56]. Nutrients from this source may decrease as the North Pacific water column heats up and becomes more stable, allowing more removal of nutrients from surface waters[57,58] before they reach the Arctic Ocean. In fact, concentrations of nitrate, phosphate and silicate were lower in 2004 than in 2002 in the western Arctic, probably because North Pacific waters entering the Arctic were warmer and poorer in nutrients in 2004 (REF. 59). However, the nutrient supply from internal Arctic sources may increase if climate change leads to the thawing of frozen tundra soils and more nutrients in rivers and run-off feeding into the Arctic Ocean. Less sea ice could allow more wind-driven upwelling of nutrient-rich deep water to the surface layer at the shelf break[60].

FIGURE 6 suggests that the possible negative effect on phytoplankton growth of lower nutrient inputs might be compensated for by the positive effect of more light reaching an Arctic Ocean with less sea ice. This seems to have been the case recently for the western Arctic Ocean. Even though nutrient inputs and concentrations were lower in 2004 than in 2002, primary production rates were higher in 2004, probably because of the increase in availability of light made possible by the lower ice and snow coverage in that year[13]. Bacterial production was also higher, as were ratios of bacterial production to primary production, bringing these values closer to those observed in lower-latitude oceans. FIGURE 6 also illustrates the potential negative effect of higher microbial loop activity on other marine food webs. Reminiscent of the Pomeroy hypothesis[7], climate change may lead to higher microbial activity and less energy and material for supporting larger organisms and higher trophic levels.

Climate change is likely to have several other impacts on polar marine food webs that cannot be captured in a simple diagram such as FIG. 6. These impacts include changes in microbial community structure and cell size, which would affect production rates and the coupling between primary production and heterotrophic microorganisms, the biogeography of microbial species, the timing and spatial extent of phytoplankton blooms and the export of primary production to the benthos as the ice-free surface layer moves north into the Arctic basins[60]. Higher inputs of terrestrial organic material are unlikely to alter the metabolic balance of the Arctic Ocean, although work in freshwaters[61] suggests that oceanic microorganisms might use this material more readily in a warmer Arctic.

Although all of these complicated processes and impacts should be examined in more detail, we suggest that the data on microbial biomass and production presented here capture many important features of oceanic food webs. The data and our analyses revealed fundamental differences between the two polar systems and the rest of the oceanic regions, but few differences in microbial properties between the Ross Sea and the western Arctic Ocean. Bacterial

Benthos
The community of organisms that live at the sea floor.

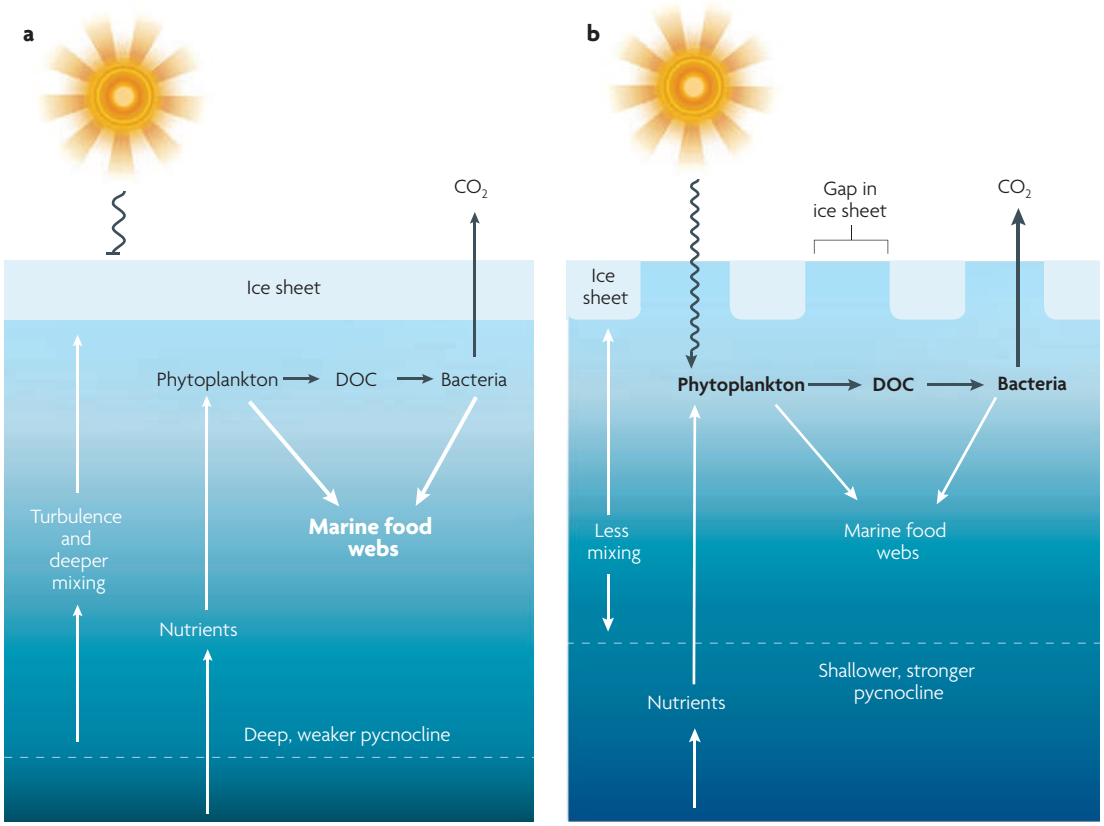

Figure 6 | **Possible responses in the oceanic microbial food web and fluxes owing to climate change in polar systems.** We postulate that compared with current conditions (**a**) decreasing ice and higher temperatures will lead to more light and higher primary production even though fluxes of new nutrients will be lower owing to a more stable water column (decreased mixing) (**b**). With these changes, more carbon will be routed through dissolved organic carbon (DOC) and bacteria, as indicated by the thicker font, at the expense of other food webs with larger organisms.

growth and microbial loop activity are substantially lower in the two polar systems than observed elsewhere, in part owing to cold temperatures, but mainly owing to lower DOM inputs. The Ross Sea and Arctic Ocean may soon diverge, as the Ross Sea is not currently warming or losing ice[62], whereas the marine ecosystem of the western Antarctic Peninsula is changing as rapidly as the Arctic[63]. Our findings suggest that microbial processes in polar systems are particularly sensitive to small changes in their environment and have potentially large impacts on carbon flows and other ecosystem functions.

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