

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

David L. Kirchman*, Xosé Anxelu G. Morán^{†§} and Hugh Ducklow[§]

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

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.

*College of Marine and Earth Studies, University of Delaware, Lewes, Delaware 19958, USA.

[†]Centro Oceanográfico de Xixón, Instituto Español de Oceanografía, 33212 Xixón, Asturias, Spain.

[§]The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543, USA.

Correspondence to D.L.K.
e-mail: kirchman@udel.edu
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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 varies¹. At one extreme are data indicating high rates of bacterial production, and even cases in which total consumption of organic carbon exceeds contemporaneous primary production², 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 respiration⁶. 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 Deibel⁷ 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 Sea⁸ and the ratio of bacterial production to primary production in this Antarctic sea is among the lowest of all marine systems⁶. 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

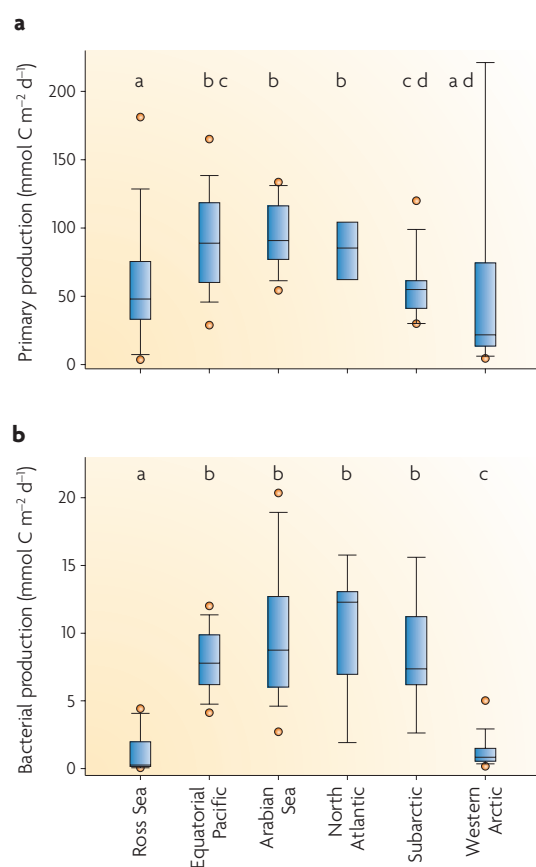


Figure 2 | Box and whisker plot of biomass production integrated through the euphotic zone in six regions. Primary production (**a**) and bacterial production (**b**). The ranges of the original data (not log transformed) are represented by points (5–95%), bars (10–90%) and boxes (25–75%). The line in 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 light¹⁶, 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 oceans¹⁷.

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 Sea²⁴ and 0.25 ± 0.13 ($n = 6$) in the Ross Sea²⁵. These values are similar (bearing in mind experimental uncertainties) to those observed in warmer, lower-latitude systems¹⁷.

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 hypothesis⁷, 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.

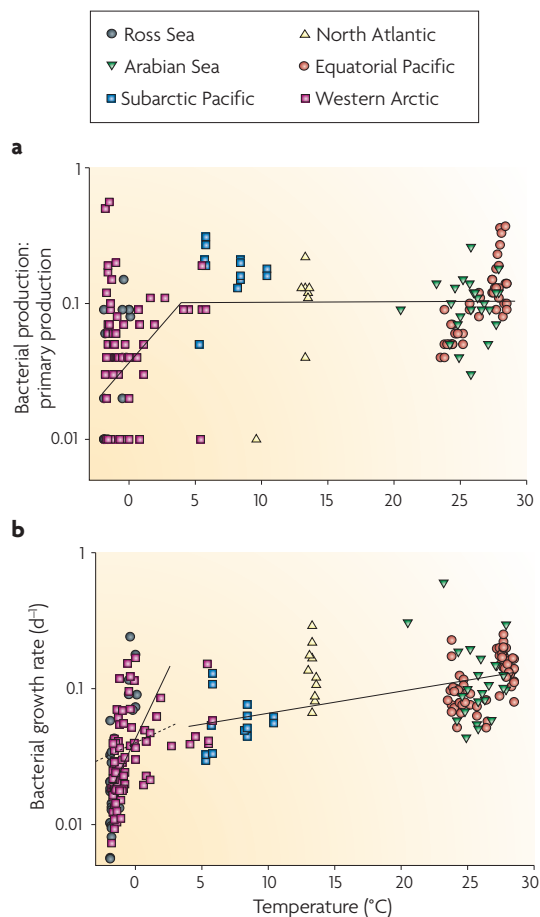


Figure 3 | Effect of temperature on the bacterial production to primary production ratio and the bacterial growth rate. a | Ratio of bacterial production to primary production as a function of temperature. Each point is the estimate for a sampling station in the indicated marine region. The lines are based on a segmented regression analysis that determined the break point to be 3.9 ± 2.8 °C (\pm the standard error). The slopes of $\log(\text{bacterial production}:\text{primary production})$ 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 $\log(\text{growth rate})$ 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 systems²⁸ 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 experimentally³¹ 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

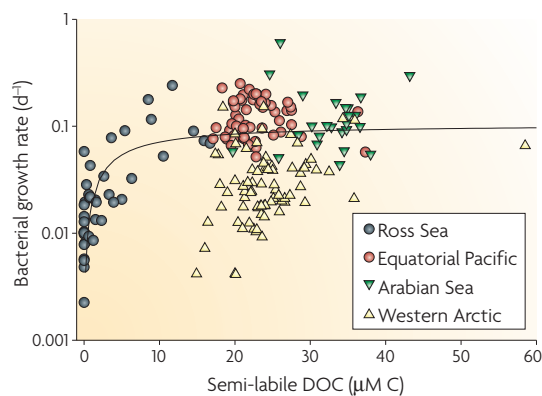


Figure 4 | Bacterial growth rate as a function of semi-labile DOC concentrations. Each point is the average growth rate and concentration for the euphotic zone at a sampling station in the indicated marine region. Dissolved organic carbon (DOC) data are not available for the North Atlantic and subarctic 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 $\mu_{\max} = 0.104 \pm 0.018 \text{ d}^{-1}$ and $K_s = 4.6 \pm 4.4 \text{ } \mu\text{M C}$ (\pm 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 low³⁴. 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 DOC³⁵, 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 DOC³⁶, which is $>1,000$ years old³⁷ 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 $5 \text{ } \mu\text{M C}$ (FIG. 4). The variability of semi-labile DOC in the Ross Sea reflects the seasonal cycle of its production and consumption³⁸. 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 $25 \text{ } \mu\text{M C}$ in the growth rate versus semi-labile

DOC graph (FIG. 4). This $25 \text{ } \mu\text{M C}$ 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 $25 \text{ } \mu\text{M C}$ 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 Ocean³⁹. 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 material⁴² 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 discharge⁴³.

The standard explanation for the low growth in polar waters is that heterotrophic bacteria are limited by some combination of temperature and low DOM concentrations¹⁵, a hypothesis that is supported by laboratory work^{15,44} and experimental studies in the Arctic⁴¹. 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 $4 \text{ } ^\circ\text{C}$ 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 $1,000 \text{ m}$ 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 blooms⁴⁵. Also, the number of potential bacteriovores was found to be high, relative to bacterial abundance, in West Antarctic Peninsula coastal waters⁴⁶. 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 Sea⁴⁸, and Rose and Caron⁴⁹ 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 Arctic⁵².

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, bacteriovores are mostly protists.

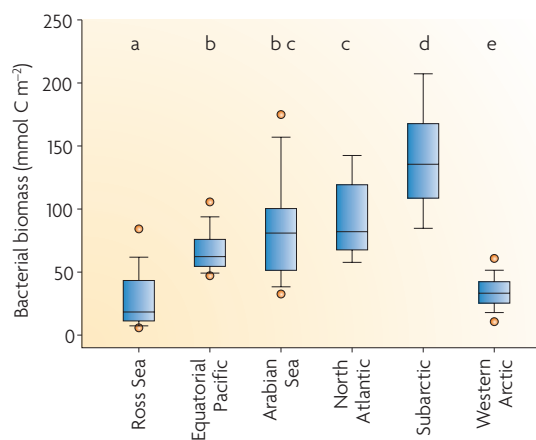


Figure 5 | Box and whisker plot of bacterial biomass integrated through the euphotic zone in six regions. The ranges of the original data (not log transformed) are represented by points (5–95%), bars (10–90%) and boxes (25–75%). The line in the box represents the median. Values for regions with the same 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 years⁵³. That year also saw a record low for sea ice coverage⁵⁴ 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 Strait⁵⁶. 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 break⁶⁰.

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 year¹³. 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 hypothesis⁷, 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 basins⁶⁰. Higher inputs of terrestrial organic material are unlikely to alter the metabolic balance of the Arctic Ocean, although work in freshwaters⁶¹ 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.

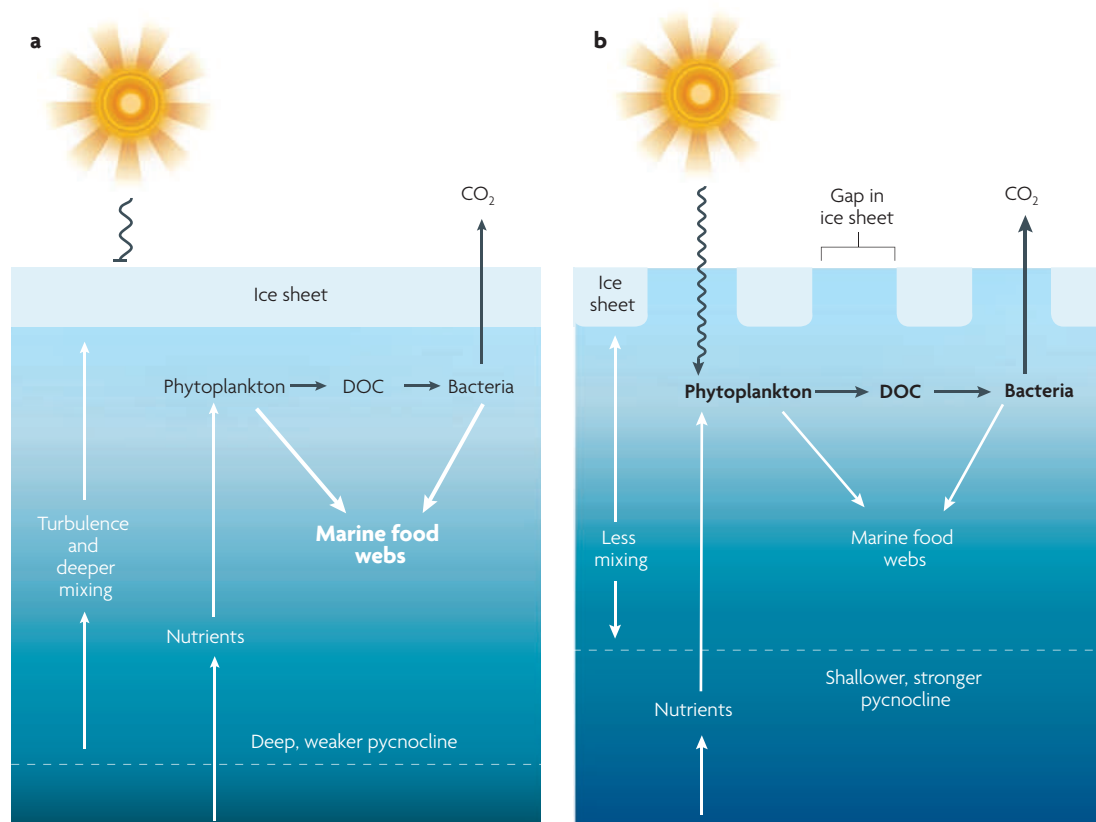


Figure 6 | Possible responses in the oceanic microbial food web and fluxes owing to climate change in polar systems. We postulate that compared with current conditions (a) decreasing ice and higher temperatures will lead to more light and higher primary production even though fluxes of new nutrients 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 ice⁶², whereas the

marine ecosystem of the western Antarctic Peninsula is changing as rapidly as the Arctic⁶³. 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.

- Robinson, C. in *Microbial Ecology of the Oceans* (ed. Kirchman, D. L.) 299–334 (Wiley-Blackwell, New York, 2008).
- del Giorgio, P. A. & Duarte, C. M. Respiration in the open ocean. *Nature* **420**, 379–384 (2002).
Respiration is the most common physiological process in the biosphere, yet it is one of the least studied. This paper highlights methods and results of studies carried out in the open sea, especially in waters below the euphotic zone, where most of the world's respiration occurs.
- Chen, F. Z. *et al.* The carbon dioxide system and net community production within a cyclonic eddy in the lee of Hawaii. *Deep-Sea Res. II* **55**, 1412–1425 (2008).
- Williams, P. J. L. The balance of plankton respiration and photosynthesis in the open oceans. *Nature* **394**, 55–57 (1998).
In this synthesis of data on primary production and respiration, the author argues that the two processes are balanced in the open sea, which is away from the direct influence of terrestrial inputs.
- Claustre, H. *et al.* Gross community production and metabolic balance in the South Pacific Gyre, using a non intrusive bio-optical method. *Biogeosciences* **5**, 463–474 (2008).
- Ducklow, H. in *Microbial Ecology of the Oceans* (ed. Kirchman, D. L.) 85–120 (John Wiley & Sons, New York, 2000).
- Pomeroy, L. R. & Deibel, D. Temperature regulation of bacterial activity during the spring bloom in Newfoundland coastal waters. *Science* **233**, 359–361 (1986).
Pomeroy and Deibel provide the original statement of the Pomeroy hypothesis, outlining temperature effects on bacterial growth rates and the consequences of low bacterial growth for marine food webs.
- Ducklow, H. *et al.* The seasonal development of the bacterioplankton bloom in the Ross Sea, Antarctica 1994–1997. *Deep-Sea Res. II* **48**, 4199–4221 (2001).
- Wheeler, P. A. *et al.* Active cycling of organic carbon in the central Arctic Ocean. *Nature* **380**, 696–699 (1996).
- Yager, P. L. *et al.* Dynamic bacterial and viral response to an algal bloom at subzero temperatures. *Limnol. Oceanogr.* **46**, 790–801 (2001).
- Morán, X. A. G., Sebastian, M., Pedros-Alio, C. & Estrada, M. Response of Southern Ocean phytoplankton and bacterioplankton production to short-term experimental warming. *Limnol. Oceanogr.* **51**, 1791–1800 (2006).
- Hoppe, H. G. *et al.* Climate warming in winter affects the coupling between phytoplankton and bacteria during the spring bloom: a mesocosm study. *Aquat. Microb. Ecol.* **51**, 105–115 (2008).
Together with Reference 11, this study describes different experimental approaches to investigate the physiological and ecological effects of temperature on bacterial processes in the oceans.
- Kirchman, D. L. *et al.* Standing stocks, production and respiration of phytoplankton and bacteria in the western Arctic Ocean. *Deep-Sea Res. II* **11** Nov 2008 (doi: 10.1016/j.dsr2.2008.10.018).
- Garneau, M.É., Roy, S., Lovejoy, C., Gratton, Y. & Vincent, W. F. Seasonal dynamics of bacterial biomass and production in a coastal arctic ecosystem: Franklin Bay, western Canadian Arctic. *J. Geophys. Res.* **113**, C07S91 (2008).
- Pomeroy, L. R. & Wiebe, W. J. Temperature and substrates as interactive limiting factors for marine heterotrophic bacteria. *Aquat. Microb. Ecol.* **23**, 187–204 (2001).
- Pedros-Alió, C., Calderon-Paz, J. I., Guixa-Boixereu, N., Estrada, M. & Gasol, J. M. Bacterioplankton and phytoplankton biomass and production during summer stratification in the northwestern Mediterranean Sea. *Deep-Sea Res. I* **46**, 985–1019 (1999).

17. del Giorgio, P. A. & Cole, J. J. in *Microbial Ecology of the Ocean* (ed. Kirchman, D. L.) 289–325 (Wiley-Liss, New York, 2000).
18. Rivkin, R. B. & Legendre, L. Biogenic carbon cycling in the upper ocean: effects of microbial respiration. *Science* **291**, 2398–2400 (2001).
19. Apple, J. K., del Giorgio, P. A. & Kemp, W. M. Temperature regulation of bacterial production, respiration, and growth efficiency in a temperate salt-marsh estuary. *Aquat. Microb. Ecol.* **43**, 243–254 (2006).
20. Hall, E. K. & Cotner, J. B. Interactive effect of temperature and resources on carbon cycling by freshwater bacterioplankton communities. *Aquat. Microb. Ecol.* **49**, 35–45 (2007).
21. Alonso-Saez, L. *et al.* Factors controlling the year-round variability in carbon flux through bacteria in a coastal marine system. *Ecosystems* **11**, 397–409 (2008). **The most complete study published so far about the environmental factors that control bacterial production rates in a marine system, including bacterial community composition.**
22. Vazquez-Dominguez, E., Vaque, D. & Gasol, A. M. Ocean warming enhances respiration and carbon demand of coastal microbial plankton. *Glob. Change Biol.* **13**, 1327–1334 (2007).
23. López-Urrutia, A. & Moran, X. A. G. Resource limitation of bacterial production distorts the temperature dependence of oceanic carbon cycling. *Ecology* **88**, 817–822 (2007).
24. Meon, B. & Amon, R. M. W. Heterotrophic bacterial activity and fluxes of dissolved free amino acids and glucose in the Arctic rivers Ob, Yenisei and the adjacent Kara Sea. *Aquat. Microb. Ecol.* **37**, 121–135 (2004).
25. Carlson, C. A., Bates, N. R., Ducklow, H. W. & Hansell, D. A. Estimation of bacterial respiration and growth efficiency in the Ross Sea, Antarctica. *Aquat. Microb. Ecol.* **19**, 229–244 (1999).
26. Hoch, M. P. & Kirchman, D. L. Seasonal and interannual variability in bacterial production and biomass in a temperate estuary. *Mar. Ecol. Prog. Ser.* **98**, 283–295 (1993).
27. Shiah, F. K. & Ducklow, H. W. Multiscale variability in bacterioplankton abundance, production, and specific growth rate in a temperate salt-marsh tidal creek. *Limnol. Oceanogr.* **40**, 55–66 (1995).
28. Rivkin, R. B., Anderson, M. R. & Lajzerowicz, C. Microbial processes in cold oceans. I. Relationship between temperature and bacterial growth rate. *Aquat. Microb. Ecol.* **10**, 243–254 (1996).
29. Kirchman, D. L., Malmstrom, R. R. & Cottrell, M. T. Control of bacterial growth by temperature and organic matter in the Western Arctic. *Deep-Sea Res. II* **52**, 3386–3395 (2005).
30. Pedrós-Alió, C., Vaque, D., Guixa-Boixereu, N. & Gasol, J. M. Prokaryotic plankton biomass and heterotrophic production in western Antarctic waters during the 1995–1996 Austral summer. *Deep-Sea Res. II* **49**, 805–825 (2002).
31. Kirchman, D. L. & Rich, J. H. Regulation of bacterial growth rates by dissolved organic carbon and temperature in the equatorial Pacific Ocean. *Microb. Ecol.* **33**, 22–30 (1997).
32. Davis, J. & Benner, R. Seasonal trends in the abundance, composition and bioavailability of particulate and dissolved organic matter in the Chukchi/Beaufort Seas and western Canada Basin. *Deep-Sea Res. II* **52**, 3396–3410 (2005).
33. Kirchman, D. L. *et al.* Glucose fluxes and concentrations of dissolved combined neutral sugars (polysaccharides) in the Ross Sea and Polar Front Zone, Antarctica. *Deep-Sea Res. II* **48**, 4179–4197 (2001).
34. Benner, R. in *Biogeochemistry of Marine Dissolved Organic Matter* (eds Hansell, D. A. & Carlson, C. A.) 59–90 (Academic Press, New York, 2002).
35. Kirchman, D. L. *et al.* in *Towards a Model of Biogeochemical Ocean Processes* (eds Evans, G. T. & Fasham, M. J. R.) 209–225 (Springer-Verlag, Berlin, 1993).
36. Hansell, D. A. & Carlson, C. A. Deep-ocean gradients in the concentration of dissolved organic carbon. *Nature* **395**, 263–266 (1998).
37. Williams, P. M. & Druffel, E. R. M. Radiocarbon in dissolved organic matter in the central North Pacific Ocean. *Nature* **330**, 246–248 (1987).
38. Carlson, C. A., Hansell, D. A., Peltzer, E. T. & Smith, W. O. J. Stocks and dynamics of dissolved and particulate organic matter in the Southern Ross Sea, Antarctica. *Deep-Sea Res. II* **47**, 3201–3225 (2000).
39. Hansell, D. A., Kadko, D. & Bates, N. R. Degradation of terrigenous dissolved organic carbon in the western Arctic Ocean. *Science* **304**, 858–861 (2004).
40. Opsahl, S., Benner, R. & Amon, R. M. W. Major flux of terrigenous dissolved organic matter through the Arctic Ocean. *Limnol. Oceanogr.* **44**, 2017–2023 (1999).
41. Middelboe, M. & Lundsgaard, C. Microbial activity in the Greenland Sea: role of DOC lability, mineral nutrients and temperature. *Aquat. Microb. Ecol.* **32**, 151–163 (2003).
42. Rachold, V. *et al.* in *The Organic Carbon Cycle in the Arctic Ocean* (eds Stein, R. & Macdonald, R. W.) 33–55 (Springer-Verlag, New York, 2003).
43. Kirchman, D. L., Elifantz, H., Dittel, A., Malmstrom, R. R. & Cottrell, M. T. Standing stocks and activity of archaea and bacteria in the western Arctic Ocean. *Limnol. Oceanogr.* **52**, 495–507 (2007).
44. Nedwell, D. B. Effect of low temperature on microbial growth: lowered affinity for substrates limits growth at low temperature. *FEMS Microbiol. Ecol.* **30**, 101–111 (1999).
45. Duarte, C. M. *et al.* Experimental test of bacteria-phytoplankton coupling in the Southern Ocean. *Limnol. Oceanogr.* **50**, 1844–1854 (2005).
46. Bird, D. F. & Karl, D. M. Uncoupling of bacteria and phytoplankton during the austral spring bloom in Gerlache Strait, Antarctic Peninsula. *Aquat. Microb. Ecol.* **19**, 13–27 (1999).
47. Anderson, M. R. & Rivkin, R. B. Seasonal patterns in grazing mortality of bacterioplankton in polar oceans: a bipolar comparison. *Aquat. Microb. Ecol.* **25**, 195–206 (2001).
48. Ducklow, H. W. & Yager, P. L. in *Polynyas: Windows into Polar Oceans* (eds Smith, W. O. J. & Barber, D. G.) 323–361 (Elsevier/CRC, New York, 2007).
49. Rose, J. M. & Caron, D. A. Does low temperature constrain the growth rates of heterotrophic protists? Evidence and implications for algal blooms in cold waters. *Limnol. Oceanogr.* **52**, 886–895 (2007).
50. Payet, J. P. & Suttle, C. A. Physical and biological correlates of virus dynamics in the southern Beaufort Sea and Amundsen Gulf. *J. Mar. Syst.* **74**, 933–945 (2008).
51. Wells, L. E. & Deming, J. W. Significance of bacterivory and viral lysis in bottom waters of Franklin Bay, Canadian Arctic, during winter. *Aquat. Microb. Ecol.* **43**, 209–221 (2006).
52. Steward, G. F., Fandino, L. B., Hollibaugh, J. T., Whittedge, T. E. & Azam, F. Microbial biomass and viral infections of heterotrophic prokaryotes in the subsurface layer of the central Arctic Ocean. *Deep-Sea Res. I* **54**, 1744 (2007).
53. Steele, M., Ermold, W. & Zhang, J. L. Arctic Ocean surface warming trends over the past 100 years. *Geophys. Res. Lett.* **35**, L02614 (2008).
54. Perovich, D. K., Richter-Menge, J. A., Jones, K. F. & Light, B. Sunlight, water, and ice: extreme Arctic sea ice melt during the summer of 2007. *Geophys. Res. Lett.* **35**, L11501 (2008).
55. Holland, M. M., Bitz, C. M. & Tremblay, B. Future abrupt reductions in the summer Arctic sea ice. *Geophys. Res. Lett.* **33**, L23503 (2006).
56. Codispoti, L. A., Flagg, C., Kelly, V. & Swift, J. H. Hydrographic conditions during the 2002 SBI process experiments. *Deep-Sea Res. II* **52**, 3199–3226 (2005).
57. Falkowski, P. G. & Oliver, M. J. Mix and match: how climate selects phytoplankton. *Nature Rev. Microbiol.* **5**, 813–819 (2007).
58. Cermeño, P. *et al.* The role of nutricline depth in regulating the ocean carbon cycle. *Proc. Natl Acad. Sci. USA* **105**, 20344–20349 (2008). **Together with Reference 57, this study explains how climate change will affect mixing in the oceans.**
59. Codispoti, L. A., Flagg, C. N. & Swift, J. H. Hydrographic conditions during the 2004 SBI process experiments. *Deep-Sea Res. II* **11 Nov 2008** (doi:10.1016/j.dsr2.2008.10.013).
60. Carmack, E. & Wassmann, P. Food webs and physical-biological coupling on pan-Arctic shelves: unifying concepts and comprehensive perspectives. *Prog. Oceanogr.* **71**, 446–477 (2006). **This paper is a good introduction to how physics affects plankton communities in the Arctic Ocean.**
61. Jansson, M., Hickler, T., Jonsson, A. & Karlsson, J. Links between terrestrial primary production and bacterial production and respiration in lakes in a climate gradient in subarctic Sweden. *Ecosystems* **11**, 367–376 (2008).
62. Stammerjohn, S. E., Martinson, D. G., Smith, R. C., Yuan, X. & Rind, D. Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño–Southern Oscillation and Southern Annular Mode variability. *J. Geophys. Res.* **113**, C03590 (2008).
63. Ducklow, H. W. *et al.* Marine pelagic ecosystems: the west Antarctic Peninsula. *Philos. Trans. R. Soc. Lond. B* **362**, 67–94 (2007).
64. Pedros-Alió, C., Vaque, D., Guixa-Boixereu, N. & Gasol, J. M. Prokaryotic plankton biomass and heterotrophic production in western Antarctic waters during the 1995–1996 Austral summer. *Deep-Sea Res. II* **49**, 805–825 (2002).
65. Ducklow, H., Carlson, C. & Smith, W. Bacterial growth in experimental plankton assemblages and seawater cultures from the *Phaeocystis antarctica* bloom in the Ross Sea, Antarctica. *Aquat. Microb. Ecol.* **19**, 215–227 (1999).

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FURTHER INFORMATION

David L. Kirchman's homepage: <http://www.ocean.udel.edu/people/profile.aspx?kirchman>

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