

Bacteria in the Greenhouse: Marine Microbes and Climate Change

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1.1 INTRODUCTION: A MICROBIAL OCEAN IN A WARMING WORLD

The global ocean covers 70% of Earth's surface and comprises most of the volume of the biosphere (except the deep subsurface). It supports about half the annual net primary production (NPP) on the planet (Figure 1.1) (Field et al., 1998). This vast, interconnected network of marine ecosystems is warming in response to anthropogenic climate change, with uncertain consequences for human societies. In this chapter we address the possible responses of ocean warming on marine microbes (protists, phytoplankton, bacteria, and archaea, with emphasis on the bacteria). Other anthropogenic changes related to CO₂ accumulation in the atmosphere, such as ocean acidification (Orr et al., 2005), will also have uncertain effects on ocean microbes.

The ocean is, and always has been, dominated by microbes. Microscopic unicellular phytoplankton and cyanobacteria inhabiting the sunlit upper approximate 100 m of the water column carry out nearly all the photosynthesis on which oceanic life depends (Falkowski et al., 1998, 2000). NPP on land and in the oceans is the process dominating solar energy and CO₂ fixation into organic matter, thus driving the global carbon cycle (Houghton, 2007). Nearly all of the approximately 50 Pg (1 petagram = 1 Pg = 10¹⁵ g = 10⁹ tons) of carbon fixed annually in marine photosynthesis is ultimately oxidized by bacterioplankton, protozoans, and zooplankton (Ducklow and Carlson, 1992) with a very small fraction (<0.1%) escaping heterotrophic metabolism in the deep water column to be buried in the sedimentary record and hydrocarbons. The myriad pathways by which marine organic matter is cycled through particulate and dissolved forms and

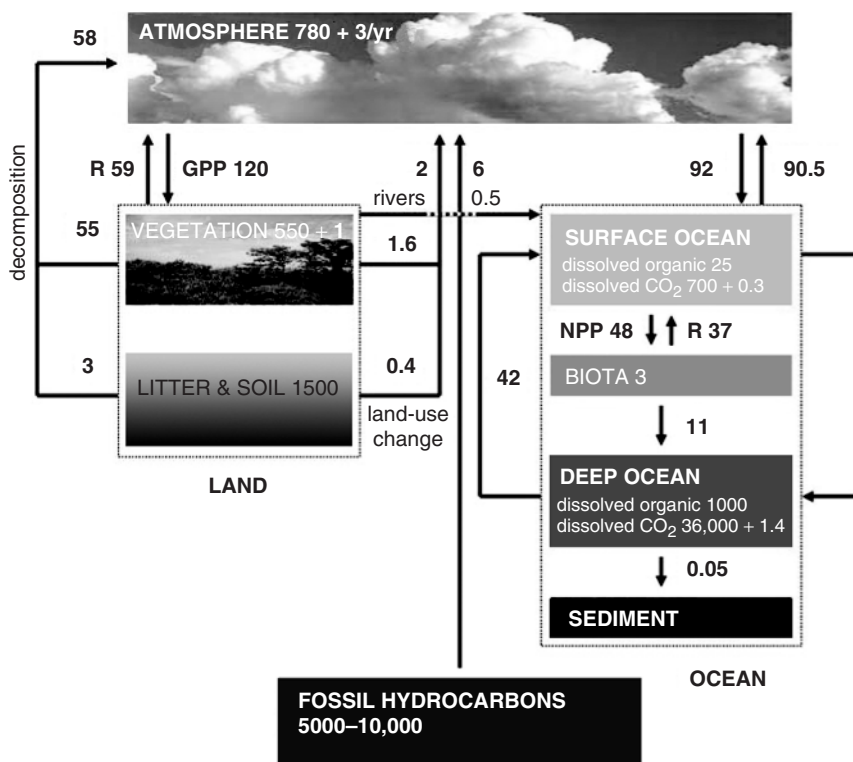


Figure 1.1 The global carbon cycle, including human perturbations in the 1990s. The quantities in the boxes are the size of the carbon reservoir in petagrams (Pg; 10^{15} g), with the annual growth, if any, due to the perturbations. Note that there is direct exchange between the atmosphere and terrestrial ecosystems, whereas exchange with the ocean is mediated by the physicochemical exchange across the air–sea interface. The downward transport of organic carbon, both particulate and dissolved, constitutes the biological pump. There is a riverine input of about 0.5 Pg from the land to ocean, balanced by outgassing and burial in sediments. Currently, the annual net land sink for atmospheric CO₂ is 1 Pg and the ocean sink is 2 Pg, leaving an annual net anthropogenic accumulation in the atmosphere of 3.2 Pg. (Modified from Houghton, 2007.) (See insert for color representation.)

back into CO₂ overwhelmingly involve microbial exchanges among organisms less than 1 to 5 μm in diameter—the microbial loop (Pomeroy, 1974; Azam et al., 1983; Azam and Worden, 2004; Azam and Malfatti, 2007). This large-scale view of global biogeochemistry makes the point that microbial ecology depends ultimately on the patterns and products of photosynthesis. In metabolizing the products of photosynthesis on land and in the sea, bacteria perform important ecosystem services, such as decomposition, nutrient cycling, regulating the composition of the atmosphere, enhancing soil fertility, and purifying water, on which human societies depend for healthy and sustainable existence (Ducklow, 2008). Here we review marine plankton and microbial ecology to understand how marine bacteria may respond to anthropogenic climate change, and suggest potential research directions for making more informed projections.

Bacteria respond directly to changes in environmental temperature, but these responses occur in complex communities with phytoplankton and zooplankton and in

a complex biogeochemical milieu. After reviewing the microbial loop to set the stage for a more detailed look at the connections between climate and plankton processes, we take two complementary approaches. First, we examine how bacterial activity varies as a function of temperature. Then we examine how marine phytoplankton respond to climate variability in the ocean and how these responses modulate the effects of climate change on bacterial and animal consumers. We have a reasonable understanding of the mechanisms by which phytoplankton (especially eukaryotes) will respond to climate change, based on physical theory and knowledge of past changes from the fossil record. But as Falkowski and Oliver (2007) stated in their review of phytoplankton and climate, “Whether this fundamental principle holds for marine prokaryotes remains to be seen, because the spatial and temporal distribution of prokaryotic taxa, as well as their relevant ecophysiological attributes, is not yet well characterized.” Our knowledge of the mechanisms linking phytoplankton to bacterial variability is still fragmentary, but much new research is directed at this problem. We use this nascent understanding to suggest how bacterial carbon cycling may change and what knowledge is needed for better predictions of such changes. Finally, we synthesize these approaches and consider scenarios of how microbial communities will respond (or may already be responding) to climate change in the coastal seas, cold polar seas, and in warm oligotrophic subtropical gyres. First, we sketch briefly the projected physical changes to the global oceans in response to anthropogenic climate forcing.

1.1.1 Impact of Climate Change on the Oceans

The world is warming in response to climate change driven by the accumulation of anthropogenic greenhouse gases (Kerr, 2007). The 2007 IPCC Assessment projects that the mean global surface atmospheric temperature will rise by 1 to 6°C by 2099, depending on various assumptions or scenarios of population growth, economic and technological development, energy use, and greenhouse gas emissions (IPCC, 2007b). The projected warming is not uniform in space or time, with different rates forecast for various regions and seasons. Surface ocean temperatures may rise by 3 to 7°C in some regions, with the largest increases (although not necessarily the largest *effects*; see below) in polar seas (Figure 1.2). Climate warming will take longer to percolate into the deep ocean. The surface ocean west of the Antarctic Peninsula has already increased by 1°C since the 1950s (Meredith and King, 2005), and Arctic sea ice has declined alarmingly in the past few years (Serreze et al., 2007). Enhanced greenhouse warming is projected to cause impacts ranging from changes in winds, clouds, sea level, precipitation, storm frequency and intensity to more complex alterations in long-term climate modes (e.g., ENSO), ecosystems, biodiversity, and human well-being (Millennium Ecosystem Assessment, 2005; IPCC, 2007a). The impact of changes in surface temperatures, clouds, and wind on ocean stratification, mixing, and circulation has been examined using coupled atmosphere–ocean general circulation models (AOGCM) (Meehl et al., 2007). In addition to atmospheric warming, major changes predicted by many different AOGCMs include increases in ocean surface stratification in the tropics and subtropics; and reductions in mixed-layer depth in the middle to upper latitudes (Figure 1.3; Boyd and Doney, 2002). Other changes include loss of sea ice in both hemispheres (especially in the north), and increases in westerly winds and coastal upwelling (Sarmiento et al., 2004). As the temperature fields shown

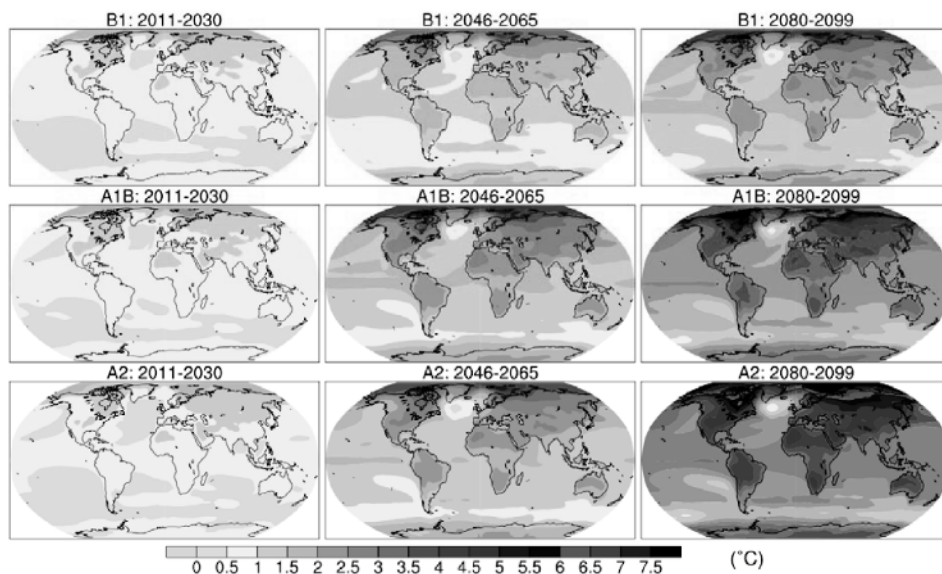


Figure 1.2 Multimodel mean of annual mean surface warming (surface air temperature change, °C) for scenarios B1, A1B, and A2, and three time periods, 2011 to 2030 (left), 2046 to 2065 (middle), and 2080 to 2099 (right). Stippling is omitted for clarity (see the text). Anomalies are relative to the average of the period 1980–1999. (From IPCC, 2007b, with permission of the IPCC, <http://www.ipcc.ch/graphics/graphics.htm>.) (See insert for color representation.)

in Figures 1.2 and 1.3 indicate, projected changes are far from uniform. Specification of the changes in any particular region is more uncertain than projections of the global means. Responses of ocean ecosystems and biogeochemistry are less certain than physical changes.

1.1.2 The Microbial Loop and Marine Bacterioplankton Communities

A typical milliliter of seawater harbors about 10^6 bacterial and archaeal cells, the great majority of which are revealed to be active based on fluorescent in situ hybridization and visualization of intact ribosomes (Church et al., 2003). This assemblage contains extraordinary genetic and metabolic diversity (Venter, 2004; Sogin et al., 2006), and with it the potential for adaptation to wide ranges and combinations of environmental conditions. The planktonic archaea make up a variable fraction of the prokaryote assemblage, comprising up to about 50% of the total abundance in deep-ocean waters, but less in the more active surface layer (Karner et al., 2001). Recent work has revealed new insights concerning the metabolism and ecological roles of planktonic GI marine crenarchaeota and GII marine euryarchaeota. Collective evidence suggests that perhaps a significant portion of the GI marine crenarchaeota are ammonia oxidizers (Francis et al., 2005; Konneke et al., 2005; Hallam et al., 2006; Wuchter et al., 2006), while the first environmental genomic sequence from a GII marine euryarchaeote identified a proteorhodopsin-encoding gene (Frigaard et al., 2006). Both of these metabolisms are consistent with the ecological distributions of these organisms in the ocean, where the GI marine crenarchaeota are typically found below the photic zone, and the GII

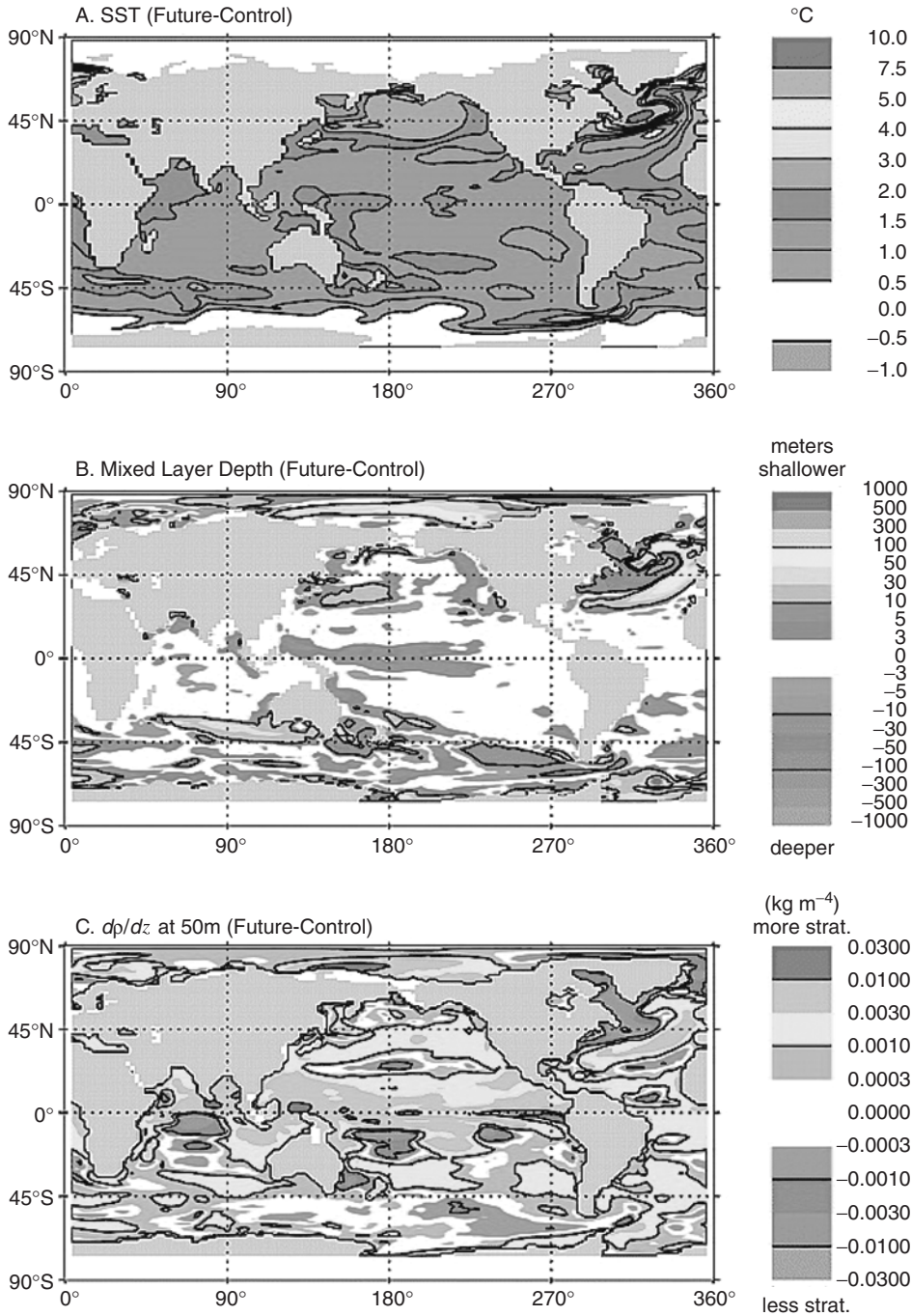


Figure 1.3 Projected climate-mediated changes in ocean physical forcing (future-control, i.e., 2060–2070 minus the present) from the NCAR Community Climate System Model for (A) sea surface temperature, (B) mixed-layer depth, and (C) upper ocean (50 m) stratification. (From Boyd and Doney, 2002, with permission of the American Geophysical Union.) (See insert for color representation.)

marine euryarchaeota are found in oceanic surface waters. Marine aerobic heterotrophic bacteria directly take up and metabolize low-molecular-weight (LMW, <500 MW) dissolved organic matter (DOM) such as easily metabolized mono- and oligosaccharides, free amino acids, and small peptides (Kirchman et al., 2001). Most bacterial cells in the ocean are free-living and thus dependent on DOM (Azam and Hodson, 1977). Free and attached bacteria hydrolyze polymeric substances and particulate matter into LMW compounds that can be passed through cell membranes (Hoppe et al., 1993). Bacterial metabolism in the surface ocean depends predominantly on uptake of labile LMW and HMW compounds with turnover times of minutes to days (Fuhrman, 1990). However bacterial metabolism may be supplemented by a variable contribution from semilabile DOM that turns over on approximately seasonal time scales (Kirchman et al., 1993; Carlson and Ducklow, 1996). Bacterial turnover of DOM and the associated remineralization of micro- and macronutrients such as iron, nitrogen, and phosphorus close the major biogeochemical cycles of these elements in the sea (Falkowski et al., 2008).

Marine net primary production is processed through a complex trophic network of consumers, with a global average 15 to 20% escaping microbial respiration in the euphotic surface layer (upper approximately 100 to 200 m) to be exported to the ocean interior. A change in this fraction would have a major impact on the global carbon cycle (Sarmiento and Toggweiler, 1984). In the open sea and in many coastal and shelf seas under stratified conditions, carbon and nitrogen flows are dominated by microbial food webs (Figure 1.4). The intensive recycling of the dissolved and particulate fractions of the NPP through consumers results in a large fraction (about 50%) of the NPP passing through bacteria and the dissolved pool (Pomeroy, 1974; Williams, 1981). In the open sea, most grazing is by microzooplankton (Landry and Kirchman, 2002; Calbet and Landry, 2004); thus most heterotrophic consumption and respiration is microbial. Microbial dominance of marine food webs appears to hold even for the Antarctic seas, previously thought to be the last bastion of the classical diatom–krill–whale food chain based on large plankton (Daniels et al., 2006).

As this discussion and Figure 1.4 suggest, a large fraction of the organic matter fixed in marine NPP is cycled through dissolved pools and metabolized by bacteria. All organisms leak DOM into the environment via passive diffusion, cell lysis and breakage, and active metabolic processes (Bjørnsen, 1988; Nagata, 2000). Phytoplankton actively exude dissolved organic carbon (DOC) to dispose of excess photosynthetically fixed carbon not combined with nitrogen and phosphorus into biomass in the approximate Redfield ratio 106 : 16 : 1 (C/N/P). Phytoplankton exudation is the process most directly coupling primary to bacterial production (Morán et al., 2002), but not the only process. Larger-celled phytoplankton such as diatoms may be broken between capture and ingestion by crustacean predators, spilling their fluid contents, in a process known as *sloppy feeding* (Lampert, 1978). According to Nagata (2000), egestion and excretion during feeding by protistan grazers may be the greatest relative contribution to photosynthetically derived DOC fluxes. Clearly, passive diffusion across phytoplankton cell membranes, active exudation, egestion, and sloppy feeding will produce DOM with different chemical composition and at different rates. Following ingestion and digestion, zooplankton grazers excrete DOM, and it also diffuses out of fresh fecal material (Jumars et al., 1989). Additional DOM may be released during viral lysis, abiotic dissolution, or bacterial hydrolysis of suspended and sinking detrital particles and marine snow. Figure 1.4 suggests one scenario for the relative

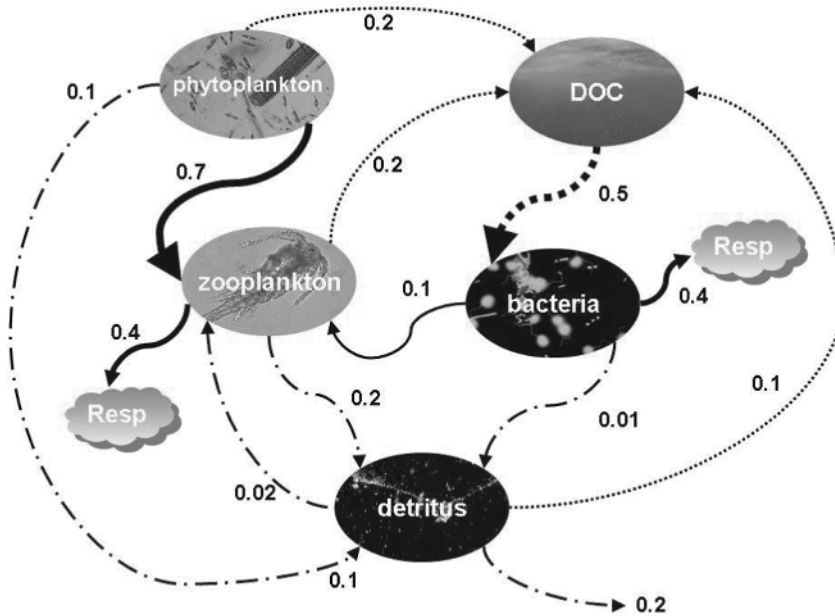


Figure 1.4 Microbial food-web diagram, showing exchanges of carbon in the oceanic surface layer. The flows are normalized to $NPP = 1.0$. The partitioning of flows among compartments is based on the physiological budget model given in Anderson and Ducklow (2001). Note that the carbon flows are dominated by zooplankton grazing (70% of NPP), DOC uptake by bacteria (50%), and heterotrophic respiration (80%). In this depiction the respiration is divided evenly among zooplankton and bacteria, but note that oceanic zooplankton may be dominated by protozoans smaller than $20\ \mu\text{m}$. Here the bacterial production is 12% of the particulate NPP, the fraction approximated by traditional ^{14}C assays, and a typical value for the open sea (Ducklow, 1999). Solid lines, biomass flows and respiration; dotted lines, dissolved flows; dashed–dotted lines, detrital flows and mortality. (See insert for color representation.)

magnitudes of DOC fluxes from these diverse sources. This model explains how the level of bacterial production (BP) is limited by how much DOC flows through the food web to bacteria, and by the bacterial allocation of the carbon ingested between production and respiration (bacterial growth efficiency; see below). Phytoplankton extracellular release (PER) may vary widely even in healthy cells, ranging from less than 5 to more than 50% of the total (dissolved plus particulate) primary production (Morán and Estrada, 2002). Anderson and Ducklow (2001) outlined the importance of PER vs. grazer-related sources in setting the overall level of bacterial metabolism in the sea. Williams (1981) hypothesized a larger role for PER, whereas Jumars et al. (1989) emphasized the primacy of grazers as DOM sources. Depending on the season, location, and particular environmental conditions of nutrient and light levels, grazing intensity, and other factors, many different scenarios are possible. Specifying how bacteria may respond to climate change requires better understanding of these rates, and the chemical composition of DOM released from a multitude of sources. For example, DOM released by grazing activities is probably of lower quality for bacterial nutrition, due to enzymatic attack, than that released by phytoplankton or viral

lysis (Nagata, 2000). Changes in the physical or ecological state of ocean ecosystems affecting herbivores may cascade to changes in bacterial activity or community composition.

Our understanding of microbial life in the oceans has escalated rapidly following the application of molecular tools (e.g., gene or whole genome sequencing, molecular profiling, fluorescent in situ hybridization), many of which have targeted the SSU rRNA gene, a phylogenetically informative molecule in which all forms of life can be compared. Marine microbial communities are diverse, although moreso at finer taxonomic scales than at gross phylum levels. Overall at the phylum level, there are some differences between ocean realms and between coastal vs. open ocean. Some distribution and biogeographically-based patterns are now emerging following extensive surveys of the world's ocean with these new tools. The upper oceans are dominated (25 to 33%) by SAR11-related bacteria members of the α -proteobacteria (Morris et al., 2002), and the deeper oceans below 150 m harbor abundant marine GI crenarchaeotal populations (20 to 40% of DAPI-stained cells; Karner et al., 2001; Teira et al., 2006). Another numerous group of α -proteobacteria, common to both coastal and open ocean regions, the Roseobacter clade is often abundant (about 15% of the community; Buchan et al., 2005). There is high phylogenetic and functional diversity of marine γ -proteobacteria, which comprise a significant fraction of the bacterioplankton. Interestingly, though, γ -proteobacteria are often the most commonly cultivated marine bacteria, yet the cultivated species are rarely detected in molecular surveys. The more commonly detected γ -proteobacteria in cultivation-independent surveys on global scale harbor diverse metabolisms, and are in a number of cases strictly oligotrophic (Cho and Giovannoni, 2004). Marine Bacterioidetes-related organisms are a third group that includes diverse members that are not well represented in culture collections but can be numerically dominant (Cottrell et al., 2000). Interestingly, we now also know that species in each of these major phylogenetic groups found in oceanic photic zones contain proteorhodopsin, a membrane-associated light-driven proton pump. How these organisms utilize proteorhodopsin to supplement growth is still not well understood, although it may be a theme for organisms living in the upper ocean. Campbell et al. (2008) estimated that at least 14% of organisms living in the photic zone contain proteorhodopsin homologs.

Biogeographic, temporal, and spatial surveys have also revealed considerable diversity and dynamics in community composition. For example, Pommier et al. (2007) compared the diversity of bacterioplankton assemblage at nine different sites around the world. Their findings suggest that despite the fact that the major phyla detected were similar, there were very few sequences that were detected repeatedly. Seasonal variation in coastal Antarctic waters is dramatic, with bacterial richness shifting significantly (Murray et al., 1998; Murray and Grzymski, 2007) and archaeal populations increasing in relative proportions in winter (Massana et al., 1998; Murray et al., 1998; Church et al., 2003). Vertical density stratification in the ocean (see below) has the most apparent impact on gradients of diversity in the ocean, however, as community diversity shifts most significantly with depth rather than with longitude or latitude. One of the caveats of nearly all studies is that the diversity is undersampled but new technologies in massively parallel DNA sequencing promise to reshape our views of species richness and our ability to compare in detail community composition from many sites using the same deep sequencing approach (Sogin et al., 2006; Huber et al., 2007).

1.2 BACTERIAL ACTIVITY AND TEMPERATURE

Temperature is a critical property affecting virtually all metabolic processes of organisms (Gillooly et al., 2001; Brown et al., 2004), especially those of microbes (Price and Sowers, 2004). However, by concentrating solely on temperature as a key control of bacterial properties, we are necessarily neglecting other biological interactions that shape bacterial communities in the oceans (Strom, 2008). Theoretically, with no other constraints and unlimited resources, increases in temperature should result through increased enzymatic activity in higher growth rates and eventually, larger abundances of cells. Thus, a first and indirect approach to the possible effects of climate warming on heterotrophic bacteria could be the examination of how their abundance or activity changes with temperature in present-day natural conditions (Figure 1.5). A corollary to this reasoning is that if resources (nutrients and organic matter) are limiting, increased temperature will not necessarily cause increased activity.

The major problem with trying to describe the response of bacteria to temperature is to separate it from other environmental factors that actually covary with temperature, such as nutrient concentration or primary productivity, which may themselves have a larger effect on bacterial properties (Lomas et al., 2002). In permanently warm regions or during summer in temperate waters, strong stratification of the upper layers of the water column precludes the input of inorganic nutrients from below the euphotic zone, thus severely limiting the photosynthetic fixation of CO₂ (Longhurst, 1998). A simple way around this complication is to correct by the other limiting factor, such as examining the relationship of the ratio of bacteria to phytoplankton biomass or activity versus temperature (Li et al., 2004; Apple et al., 2008). In Li's analysis, the bacteria/phytoplankton biomass ratio increases with increasing temperature up to an estimated upper limit of 1, consistent with the predictions of the food-web model of Laws et al. (2000).

Despite the complex nature of interactions between temperature, substrate availability, cell size and abundance in the ocean, strong apparent increases with temperature in the abundance of picoplankton, the smallest size class of planktonic organisms (< 2 µm in diameter) comprising all free-living heterotrophic bacteria, have consistently been reported for different aquatic ecosystems (Li, 1998; Rae and Vincent, 1998; Agawin et al., 2000; Li et al., 2006; Morán et al., 2008). Heterotrophic bacterial numbers generally peak in the summer months, while minima are frequently found during winter in most regions (Li, 1998; Steinberg et al., 2001; Calvo-Díaz and Morán, 2006; Alonso-Sáez et al., 2008; Garneau et al., 2008). This relationship is, however, not constant through the entire -2 to 30°C temperature range. Usually, the initial increase in abundance with temperature in colder conditions is followed by more constant or even decreasing abundance (Hoch and Kirchman, 1993; Shiah and Ducklow, 1995), and with considerably more variation, as temperature rises above some value around 15°C (Figure 1.5A). Bacterial growth rates calculated as production/biomass ratios also show a remarkably similar response to temperature, with no further significant increases at temperatures above 15°C (Figure 1.5B). This figure implies that climate warming may alter the microbial ecology of both polar and tropical environments, representatives of extreme temperature conditions of Earth's marine ecosystems, in different ways. We use these environments as case examples of possible changes in carbon fluxes mediated by bacteria in a warmer ocean (see below).

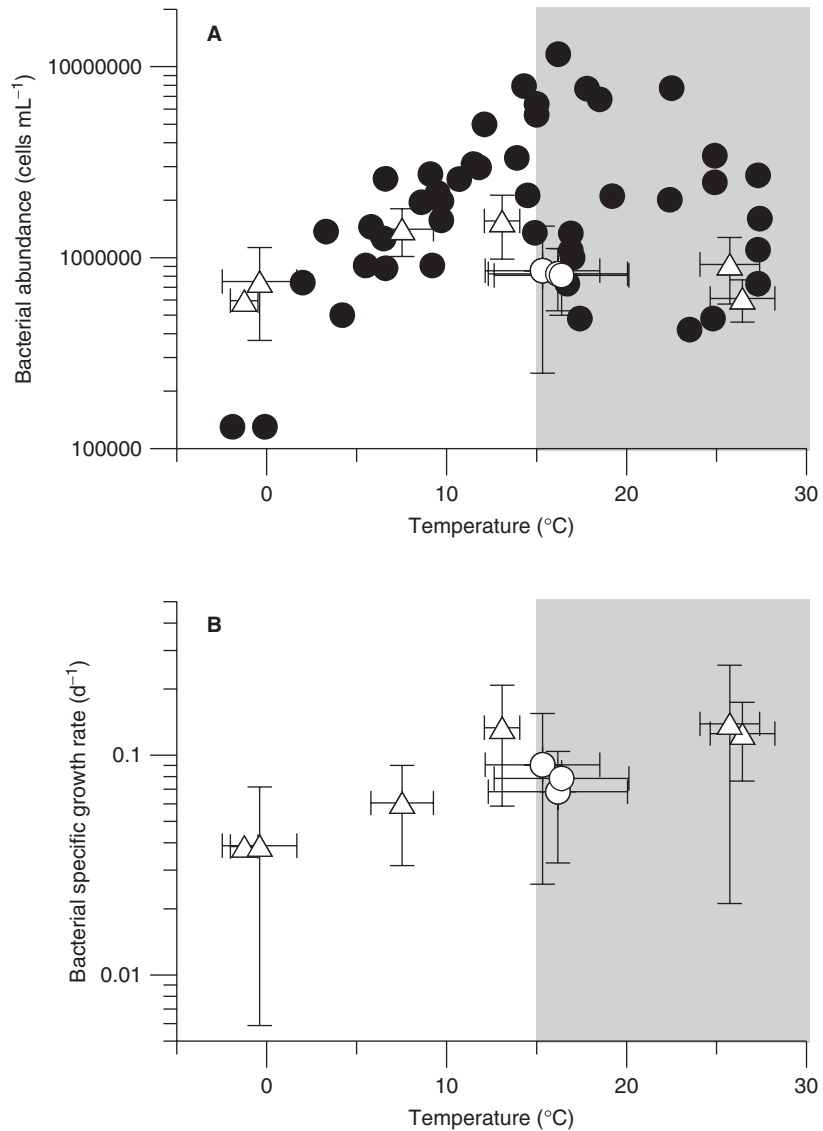


Figure 1.5 (A) Relationship between bacterial abundance and temperature. Closed circles are mean annual values at the surface of different regions of the world ocean. Open circles are mean \pm SE annual values in 2006 at the surface of three stations in the southern Bay of Biscay. Open triangles are mean \pm SE values averaged for the euphotic layer from studies that partially covered the annual cycle in the Antarctic, Arctic, subarctic Pacific, North Atlantic, Arabian, and equatorial Pacific. (B) Bacterial specific growth rates (BP/BB per day) vs. temperature of the two data sets added to Li's original figure. The shaded area represents the general change in response at temperatures at or above 15°C. (Modified from Li, 1998.)

Since bacterial abundance is the result of in situ growth minus losses due to predation and lysis, not necessarily involving the same temperature dependences (Sherr et al., 1988), we now focus on the intrinsic physiological processes of bacteria that are affected directly by temperature. The two fluxes mediated by bacteria that are most relevant from the perspective of biogeochemical cycling of organic matter are bacterial production (BP) and respiration (BR). BP and BR are related by bacterial growth efficiency (BGE), which is the fraction of the total organic carbon assimilated or bacterial carbon demand (BCD) that is used to build up biomass: $BGE = BP/BCD = BP/(BP + BR)$. A more mechanistic approach involves the use of mathematical descriptions of the temperature dependence of BP and BR. The simplest is the temperature coefficient, Q_{10} , the factor by which a biological reaction changes with a temperature increase of 10°C. Although as for other planktonic groups, the mean Q_{10} for BP, BR, and growth rates clusters around 2 (Robinson and Williams, 1993; Kirchman et al., 1995; Lomas et al., 2002; Kirchman et al., 2005), actual values may vary considerably as much within as across regions (Pedros-Alió et al., 2002; Middelboe and Lundsgaard, 2003). This pattern argues against the use of a fixed Q_{10} value in models predicting biogeochemical responses to rising sea temperatures.

A more rigorous description of the temperature dependence of metabolic rates stems from the work of van't Hoff and Arrhenius in the late nineteenth century on chemical reactions, later applied to biological processes. The *van't Hoff–Arrhenius equation* (Arrhenius, 1915) ($Q = Q_0 e^{-E_a/kT}$), also called *Boltzmann's factor* (Gillooly et al., 2001; Brown et al., 2004; Allen et al., 2005), describing the exponential increase in metabolic rates with temperature was recently extended into the more general framework of the metabolic theory of ecology (MTE) (Brown et al., 2004). The MTE predicts a value of activation energy E_a of 0.65 eV for heterotrophic organisms (Brown et al., 2004; Allen et al., 2005). In a recent review of published data on temperature and bacterial metabolism, López-Urrutia and Morán (2007) showed that the temperature dependencies of cell-specific BP and BR rates were statistically indistinguishable, with E_a values close to the predicted 0.65 eV (0.42 to 0.59 eV) (Figure 1.6). In other words, although the absolute amount of organic carbon processed by bacteria may change in the future, they would essentially be allocating the same fraction of resources to growth (BP) and metabolism (BR) in a warmer scenario, contradicting previous claims of a strong inverse relationship of BGE with temperature (Rivkin and Legendre, 2001). Invariant BGE values with an increase of 2°C over in situ temperatures have been shown recently in an annual cycle in Mediterranean coastal waters (Vázquez-Dominguez et al., 2007). The relationship between BGE and temperature observed by Rivkin and Legendre (2001) probably reflects variations in regional ecology rather than a direct temperature effect.

However, resource limitation strongly affected the temperature-corrected BP, while BR remained unaltered (López-Urrutia and Morán, 2007). Hence under resource-limiting conditions, assimilated organic carbon (BCD) would decrease solely at the expense of BP. Although the response of BP to temperature was constant at three levels of resource availability using chlorophyll as a proxy for bacterial substrates (<0.5, 0.5 to 2, >2 mg of chlorophyll per cubic meter), the intercepts were significantly different (1.6). The implication of this result is that low-productivity areas (<0.5 mg chlorophyll per cubic meter) will have lower BP than that of eutrophic regions (>2 mg m⁻³) but essentially the same BR. As a consequence, BGE would decrease with decreasing chlorophyll concentrations, from about 30% at values greater

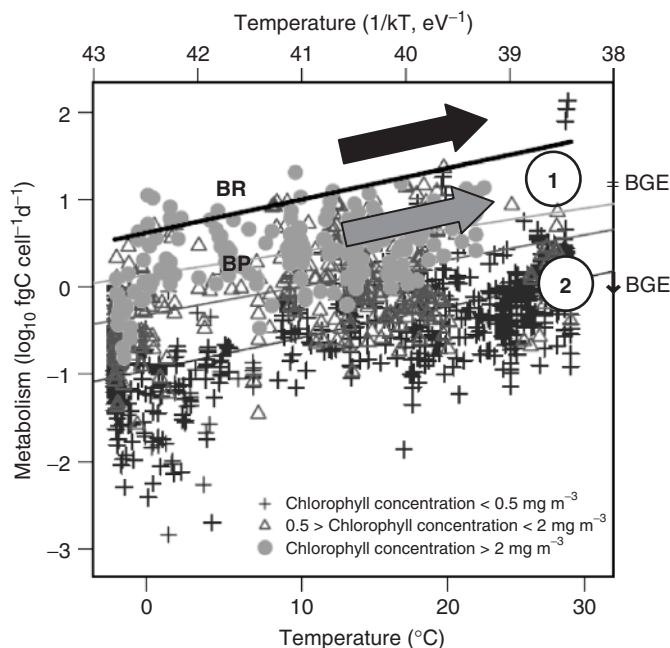


Figure 1.6 Individual rates of bacterial production (BP_i) and respiration (BR_i) versus temperature at three levels of chlorophyll concentration. The black line represents the relationship between $\ln BR_i$ and $1/kT$ ($y = 26.49 - 0.59x$) and the colored lines represent the $\ln BP_i$ –temperature relationships for each data subset (green, $y = 18.14 - 0.42x$; red, $20.54 - 0.50x$; blue, $22.58 - 0.58x$). An increase in temperature with no changes in resource availability would result in similar increases in BP_i and BR_i (i.e., the same BGE: case 1). Resource limitation would slow the rate of increase of BP_i with temperature compared to BR_i , thus lowering BGE (case 2). (Modified from López-Urrutia and Morán, 2007.) (See insert for color representation.)

than $5 \mu\text{g/L}$ to values about 5% at lower chlorophyll levels, confirming previous work on systematic changes of the BGE with resource availability (del Giorgio and Cole, 1998). We suggest that a climate-induced change toward lower phytoplankton biomass and production in vast areas of the oligotrophic ocean (Bopp et al., 2001; Behrenfeld et al., 2006) or a shift in composition to smaller organisms (Karl, 1999a) (see below) would affect BGE by changing the resource level at which the BP–temperature relationship operates. That is, if we collected data in a warmer ocean in 2100 at exactly the same locations as those used for plotting Figure 1.6, substantially more of the data would fall in the oligotrophic and mesotrophic categories, so the BGE would decrease—but due to resource limitation rather than to a direct temperature effect. To sum up, increases in temperature will undoubtedly increase BR and BP, but respiration would proceed unabated while production will probably level off. This is because BP is affected by resource availability, which is influenced by temperature. The obvious consequence is that proportionally more dissolved organic carbon would be released as CO_2 by bacteria than is made available as biomass to bacteriovores in marine food webs. This shift would have follow-on effects for nutrient limitation and upper trophic levels (Ducklow et al., 1986).

Some of the models aimed at predicting how biogeochemical cycles in the ocean will respond to global warming use the functional groups approach (e.g., Hood et al., 2006), where bacteria appear as the major respirers. This view has been held by most researchers (Rivkin and Legendre, 2001; del Giorgio and Duarte, 2002), although recent work suggests a slightly lower mean contribution of bacterial respiration to total values (Robinson, 2008). Yet since respiration at the community level would be largely bacterial, the consequences for the metabolic balance of the oceans of a differential regulation of BP and BR are potentially large. Using the MTE approach (see above) to model gross primary production and respiration of planktonic communities, López-Urrutia et al. (2006) predict a significant (21%) reduction in ocean uptake of atmospheric CO₂ as a result of changing metabolic balance.

An important issue regarding temperature and substrate availability interactions as factors determining bacterial activity is the claimed difference between permanently cold (<5°C) waters and elsewhere. The hypothesis developed by Pomeroy and co-workers (Pomeroy and Deibel, 1986; Pomeroy et al., 1990; Wiebe et al., 1992) states that polar bacteria need comparatively higher concentrations of DOM for efficient uptake than do those inhabiting lower latitudes, and hence would process a lower proportion of primary production (Pomeroy and Wiebe, 1988), with the remainder sedimenting into the benthic food web. Changes in the kinetics of DOM uptake have been observed (Nedwell, 1999; Yager and Deming, 1999) as predicted by Pomeroy and Wiebe (2001), and low bacterial production/primary production (BP/PP) ratios have been documented frequently in cold waters (Bird and Karl, 1999; Ducklow, 1999; Morán et al., 2001). However, there is no such clear pattern of systematic changes in BP/PP with temperature (Figure 1.7) as observed for abundance or growth rates (Figure 1.5). The lack of consistent occurrence of low BP/PP values in cold waters, together with contrary results reported for the Arctic (Kirchman et al., 2005) and the

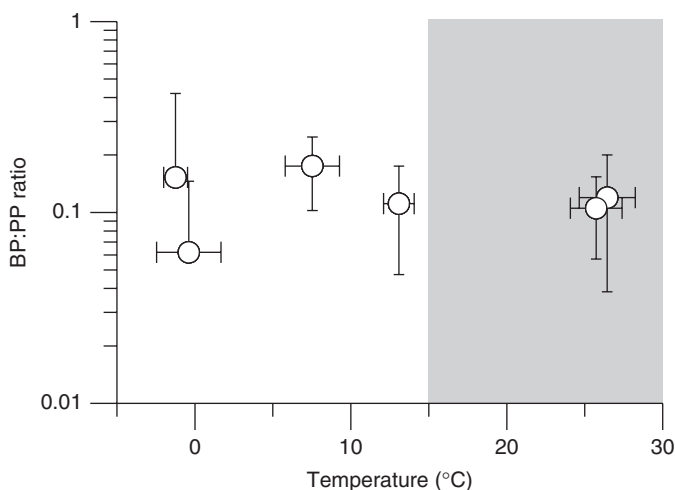


Figure 1.7 Relationship between the mean \pm SE ratio of bacterial production to primary production (BP/PP) and temperature averaged for the euphotic layer from surveys conducted in the Antarctic, Arctic, subarctic Pacific, North Atlantic, Arabian, and equatorial Pacific. Shaded area as in Figure 1.5.

independence of temperature and resource effects in the analysis shown in Figure 1.5, all argue against the universal validity of Pomeroy's hypothesis.

Another way of approaching the consequences of global warming on bacterial-mediated carbon fluxes is by conducting perturbation experiments in which experimental warming is applied over short- to medium-term-duration incubations with natural samples to capture local responses (e.g., Kirchman et al., 2005). The small number of realistic warming perturbation experiments performed to date have shown differences in the respective responses of phytoplankton and bacteria (Morán et al., 2006; Hoppe et al., 2008), suggesting the possibility of disruptions in their trophic relationship at higher temperatures. This type of experiment, together with examination of patterns across large temperature ranges, can provide us with clues about the possible directions of change. However, they obviously fail to incorporate the possibility of adaptations of extant communities over the longer term, or of shifts in community composition (see below). Interestingly, agreement in the absence of direct warming-driven changes in BGE between the results of experimental perturbations and theoretically based predictions linking metabolism and temperature (cf. López-Urrutia and Morán, 2007; Vázquez-Domínguez et al., 2007) would still encourage their use as hypothesis-generating tools.

In conclusion, although temperature is only one of the many factors affecting bacterial metabolism, current knowledge suggests that changes are expected in the amount of organic carbon being processed by bacteria in a warmer ocean. Whether these changes will be a larger amount of DOM being channeled through bacterial communities with unaltered bacterial physiology (BGE; Figure 1.6, case 1) or, more likely, a general slowdown of system metabolism, as implied by decreasing phytoplankton biomass and primary production in vast areas of the world ocean, lowering BGE (Figure 1.6, case 2) remains to be tested.

1.3 CLIMATE AND PLANKTON ECOLOGY

As we stated above, bacterial growth in the sea is regulated by the complex interplay of resource limitation (bottom-up forcing; Billen et al. 1990), temperature, and removal processes (top-down controls; Strom, 2008). Bacterial abundance in many marine environments is correlated with bacterial production rates, a proxy for resource supply, suggesting that resource limitation is the primary control on bacterial stocks (Ducklow, 1992). But the abundance seldom reaches the saturating level predicted from physiological models of growth and resource supply (Wright and Coffin, 1984; Ducklow and Hill, 1985). This effect means that predators and viruses must suppress bacterial accumulation below the saturation level set by resource supply. Together, these observations suggest that bacterial abundance is set by a dynamic balance between resource supply and removal processes, a combination of bottom-up and top-down controls. Changes in resource supply cause changes in abundance, but some of the resources are funneled to bacteriovores, and thence into the food web. Bacteria may be limited by inorganic nutrients such as phosphorus (Thingstad et al., 2005), organic matter (Carlson and Ducklow, 1996), or combinations of organic and inorganic forms, such as DOM and iron (Church et al., 2000; Kirchman et al., 2000). Similarly, removal is some combination of grazing by bacteriovores (Strom, 2000) and lysis by bacteriophages (Suttle, 2007). The balance among supplies of different limiting resources for bacteria,

and between different bacterial consumers is a function of the composition of the entire plankton community. Thus, we need to look in more detail at plankton communities to get a better understanding of how bacteria might respond to climate-driven changes in the physical environment.

Delivery of solar energy to the ocean surface determines two critical processes that structure the plankton ecosystem: vertical density stratification of the upper ocean water column; and the maximum rate of photosynthesis under ambient temperature, nutrient, and grazing conditions (Miller, 2004). Phytoplankton growth is proportional to light intensity and depletes nutrients from the surface layer, creating a vertical nutrient concentration gradient opposite to the profile of light intensity. Heating the ocean surface results in vertical stratification because warmer water is less dense and more buoyant than the colder layers below. Hence, global warming is predicted to lead to more stratification. The vertical temperature–density gradient is determined both by heating at the surface and by the temperature of deep-ocean water, which reflects temperatures at the poles. In coastal and polar regions, inputs of fresh water also contribute to enhanced stratification. The stratification, or contrast in density between shallow and deeper layers, is a barrier to turbulent mixing generated by winds. Turbulent mixing has two opposing impacts on phytoplankton growth: It mixes nutrients from deep into shallow water, and mixes phytoplankton from the illuminated surface down into darker subsurface waters. Coastal, polar, and high-latitude regions experience higher winds and more turbulence; in contrast, tropical, subtropical, and offshore waters receive more heating and tend to be more stratified. Thus, very generally, phytoplankton in higher latitudes and coastal waters with more nutrient supply are relatively more light-limited, and those in warm, stratified seas are more nutrient-limited.

These geographic patterns are set by the climate and have important implications for phytoplankton community composition (Falkowski and Oliver, 2007). Thermal gradients between the tropics and polar regions, and between the land and ocean, generate large-scale wind patterns, causing regional differences in mixing and turbulence. During periods with stronger equator-to-pole thermal contrasts, such as glacial epochs, winds are stronger and storms are more frequent, enhancing ocean turbulence. During warm periods the winds are lower and there is greater stratification, with a lower turbulence regime. In past geological history, the temperature difference between the surface and deep ocean has ranged from about 10°C, a relatively well-mixed condition 65 million years ago (65 Ma), to 25°C, a more stratified condition today. We live today in a cryosphere-influenced climate still largely set by glacial conditions with polar ice caps, sea ice, strong thermal gradients, and high winds and turbulence. Sixty-five million years ago, the world was warmer, ocean bottom temperatures were higher, and the ocean was less well stratified. It took less wind energy to mix nutrients up from deep water in the pan-tropical era of 65 Ma.

Plankton community composition is set ultimately by environmental selection of phytoplankton cell size (Cullen et al., 2002; Katz et al., 2004). In nutrient-depleted tropical seas, and in the seasonally stratified surface layer in midlatitudes in summer, small cells with high surface/volume ratios and superior ability to compete for scarce nutrients dominate the phytoplankton community (Agawin et al., 2000). The classic example of this condition is the oligotrophic North Pacific subtropical gyre (NPSG) to the north of Hawaii, a vast region dominated by *Prochlorococcus* and *Synechococcus*, photosynthetic prokaryotes about 1 µm in diameter (Karl, 1999a). Diatoms are favored under turbulent conditions because they have internal nutrient storage vacuoles and can

“stock up” during transient mixing events caused by storms and other turbulent events. In addition, because they have dense and heavy silicified shells (frustules), diatoms sink into deep water under stratified, quiescent conditions, but stay suspended in the upper water column in more turbulent conditions. There has been a long, steady increase in diatom diversity over the last 65 million years during the transition from tropical to glacial conditions, reflecting the increase in the turbulence climate over that time span (Falkowski and Oliver, 2007). Other groups, including dinoflagellates and coccolithophorids, predominate in regions and time periods with conditions intermediate between these oligotrophic and well-mixed regimes. The grazer community adapts to the size of its prey: In tropical seas, the predominant herbivores are protozoans specialized to feed efficiently on small phytoplankton (Landry and Kirchman, 2002). Where phytoplankton are larger, copepods and krill are the major grazers (Miller, 2004).

To summarize at this point: Heterotrophic bacteria depend on, and respond to, the flux of organic matter and nutrients produced by phytoplankton and processed by grazers in marine food webs. Climate sets the physical regime of wind mixing, turbulence, and stratification in marine environments. The large-scale biogeography of marine plankton ecosystems follows the global gradients of temperature and wind. The physical regime, in turn, determines the characteristic size and community composition of planktonic phytoplankton (and by extension, zooplankton) in different marine ecological provinces or biomes (Longhurst, 1998).

The projected responses of ocean phytoplankton to changes in physical properties as outlined above have been studied by adding models of plankton food webs to AOGCMs (Bopp et al., 2001; Boyd and Doney, 2002; Sarmiento et al., 2004; Boyd et al., 2008). In the early cases, the models were very simple, including only single phytoplankton, zooplankton, and bacterial compartments (e.g., Figure 1.4), using only nitrogen as a model currency (Sarmiento et al., 1993). The underlying concept embodied in these models is that plankton ecosystem response to climate variability is modulated through direct phytoplankton responses to ocean mixing, light, and nutrient supply. These simple models have a critical limitation: that only crude bulk-rate changes such as the total primary production can be modeled. Importantly, however, climate change will also affect the species and functional group composition of phytoplankton communities (Falkowski et al., 1998). For example, changes in stratification and mixing may lead to shifts in the relative importance of diatoms and other forms. Such changes have already been reported, with shifts from diatoms to cryptophytes in Antarctica (Moline et al., 2004), large blooms of coccolithophorids in the Bering Sea (Napp and Hunt, 2001; Broerse et al., 2003), and shifts toward the smallest phytoplankton in the NPSG (Karl, 1999b). To capture such ecosystem shifts, modelers have had to construct more complex models with several different classes of phytoplankton rather than a single aggregate compartment (Ducklow and Fasham, 1991; Doney et al., 2004; Follows et al., 2007).

One approach to greater articulation in model community structure and forecasting acuity has been to incorporate representations of planktonic biogeochemical functional groups: plankton groups that mediate specific chemical transformations such as diatoms (fixing silica), coccolithophorids (calcium carbonate), and diazotrophs (nitrogen fixation). In this context, heterotrophic bacteria can be thought of as a functional group that decomposes organic matter and respire CO_2 back into the water. Indeed, “bacteria,” first added to a plankton system model by Fasham et al. (1990), are included in one of the most complex plankton functional group models currently in use (Le Qué

et al., 2005). Boyd and Doney (2002) coupled diatoms, coccolithophorids, and diazotrophs in the NCAR Community Climate System AOGCM and looked at how the abundance of these groups changed in different ocean regions under a global warming scenario with increased stratification (as shown in Figure 1.3). In such an approach, all the functional forms are potentially present in any region and may become dominant, depending on their model-defined environmental preferences (“universal distribution, local selection”).

Boyd and Doney’s model predicted increases in diazotrophs in the tropics in response to decreased mixed layers and increased stratification (Figure 1.8), both of which favor the buoyant, colonial *Trichodesmium* with its high light requirement (Karl et al., 1997). Other projected changes include reductions in diatoms and increases in picoplankton in the central gyres, increases in diatoms in coastal regions (in response to increased upwelling), and increases in coccolithophorids. A caveat is that few such model studies have been performed, and the results are still speculative (Falkowski and Oliver, 2008; Peters, 2008). But they represent the current state of our understanding, with the best tools we possess. To date, models have not included different microbial functional or taxonomic groups, such as photoheterotrophs or archaea.

1.3.1 Linking Bacteria to Climate Changes

Bacteria may respond directly to increasing temperature, but their responses to other changes in the ocean climate will be modulated through the plankton community. Current knowledge about the trophic interactions between phytoplankton and bacteria, called *phytoplankton–bacterioplankton coupling* (Morán et al., 2002), may allow us to make predictions based on predicted changes in primary producer assemblages and their production rates and physiology. The composition of phytoplankton assemblages is known to affect the quality and quantity of released photosynthate (Lancelot, 1979,1983) and the fraction of primary production directly available for bacterial uptake (Cole et al., 1982,1988; Baines and Pace, 1991). Shifts toward smaller phytoplankton cell sizes (see above) can be accompanied by a relatively higher proportion of photosynthate being released extracellularly. Teira et al. (2001) and Morán et al. (2002) have reported consistent increases in the percentage of extracellular release when phytoplankton assemblages are dominated increasingly by the picoplankton size class in subtropical and temperate regions, respectively. Thus, although lower primary production rates are anticipated in vast areas of the ocean (Behrenfeld et al., 2006), the amount of substrates readily available to bacterial assemblages might be somewhat compensated by increased extracellular release. In general, the coupling between phytoplankton growth and removal by grazers is tighter in plankton communities dominated by smaller cells. Shifts in cell size may alter the balance between DOM supplied by exudation and that originating from grazers and their feeding behavior, changing the rates and composition of the DOM supply. Below we focus on the changes predicted in phytoplankton in polar, tropical, and coastal oceans, and the potential implications for bacteria.

1.3.2 Polar Regions

In the Antarctic peninsula, one of the fastest-warming regions of the Earth (Vaughan et al., 2003), experimental 2°C warming of incubated samples collected in summer

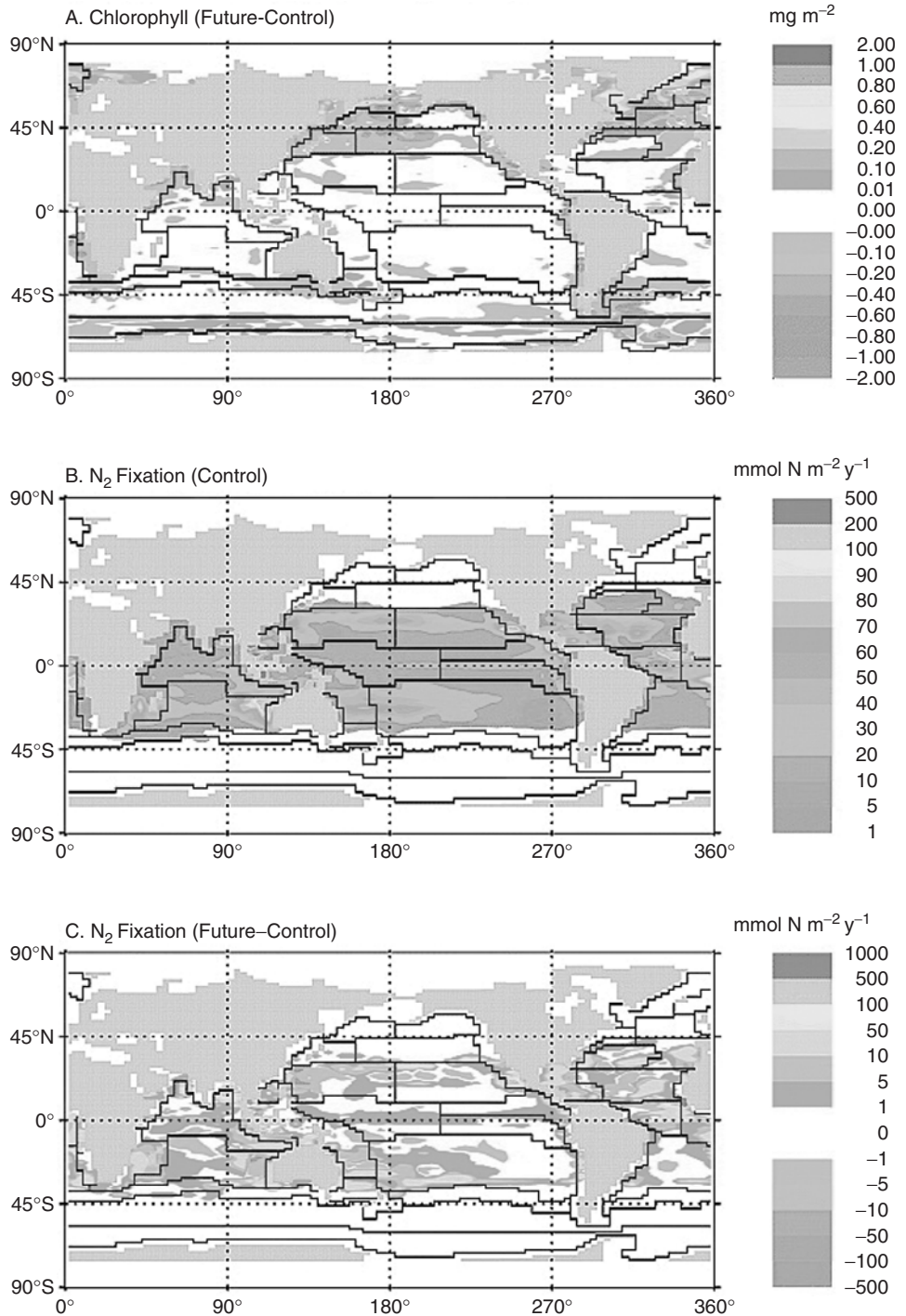


Figure 1.8 Numerical model simulations of ocean ecosystems using the CSSM (see Figure 1.3) with an off-line, multispecies pelagic ecosystem model for (A) the difference between predicted chlorophyll with warming and a control run (future-control), (B) N₂ fixation (control), and (C) N₂ fixation (future-control). (From Boyd and Doney, 2002, with permission of the American Geophysical Union.) (See insert for color representation.)

significantly changed the partitioning of primary production between the particulate and dissolved phase, but a clear effect on bacterial demand for carbon could not be demonstrated at the time scale of the experiments (Morán et al., 2006). Models predict an increase in primary production rates during the growth season due to enhanced stratification and abundance of macronutrients in both polar regions (see above). The expected impact of higher temperatures and larger amounts of fresh DOM provided to bacterial communities is an increase in bacterial abundance and consequently, in activity (Figure 1.5). Below we discuss potential shifts in bacterial species composition as well. The role of micronutrients such as iron in the response of bacteria is still uncertain (Pakulski et al., 1996; Church et al., 2000; Arrieta et al., 2004; Oliver et al., 2004), as are such changes in phytoplankton communities as the replacement of diatoms by cryptophytes already observed (Moline et al., 2000, 2004). However, the predicted lack of substrate limitation suggests that a greater DOM flux would be processed by a larger number of bacteria with essentially the same growth efficiency. According to the model of Anderson and Ducklow (2001), partitioning of food web flows in favor of extracellular release by phytoplankton would result in higher BP/PP ratios, even without concomitant alteration in the BGE. Increasing BP/PP may constitute a positive feedback, with higher bacterial biomass enhancing viral lysis, more available DOM, and so on.

The existence of strong hydrographic fronts that serve as faunal boundaries in the Southern Ocean is a singular feature of Antarctic polar waters (Tréguer and Jacques, 1992). Despite claims of unlimited dispersal across such biogeographical boundaries (Finlay, 2002), scenarios of a mean warming higher than 5°C may entail loss of Southern Ocean bacterial and archaeal species without immediate replacement by lower-latitude species (Papke and Ward, 2004; Newsham and Garstecki, 2007), due to endemism in extreme environments. However, the greatest effect of warming is likely to be loss of sea ice. The microbial communities in sea ice probably have a higher incidence of endemism than that of the pelagic community.

1.3.3 Tropical Regions

Tropical and subtropical ecosystems correspond to the right end of the bacterial vs. temperature relationship depicted in Figure 1.5, thus implying that factors other than temperature are more critical for regulating bacterial standing stocks and metabolism. We generally lack specific formulations for the temperature dependence of bacterial grazers (see Sherr et al., 1988) and how they may change in a warmer ocean, but even leaving top-down controls aside, a fundamental difference exists between most tropical–subtropical and higher-latitude environments. With the exception of the equatorial provinces, waters with a mean temperature of 25°C and higher are oligotrophic, characterized by chlorophyll values below 0.2 mg m⁻³ (Longhurst, 1998; Ducklow, 2003). Moreover, they cover the vast majority of the ocean's surface, so changes in their functioning will greatly affect biogeochemical cycles.

Inorganic nutrients not only limit phytoplankton growth, but nitrate and phosphate can also directly affect bacterial growth (Mills et al., 2008). Coupled models of ocean circulation and ecology agree strongly in predicting a general decrease in the supply of new nutrients from below the thermocline due to increased stratification (see above). The obvious consequence is that phytoplankton primary production will decrease, as already observed in the satellite record over the past decade (Behrenfeld et al., 2006).

Decreases in phytoplankton size at increased temperatures (Morán et al., 2008) could be associated with an increase in PER, as discussed previously, but it may be insufficient to support a larger bacterial demand driven by increased temperature. Although considerable scatter is seen in at temperatures higher than 15°C (Figure 1.5), the constraints exerted by lower primary productivity will probably result in lower bacterial standing stocks. Our hypothesis is that a greater proportion of the organic carbon processed by bacteria (from increased PER) would be respired rather than used to build up biomass (Figure 1.6). The decrease in BGE and increase in respiration could have an impact on global carbon cycling by enhancing ocean-to-atmosphere CO₂ fluxes.

Changes in stratification may also affect the oxygen balance in deeper waters: for example, the extensive oxygen minimum zones (OMZs) in the eastern tropical Pacific and Arabian Sea. These are habitats for chemolithotrophic bacteria that would respond to expansion or contraction of the OMZs. The key question concerning these vast areas of the global oceans is whether we can extrapolate the general patterns described so far to predict future behavior of heterotrophic bacteria in a warmer ocean. A question that remains unsolved is what will happen if, as models predict, oceanic primary production decreases in the huge oligotrophic oceanic regions as much as to severely limit the amount of substrate provided. Abundances will decrease to accommodate the supply of substrates or, alternatively, bacterial populations may adapt to using more of the large, seasonally varying pool of semilabile DOM (Hansell et al., 1995; Carlson and Ducklow, 1996; Church et al., 2002). An alternative hypothesis is that these conditions will favor organisms that utilize dissolved inorganic carbon chemolithotrophically.

1.3.4 Coastal Oceans

In the open sea, remote from external inputs of organic matter and nutrients, heterotrophic bacterial metabolism must be sustained on the flow of carbon from the primary producers, either directly, via exudation, or indirectly after passage through grazers and the detrital pool. The coastal oceans are influenced by multiple inputs from terrestrial ecosystems, and on diverse anthropogenic perturbations, in addition to, and interacting with, climate change (Robinson et al., 2004). Inputs of sediments change the local light regime. Nutrient inputs cause enrichment and eutrophication (Rabalais, 2004). Inputs of terrestrial organic matter are respired by bacteria, possibly leading to an excess of respiration (R) over production (P) (Ducklow and McCallister, 2004) and local to regional-scale hypoxia. The future P/R balance will depend on the relative amounts of inorganic nutrients and organic matter exported from land (Ver et al., 1999) and on the relative temperature sensitivities of phytoplankton and bacterial processes as the ocean warms. Recently, Hoppe et al. (2008) conducted a wintertime mesocosm experiment in which water from the Kiel Fjord (Baltic Sea) and its plankton community was warmed experimentally over a two-month period to simulate the effects of regional warming on phytoplankton–bacterial coupling. They found that the timing of the phytoplankton bloom was unchanged by temperature increases of 2 to 6°C, although the bloom magnitude declined with increasing temperature, as observed in a multiyear analysis in Chesapeake Bay (Lomas et al., 2002). In contrast, the lag period between the phytoplankton and peak bacterial production declined with increasing warming, apparently tightening the coupling between organic matter production and consumption. But they also found that the ratio of bacterial to primary production in the experimental mesocosms increased from 37% to 63% as the warming increment

was increased from $+2^{\circ}\text{C}$ to $+6^{\circ}\text{C}$. The higher BP/PP values indicate increased utilization of allochthonous DOM in the coastal water rather than use of recent products of phytoplankton bloom. This experiment illustrates that climate warming could have a major impact on the metabolic balance of coastal oceans.

1.3.5 Potential Impacts of Climate Change on Bacterioplankton Diversity and Structure

Our discussion so far has concentrated on bulk fluxes of organic matter through an undifferentiated bacterial community. Upon consideration of the scenarios developed in this chapter and by others (e.g., Falkowski and Oliver, 2007) which suggest that climate change may result in increased stratification, strengthened links between primary and secondary producers and increased DOC and bacterial respiration, it is also likely that microbial diversity and/or community structure will shift to accommodate these changes. Species competition and resource utilization in complex microbial communities may result in three possible outcomes in a situation with increased resources (such as DOC) (1) the functional complexity and diversity will increase (complementarity), (2) the resource will act as a factor of selection favoring reduced complexity and a less diverse assemblage (bloom situation), and (3) the community will absorb the increased resource, resulting in an increased growth rate and/or respiration, although diversity will remain unchanged. This last case may be the result of marine bacterial species being generalists rather than specialists (Mou et al., 2008). Unfortunately, for marine bacterial and archaeal diversity, our understanding of these interactions is still not well developed.

We can, however, propose a few rather simple examples of impacts on species diversity resulting from climate change. First is the consideration of habitat loss on marine microbial diversity. Antarctic and Arctic sea ice microbial communities are distinct from plankton communities (Bowman et al., 1997; Brinkmeyer et al., 2003), tend to be dominated by true psychrophiles and have a higher degree of endemism than that of many marine planktonic organisms. Loss of sea ice will not only result in habitat loss for marine psychrophiles, but will also affect sea ice-melt-related oceanic processes like seeding phytoplankton blooms (especially diatoms) and stratification of surface waters. A second bacterial habitat that may be at risk are large phytoplankton themselves. Species-specific relationships exist between bacteria and the extracellular zones surrounding algal cells (Jasti et al., 2005). Somewhat related to this is the particulate organic carbon that accumulates as marine snow. Large phytoplankton (e.g., diatoms) are thought to contribute most significantly to marine snow particles. These particles are home to unique microbial consortia which differ from their counterparts in the surrounding seawater (e.g., DeLong et al., 1993).

Another potential effect results from a fueling of the microbial loop (discussed previously). With increases in bacterial abundance, respiration, and growth, it is possible that viral control and lysis will result in a positive feedback to this loop, resulting in additional DOC and additional top-down control. Current concepts suggest that viruses play roles not only in control of dominant species ("kill the winner," Thingstad and Lignel, 1997) but that they also influence bacterial diversity through population control of less dominant populations in addition to being resources of lateral gene transfer (Weinbauer and Rassoulzadegan, 2004; Suttle, 2007). As resources in the ocean shift toward higher DOC, inevitably this will influence the competitive abilities of organisms in the upper ocean for carbon utilization, and likely species composition.

1.4 SUMMARY

The projections we have reviewed suggest a geographic redistribution of plankton rate processes with climate change. Primary production rates will increase in polar waters and decrease in the tropics, concentrating more of the global ocean productivity at higher latitudes. In both regimes, more primary production may be routed through the dissolved pool, resulting in a greater flux of photosynthate through bacteria over much of the world ocean, and possibly increases in bacterial stocks at higher latitudes. This may lead to alterations in food web structure as more biomass at the base of food webs is concentrated in the microbial loop, and may increase the recycling rate of carbon through the loop. In general, however, the changes we discuss would not lead to large-scale alterations of the ocean carbon balance (Falkowski and Oliver, 2007). The total amount of ocean production that is respired would ultimately change little, although the location and timing of the respiration could be affected. For example, if warming increases the recycling rate of locally produced, labile organic matter in the surface layer, less carbon will be exported to the deep sea. But a change in the bacterial use of oceanic semilabile DOC could represent a major alteration of the marine carbon cycle. A similarly large change would be seen if a change in trophic structure of marine bacteria favored chemolithotrophic organisms under these conditions. The total amount of DOC in the global ocean is about equal to the amount of CO₂ in the atmosphere (Houghton, 2007), and repartitioning of carbon in the ocean–atmosphere system is a major control on the climate system (Sarmiento and Toggweiler, 1984). Climate warming is already causing increased soil respiration in the Arctic, in which soil microbes are decomposing organic matter stored in the tundra since the last glaciation (Oechel et al., 1993). This process is potentially a major positive feedback in the climate system (Luo, 2007). Increased bacterial utilization and respiration of DOM, the “soil” of the oceans, could alter the metabolic balance of ocean ecosystems, which are currently finely balanced, with equal rates of production and respiration (Robinson, 2008). Such a change may depend on temperature selection of bacterial populations capable of decomposing the more refractory components of marine DOC, as well as temperature-mediated increases in production and respiration rates.

When it comes to marine microbial diversity, we are still knowledge limited, particularly with regard to the links between phylogenetic diversity and functional capacities and the repertoire of growth strategies characteristic of marine bacterioplankton. These limitations affect our ability to predict response of the community to increased sea surface temperature and resulting changes in the flow of organic carbon through the microbial community. Marine microbial genome (Moran et al., 2004; Giovannoni et al., 2005) and metagenome (Venter, 2004; DeLong and Karl, 2005) studies have begun to crack the door open on these processes, but we are still at the beginning of this knowledge curve. We can look to certain regions of the world’s ocean to gain further understanding of processes that may inform our predictive capabilities for understanding climate change. Two such regions are the oxygen minimum zones of the tropics, where conditions resulting from increased respiration can be studied, and the Southern Ocean, where annual primary production varies tremendously, and the responses of the marine microbial communities to a highly dynamic and predictable change in dissolved organic carbon resources can be studied. Further, improvements are needed to develop predictive coupled physical–biological models which incorporate both process (function) and species diversity information in the photic zone (Follows et al., 2007;

Moran et al., 2007) as well as inner ocean, since it is likely that changes in the upper water column, particularly with loss of larger phytoplankton that are responsible for a significant fraction of export production, will have an impact on carbon respiration in the deep sea. We are only now beginning to understand the relationships between diversity and functional capabilities to inform these models, but with the rapid advances in this field and large-scale oceanographic studies (Rusch et al., 2007) we will be poised to understand emergent properties and predict vital impacts on the marine ecosystem following anthropogenic climate change. Disentangling the multiple effects of climate warming on ocean ecosystems—changes in the physical environment, phytoplankton community composition, and bacterial processes—will be a major challenge for marine ecologists in the coming decade.

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REFERENCES

- Agawin, N. S. R., Duarte, C. M., and Agustí, S. (2000) Nutrient and temperature control of the contribution of picoplankton to phytoplankton biomass and production. *Limnol. Oceanogr.*, 45, 591–600.
- Allen, A. P., Gillooly, J. F., and Brown, J. H. (2005) Linking the global carbon cycle to individual metabolism. *Funct. Ecol.*, 19, 202–213.
- Alonso-Sáez, L., Vázquez-Domínguez, E., Cardelús, C., et al. (2008) Factors controlling the year-round variability in carbon flux through bacteria in a coastal marine system. *Ecosystems*, 11, 397–409.
- Anderson, T. R., and Ducklow, H. W. (2001) Microbial loop carbon cycling in ocean environments studied using a simple steady state model. *Aquat. Microb. Ecol.*, 26, 37–49.
- Apple, J. K., Smith, E. M., and Boyd, T. J. (2008) Temperature, salinity, nutrients, and the covariation of bacterial production and chlorophyll-*a* in estuarine ecosystems. *J. Coast. Res.*, 55 (in press).
- Arrhenius, S. (1915) *Quantitative Laws in Biological Chemistry*. C. Belland Sons, London.
- Arrieta, J. M., Weinbauer, M. G., Lute, C., and Herndl, G. J. (2004) Response of bacterioplankton to iron fertilization in the Southern Ocean. *Limnol. Oceanogr.*, 49, 799–808.
- Azam, F., and Hodson, R. E. (1977) Size distribution and activity of marine microheterotrophs. *Limnol. Oceanogr.*, 22, 492–501.
- Azam, F., and Malfatti, F. (2007) Microbial structuring of marine ecosystems. *Nat. Rev. Micro.*, 5, 782–791.
- Azam, F., and Worden, A. Z. (2004) Oceanography: microbes, molecules, and marine ecosystems. *Science*, 303, 1622–1624.
- Azam, F., Fenchel, T., Field, J. G., et al. (1983) The ecological role of water-column microbes in the sea. *Mar. Ecol. Prog. Ser.*, 10, 257–263.

- Baines, S. B., and Pace, M. L. (1991) The production of dissolved organic matter by phytoplankton and its importance to bacteria: patterns across marine and freshwater systems. *Limnol. Oceanogr.*, 36, 1078–1090.
- Behrenfeld, M. J., O'Malley, R. T., Siegel, D. A., et al. (2006) Climate-driven trends in contemporary ocean productivity. *Nature*, 444, 752–755.
- Billen, G., Servais, P., and Becquevort, S. (1990) Dynamics of bacterioplankton in oligotrophic and eutrophic aquatic environments: bottom-up or top-down control? *Hydrobiologia*, 207, 37–42.
- Bird, D. F., and Karl, D. M. (1999) Uncoupling of bacteria and phytoplankton during the austral spring bloom in Gerlache Strait, Antarctic Peninsula. *Aquat. Microb. Ecol.*, 19, 13–27.
- Bjørnsen, P. K. (1988) Phytoplankton exudation of organic matter: Why do healthy cells do it? *Limnol. Oceanogr.*, 33, 151–154.
- Bopp, L., Monfray, P., Aumont, O., et al. (2001) Potential impact of climate change on marine export production. *Glob. Biogeochem. Cycles*, 15, 81–99.
- Bowman, J. P., McCammon, S. A., Brown, M. V., et al. (1997) Diversity and association of psychrophilic bacteria in Antarctic sea ice. *Appl. Environ. Microbiol.*, 63, 3068–3078.
- Boyd, P. W., and Doney, S. C. (2002) Modelling regional responses by marine pelagic ecosystems to global climate change. *Geophys. Res. Lett.*, 29, 1806.
- Boyd, P. W., Doney, S. C., Strzepek, R., et al. (2008) Climate-mediated changes to mixed-layer properties in the Southern Ocean: assessing the phytoplankton response. *Biogeosciences*, 5, 847–864.
- Brinkmeyer, R., Knittel, K., Jurgens, J., et al. (2003) Diversity and structure of bacterial communities in Arctic vs. Antarctic pack ice. *Appl. Environ. Microbiol.*, 69, 6610–6619.
- Broerse, A. T. C., Tyrrell, T., Young, J. R., et al. (2003) The cause of bright waters in the Bering Sea in winter. *Continental Shelf Res.*, 23, 1579–1596.
- Brown, J. H., Gillooly, J. F., Allen, A. P., et al. (2004) Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789.
- Buchan, A., Gonzalez, J. M., and Moran, M. A. (2005) Overview of the marine *Roseobacter* lineage. *Appl. Environ. Microbiol.*, 71, 5665–5677.
- Calbet, A., and Landry, M. R. (2004) Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. *Limnol. Oceanogr.*, 49, 51–57.
- Calvo-Díaz, A., and Morán, X. A. G. (2006) Seasonal dynamics of picoplankton in shelf waters of the southern Bay of Biscay. *Aquat. Microb. Ecol.*, 42, 159–174.
- Campbell, B. J., Waidner, L. A., Cottrell, M. T., and Kirchman, D. L., (2008) Abundant proteorhodopsin genes in the North Atlantic Ocean. *Environ. Microbiol.* 10, 99–109.
- Carlson, C. A., and Ducklow, H. W. (1996) Growth of bacterioplankton and consumption of dissolved organic carbon in the Sargasso Sea. *Aquat. Microb. Ecol.*, 10, 69–85.
- Cho, J. C., and Giovannoni, S. J. (2004) Cultivation and growth characteristics of a diverse group of oligotrophic marine [gamma]-proteobacteria. *Appl. Environ. Microbiol.*, 70, 432–440.
- Church, M. J., Hutchins, D. A., and Ducklow, H. W. (2000) Limitation of bacterial growth by dissolved organic matter and iron in the Southern Ocean. *Appl. Environ. Microbiol.*, 66, 455–466.
- Church, M. J., Ducklow, H. W., and Karl, D. M. (2002) Temporal variability in dissolved organic matter stocks in the Central North Pacific Gyre. *Limnol. Oceanogr.*, 47, 1–10.
- Church, M. J., DeLong, E. F., Ducklow, H. W., et al. (2003) Abundance and distribution of planktonic archaea and bacteria in the waters west of the Antarctic Peninsula. *Limnol. Oceanogr.*, 48, 1893–1902.

- Cole, J. J., Likens, G. E., and Strayer, D. L. (1982) Photosynthetically produced dissolved organic carbon: an important carbon source for planktonic bacteria. *Limnol. Oceanogr.*, 27, 1080–1090.
- Cole, J. J., Findlay, S., and Pace, M. L. (1988) Bacterial production in fresh and saltwater ecosystems: a cross-system overview. *Mar. Ecol. Prog. Ser.*, 43, 1–10.
- Cottrell, M. T., Wood, D. N., Yu, L., and Kirchman, D. L. (2000) Selected chitinase genes in cultured and uncultured marine bacteria in the alpha- and gamma-subclasses of the proteobacteria. *Appl. Environ. Microbiol.*, 66, 1195–1201.
- Cullen, J. J., Franks, P. J. S., and Karl, D. M. (2002) Physical influences on marine ecosystem dynamics. In Robinson, A. R., McCarthy, J. J., and Rothschild, B. J. (eds.), *The Sea*, Vol. 12, *Biological–Physical Interactions in the Sea*. Wiley, New York, Hoboken, NJ, pp. 297–336.
- Daniels, R. M., Ducklow, H. W., and Richardson, T. L. (2006) Food web structure and biogeochemical processes during oceanic phytoplankton blooms: an inverse model analysis. *Deep-Sea Res. II*, 53, 532–554.
- del Giorgio, P. A., and Cole, J. J. (1998) Bacterial growth efficiency in natural aquatic systems. *Annu. Rev. Ecol. Syst.*, 29, 503–541.
- del Giorgio, P. A., and Duarte, C. M. (2002) Respiration in the open ocean. *Nature*, 420, 379–384.
- DeLong, E. F., and Karl, D. M. (2005) Genomic perspectives in microbial oceanography. *Nature*, 437, 336–342.
- DeLong, E. F., Franks, D. G., and Alldredge, A. L. (1993) Phylogenetic diversity of aggregate-attached vs free-living marine bacterial assemblages. *Limnol. Oceanogr.*, 38, 924–934.
- Doney, S. C., Abbott, M. R., Cullen, J. J., et al. (2004) From genes to ecosystems: the ocean's new frontier. *Front. Ecol. Environ.*, 2, 457–466.
- Ducklow, H. W. (1992) Factors regulating bottom-up control of bacterial biomass in open ocean plankton communities. *Arch. Hydrobiol.*, 37, 207–217.
- Ducklow, H. W. (1999) Minireview: The bacterial content of the oceanic euphotic zone. *FEMS Microbiol. Ecol.*, 30, 1–10.
- Ducklow, H. W. (2003) Biogeochemical provinces: towards a JGOFS synthesis. In Fasham, M. J. R. (ed.), *Ocean Biogeochemistry: A New Paradigm*. Springer-Verlag, New York, pp. 3–18.
- Ducklow, H. W. (2008) Microbial services: biodiversity-ecosystem function, ecosystem processes and sustainability. *Aquat. Microb. Ecol.*, 53, 13–19.
- Ducklow, H. W., and Carlson, C. A. (1992) Oceanic bacteria production. In Marshall, K. C. (ed.), *Advances in Microbial Ecology*. Plenum Press, New York, pp. 113–181.
- Ducklow, H. W., and Fasham, M. J. R. (1991) Bacteria in the greenhouse: modelling the role of oceanic plankton in the global carbon cycle. In Mitchell, R. (ed.), *New Concepts in Environmental Microbiology*. Wiley-Liss, New York, pp. 1–30.
- Ducklow, H. W., and Hill, S. (1985) The growth of heterotrophic bacteria in the surface waters of warm core rings. *Limnol. Oceanogr.*, 30, 241–262.
- Ducklow, H. W., and McCallister, S. L. (2004) The biogeochemistry of carbon dioxide in the coastal oceans. In Robinson, A. R., Brink, K., and Rothschild, B. J. (eds.), *The Sea*, Vol. 13, *The Global Coastal Ocean: Multiscale Interdisciplinary Processes*. Harvard University Press, Cambridge, MA, pp. 269–315.
- Ducklow, H. W., Purdie, D. A., Williams, P. J. L., and Davies, J. M. (1986) Bacterioplankton: a sink for carbon in a coastal marine plankton community. *Science*, 232, 865–867.

- Falkowski, P. G., and Oliver, M. J. (2007) Mix and match: how climate selects phytoplankton. *Nat. Rev. Microbiol.*, 5, 813–819.
- Falkowski, P. G., and Oliver, M. J. (2008) Diatoms in a future ocean—stirring it up: reply from Falkowski and Oliver. *Nat. Rev. Microbiol.*, 6, 407.
- Falkowski, P. G., Barber, R. T., and Smetacek, V. (1998) Biogeochemical controls and feedbacks on ocean primary production. *Science*, 281, 200–206.
- Falkowski, P. G., Scholes, R. J., Boyle, E., et al. (2000) The global carbon cycle: a test of our knowledge of Earth as a system. *Science*, 290, 291–296.
- Falkowski, P. G., Fenchel, T., and Delong, E. F. (2008) The microbial engines that drive Earth's biogeochemical cycles. *Science*, 320, 1034–1039.
- Fasham, M. J. R., Ducklow, H. W., and McKelvie, S. M. (1990) A nitrogen-based model of plankton dynamics in the oceanic mixed layer. *J. Mar. Res.*, 48, 1–49.
- Field, C. B., Behrenfeld, M. J., Randerson, J. T., and Falkowski, P. (1998) Primary production of the biosphere: integrating terrestrial and oceanic components. *Science*, 281, 237–240.
- Follows, M. J., Dutkiewicz, S., Grant, S., and Chisholm, S. W. (2007) Emergent biogeography of microbial communities in a model ocean. *Science*, 315, 1843–1846.
- Francis, C. A., Roberts, K. J., Beman, J. M., et al. (2005) Ubiquity and diversity of ammonia-oxidizing archaea in water columns and sediments of the ocean. *Proc. Natl. Acad. Sci. U.S.A.*, 102, 14683–14688.
- Frigaard, N. U., Martinez, A., Mincer, T. J., and DeLong, E. F. (2006) Proteorhodopsin lateral gene transfer between marine planktonic bacteria and archaea. *Nature*, 439, 847–850.
- Fuhrman, J. A. (1990) Dissolved free amino acid cycling in an estuarine outflow plume. *Mar. Ecol. Prog. Ser.*, 66, 197–203.
- Garneau, M.-E., Roy, S., Lovejoy, C., et al. (2008) Seasonal dynamics of bacterial biomass and production in a coastal arctic ecosystem: Franklin Bay, western Canadian Arctic. *J. Geophys. Res.*, 113.
- Gillooly, J. F., Brown, J. H., West, G. B., et al. (2001) Effects of size and temperature on metabolic rate. *Science*, 293, 2248–2251.
- Giovannoni, S. J., Tripp, H. J., Givan, S., et al. (2005) Genome streamlining in a cosmopolitan oceanic bacterium. *Science*, 309, 1242–1245.
- Hallam, S. J., Konstantinidis, K. T., Putnam, N., et al. (2006) Genomic analysis of the uncultivated marine crenarchaeote *Cenarchaeum symbiosum*. *Proc. Natl. Acad. Sci. U.S.A.*, 103, 18296–18301.
- Hansell, D. A., Bates, N. R., and Gundersen, K. (1995) Mineralization of dissolved organic carbon in the Sargasso Sea. *Mar. Chem.*, 51, 201–212.
- Hoch, M. P., and Kirchman, D. L. (1993) Seasonal and inter-annual variability in bacterial production and biomass in a temperate estuary. *Mar. Ecol. Prog. Ser. Oldendorf*, 98, 283–295.
- Hood, R. R., Laws, E. A., Armstrong, R. A., et al. (2006) Pelagic functional group modeling: progress, challenges and prospects. *Deep-Sea Res. II*, 53, 459–512.
- Hoppe, H.-G., Ducklow, H. W., and Karrasch, B. (1993) Evidence for dependency of bacterial growth on enzymatic hydrolysis of particulate organic matter in the mesopelagic ocean. *Mar. Ecol. Prog. Ser.*, 93, 277–283.
- Hoppe, H. G., Breithaupt, P., Walther, K., et al. (2008) Climate warming in winter affects the coupling between phytoplankton and bacteria during the spring bloom: a mesocosm study. *Aquat. Microb. Ecol.*, 51, 105–115.
- Houghton, R. A. (2007) Balancing the global carbon budget. *Annu. Rev. Earth Planet. Sci.*, 35, 313–347.

- Huber, J. A., Mark Welch, D., Morrison, H. G., et al. (2007) Microbial population structures in the deep marine biosphere. *Science*, 318, 97–100.
- IPCC (Intergovernmental Panel on Climate Change) (2007a) *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- IPCC (2007b) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Jasti, S., Sieracki, M. E., Poulton, N. J., et al. (2005) Phylogenetic diversity and specificity of bacteria closely associated with *Alexandrium* spp. and other phytoplankton. *Appl. Environ. Microbiol.*, 71, 3483–3494.
- Jumars, P. A., Penry, D. L., Baross, J. A., Perry, M. J., and Frost, B. W. (1989) Closing the microbial loop: dissolved organic carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion and absorption in animals. *Deep-Sea Res.*, 36, 483–495.
- Karl, D. M. (1999a) Minireviews: a sea of change: biogeochemical variability in the North Pacific subtropical gyre. *Ecosystems*, 2, 181–214.
- Karl, D. M. (1999b) A sea of change: biogeochemical variability in the North Pacific subtropical gyre. *Ecosystems*, 2, 181–214.
- Karl, D. M., Letelier, R., Tupas, L., et al. (1997) The role of nitrogen fixation in biogeochemical cycling in the subtropical North Pacific Ocean. *Nature*, 388, 533–538.
- Karner, M. B., DeLong, E. F., and Karl, D. M. (2001) Archaeal dominance in the mesopelagic zone of the Pacific Ocean. *Nature*, 409, 507–510.
- Katz, M. E., Finkel, Z. V., Grzebyk, D., et al. (2004) Evolutionary trajectories and biogeochemical impacts of marine eukaryotic phytoplankton. *Ann. Rev. Ecol. Evol. Syst.*, 35, 523–556.
- Kerr, R. A. (2007) Climate change: Global warming is changing the world. *Science*, 316, 188–190.
- Kirchman, D. L., Lancelot, C., Fasham, M., et al. (1993) Dissolved organic matter. In Evans, G. T., and Fasham, M. J. R. (eds.), *Towards a Model of Ocean Biogeochemical Processes*. Springer-Verlag, Berlin, pp. 209–225.
- Kirchman, D. L., Rich, J. H., and Barber, R. T. (1995) Biomass and biomass production of heterotrophic bacteria along 140 degree W. in the equatorial Pacific: effect of temperature on the microbial loop. *Deep-Sea Res. II*, 42, 603–619.
- Kirchman, D. L., Meon, B., Cottrell, M. T., et al. (2000) Carbon versus iron limitation of bacterial growth in the California upwelling regime. *Limnol. Oceanogr.*, 45, 1681–1688.
- Kirchman, D. L., Meon, B., Ducklow, H. W., et al. (2001) 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.
- Kirchman, D. L., Malmstrom, R. R., and Cottrell, M. T. (2005) Control of bacterial growth by temperature and organic matter in the western Arctic. *Deep-Sea Res. II*, 52, 3386–3395.
- Konneke, M., Bernhard, A. E., de la Torre, J. R., et al. (2005) Isolation of an autotrophic ammonia-oxidizing marine archaeon. *Nature*, 437, 543–546.
- Lampert, W. (1978) Release of dissolved organic carbon by grazing zooplankton. *Limnol. Oceanogr.*, 23, 831–834.
- Lancelot, C. (1979) Gross excretion rates of natural marine phytoplankton and heterotrophic uptake of excreted products in the southern North Sea, as determined by short-term kinetics. *Mar. Ecol. Prog. Ser.*, 1, 179–186.

- Lancelot, C. (1983) Factors affecting phytoplankton extracellular release in the Southern Bight of the North Sea. *Mar. Ecol. Prog. Ser.*, 12, 115–121.
- Landry, M. R., and Kirchman, D. L. (2002) Microbial community structure and variability in the tropical Pacific. *Deep-Sea Res. II*, 49, 2669–2693.
- Laws, E. A., Falkowski, P. G., Smith, W. O., Jr., et al. (2000) Temperature effects on export production in the open ocean. *Glob. Biogeochem. Cycles*, 14, 1231–1246.
- Le Quéré, C., Harrison, S. P., Colin Prentice, I., et al. (2005) Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models. *Glob. Change Biol.*, 11, 2016–2040.
- Li, W. K. W. (1998) Annual average abundance of heterotrophic bacteria and *Synechococcus* in surface ocean waters. *Limnol. Oceanogr.*, 43, 1746–1753.
- Li, W. K. W., Head, E. J. H., and Harrison, W. G. (2004) Macroecological limits of heterotrophic bacterial abundance in the ocean. *Deep-Sea Res. I*, 51, 1529–1540.
- Li, W. K. W., Harrison, W. G., and Head, E. J. H. (2006) Coherent assembly of phytoplankton communities in diverse temperate ocean ecosystems. *Proc. Roy. Soc. B*, 273, 1953–1960.
- Lomas, M. W., Glibert, P. M., Shiah, F. K., and Smith, E. M. (2002) Microbial processes and temperature in Chesapeake Bay: current relationships and potential impacts of regional warming. *Glob. Change Biol.*, 8, 51–70.
- Longhurst, A. (1998). *Ecological Geography of the Sea*. Academic Press, San Diego, CA.
- López-Urrutia, Á., and Morán, X. A. G. (2007) Resource limitation of bacterial production distorts the temperature dependence of oceanic carbon cycling. *Ecology*, 88, 817–822.
- López-Urrutia, Á., Martin, E. S., Harris, R. P., and Irigoien, X. (2006) Scaling the metabolic balance of the oceans. *Proc. Natl. Acad. Sci. U.S.A.*, 103, 8739–8744.
- Luo, Y. Q. (2007) Terrestrial carbon-cycle feedback to climate warming. *Annu. Rev. Ecol. Evol. Syst.*, 38, 683–712.
- Massana, R., Taylor, L. T., Murray, A. E., et al. (1998) Distribution of marine planktonic archaea in the Gerlache strait, Antarctic Peninsula, during early spring. *Limnol. Oceanogr.*, 43, 607–617.
- Meehl, G. A., Stocker, T. F., Collins, W. D., et al. (2007) Global climate projections. In Solomon, S., Qin, D., Manning, M., et al. (eds.), *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK, pp. 747–846.
- Meredith, M. P., and King, J. C. (2005) Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophys. Res. Lett.*, 32, doi: 10.1029/2005GL024042.
- Middelboe, M., and Lundsgaard, C. (2003) Microbial activity in the Greenland Sea: role of DOC lability, mineral nutrients and temperature. *Aquat. Microb. Ecol.*, 32, 151–163.
- Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-Being: Synthesis*. Island Press, Washington, DC.
- Miller, C. B. (2004). *Biological Oceanography*. Blackwell, Malden, MA.
- Mills, M. M., Moore, C. M., Langlois, R., et al. (2008) Nitrogen and phosphorus co-limitation of bacterial productivity and growth in the oligotrophic subtropical North Atlantic. *Limnol. Oceanogr.*, 53, 824–834.
- Moline, M. A., Claustre, H., Frazer, T. K., et al. (2000) Changes in phytoplankton assemblages along the Antarctic Peninsula and potential implications for the Antarctic food web. In Davidson, W., Howard-Williams, C., Broady, P. (eds.), *Antarctic Ecosystems: Models for Wider Ecological Understanding*. Caxton Press, Caldwell, ID, 263–271.

- Moline, M. A., Claustre, H., Frazer, T. K., et al. (2004) Alteration of the food web along the Antarctic Peninsula in response to a regional warming trend. *Glob. Change Biol.*, 10, 1973–1980.
- Moran, M. A., Buchan, A., Gonzalez, J. M., et al. (2004) Genome sequence of *Silicibacter pomeroyi* reveals adaptations to the marine environment. *Nature*, 432, 910–913.
- Moran, M. A., Belas, R., Schell, M. A., et al. (2007) Ecological genomics of marine roseobacters. *Appl. Environ. Microbiol.*, 73, 4559–4569.
- Morán, X. A. G., and Estrada, M. (2002) Phytoplanktonic DOC and POC production in the Bransfield and Gerlache Straits as derived from kinetic experiments of ¹⁴C incorporation. *Deep-Sea Res. II*, 49, 769–786.
- Morán, X. A. G., Gasol, J. M., Pedrós-Alió, C., and Estrada, M. (2001) Dissolved and particulate primary production and bacterial production in offshore Antarctic waters during Austral summer: coupled or uncoupled? *Mar. Ecol. Prog. Ser.*, 222, 25–39.
- Morán, X. A. G., Gasol, J. M., Pedrós-Alió, C., and Estrada, M. (2002) Partitioning of phytoplanktonic organic carbon production and bacterial production along a coastal-offshore gradient in the NE Atlantic during different hydrographic regimes. *Aquat. Microb. Ecol.*, 29, 239–252.
- Morán, X. A. G., Sebastián, M., Pedrós-Alió, C., and Estrada, M. (2006) Response of Southern Ocean phytoplankton and bacterioplankton production to short-term experimental warming. *Limnol. Oceanogr.*, 51, 1791–1800.
- Morán, X. A. G., López-Urrutia, Á., Calvo-Díaz, A., and Li, W. K. W. (2009) Increasing importance of small phytoplankton in a warmer ocean. *Ecol. Lett.*, in press.
- Morris, R. M., Rappé, M. S., Connon, S. A., et al. (2002) SAR11 clade dominates ocean surface bacterioplankton communities. *Nature (London)*, 420, 806–810.
- Mou, X. Z., Sun, S. L., Edwards, R. A., et al. (2008) Bacterial carbon processing by generalist species in the coastal ocean. *Nature*, 451, 708–711.
- Murray, A. E., and Grzymiski, J. J. (2007) Diversity and genomics of Antarctic marine microorganisms. *Philos. Trans. R. Soc. B*, 362, 2259–2271.
- Murray, A. E., Preston, C. M., Massana, R., et al. (1998) Seasonal and spatial variability of bacterial and archaeal assemblages in the coastal waters off Anvers Island, Antarctica. *Appl. Environ. Microbiol.*, 64, 2585–2595.
- Nagata, T. (2000) Production mechanisms of dissolved organic matter. In Kirchman, D. L., (ed.), *Microbial Ecology of the Oceans*. Wiley-Liss, New York, pp. 121–152.
- Napp, J. M., and Hunt, G. L. (2001) Anomalous conditions in the south-eastern Bering Sea 1997: linkages among climate, weather, ocean, and biology. *Fish. Oceanogr.*, 10, 61–68.
- Nedwell, D. B. (1999) Effect of low temperature on microbial growth: lowered affinity for substrates limits growth at low temperature. *FEMS Microbiol. Ecol.*, 30, 101–111.
- Newsham, K. K., and Garstecki, T. (2007) Interactive effects of warming and species loss on model Antarctic microbial food webs. *Funct. Ecol.*, 21, 577–584.
- Oechel, W. C., Hastings, S. J., Vourlitis, G., et al. (1993) Recent change of arctic tundra ecosystems from a net carbon dioxide sink to a source. *Nature*, 361, 520–523.
- Oliver, J. L., Barber, R. T., Smith, W. O., Jr., and Ducklow, H. W. (2004) The heterotrophic bacterial response during the Southern Ocean iron experiment (SOFEX). *Limnol. Oceanogr.*, 49, 2129–2140.
- Orr, J. C., Fabry, V. J., Aumont, O., et al. (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature*, 437, 681–686.
- Pakulski, J. D., Coffin, R. B., Kelley, C. A., et al. (1996) Iron stimulation of Antarctic bacteria. *Nature*, 383, 133–134.

- Papke, R. T., and Ward, D. M. (2004) The importance of physical isolation to microbial diversification. *FEMS Microbiol. Ecol.*, 48, 293–303.
- Pedros-Alió, C., Vaqué, D., Guixa-Boixereu, N., and Gasol, J. M. (2002) Prokaryotic plankton biomass and heterotrophic production in western Antarctic waters during the 1995–1996 Austral summer. *Deep-Sea Res. II*, 49, 805–825.
- Peters, F. (2008) Diatoms in a future ocean: stirring it up. *Nat. Rev. Micro*, 6, 407–407.
- Pomeroy, L. R. (1974) The ocean's food web, a changing paradigm. *BioScience*, 24, 499–504.
- Pomeroy, L. R., and Deibel, D. (1986) Temperature regulation of bacterial activity during the spring bloom in Newfoundland coastal waters. *Science (Washington)*, 233, 359–361.
- Pomeroy, L. R., and Wiebe, W. J. (1988) Energetics of microbial food webs. *Hydrobiologia*, 159, 7–18.
- Pomeroy, L. R., and Wiebe, W. J. (2001) Temperature and substrates as interactive limiting factors for marine heterotrophic bacteria. *Aquat. Microb. Ecol.*, 23, 187–204.
- Pomeroy, L. R., Macko, S. A., Ostrom, P. H., and Dunphy, J. (1990) The microbial food web in Arctic seawater: concentration of dissolved free amino acids and bacterial abundance and activity in the Arctic Ocean and in Resolute Passage. *Mar. Ecol. prog. Ser. Oldendorf*, 61, 31–40.
- Pommier, T., Canback, B., Riemann, L., et al. (2007) Global patterns of diversity and community structure in marine bacterioplankton. *Mol. Ecol.*, 16, 867–880.
- Price, P. B., and Sowers, T. (2004) Temperature dependence of metabolic rates for microbial growth, maintenance, and survival. *Proc. Natl. Acad. Sci. U.S.A.*, 101, 4631–4636.
- Rabelais, N. (2004) Eutrophication. In Robinson, A. R., Brink, K., and Rothschild, B. J. (eds.), *The Sea*, Vol. 13, *The Global Coastal Ocean: Multiscale Interdisciplinary Processes*. Harvard University Press, Cambridge, MA, pp. 821–866.
- Rae, R., and Vincent, W. F. (1998) Phytoplankton production in subarctic lake and river ecosystems: development of a photosynthesis–temperature–irradiance model. *J. Plankton Res.*, 20, 1293–1312.
- Rivkin, R. B., and Legendre, L. (2001) Biogenic carbon cycling in the upper ocean: effects of microbial respiration. *Science*, 291, 2398–2400.
- Robinson, C. (2008) Heterotrophic bacterial respiration. In Kirchman, D. L. (ed.), *Microbial Ecology of the Oceans*, 2nd ed. Wiley, Hoboken, NJ, pp. 299–334.
- Robinson, C., and Williams, P. (1993) Temperature and Antarctic plankton community respiration. *J. Plankton Res.*, 15, 1035–1051.
- Robinson, A. R., Brink, K. H., Ducklow, H. W., et al. (2004) Interdisciplinary multiscale coastal dynamical processes and interactions. In Robinson, A. R., Brink, K. H., and Rothschild, B. J. (eds.), *The Sea*. Harvard University Press, Cambridge, MA.
- Rusch, D. B., Halpern, A. L., Sutton, G., et al. (2007) The Sorcerer II global ocean sampling expedition: northwest Atlantic through eastern tropical Pacific. *PLoS Biology*, 5, 398–431.
- Sarmiento, J. L., and Toggweiler, J. R. (1984) A new model for the role of the oceans in determining atmospheric pCO₂. *Nature*, 308, 621–624.
- Sarmiento, J. L., Slater, R. D., Fasham, M. J. R., et al. (1993) A seasonal three-dimensional ecosystem model of nitrogen cycling in the North Atlantic euphotic zone. *Glob. Biogeochem. Cycles*, 7, 417–450.
- Sarmiento, J. L., Barber, R., Bopp, L., et al. (2004) Response of ocean ecosystems to climate warming. *Glob. Biogeochem. Cycles*, 18. doi: 10.1029/2003/GB002134.
- Serreze, M. C., Holland, M. M., and Stroeve, J. (2007) Perspectives on the Arctic's shrinking sea-ice cover. *Science*, 315, 1533–1536.
- Sherr, B. F., Sherr, E. B., and Rassoulzadegan, F. (1988) Rates of digestion of bacteria by marine phagotrophic protozoa: temperature dependence? *Appl. Environ. Microbiol.*, 54, 1091–1095.

- Shiah, F.-K., and Ducklow, H. W. (1995) Multiscale variability in bacterioplankton abundance, production and specific growth rate in a temperate salt-marsh creek. *Limnol. Oceanogr.*, 40, 55–66.
- Sogin, M. L., Morrison, H. G., Huber, J. A., et al. (2006) Microbial diversity in the deep sea and the underexplored “rare biosphere.” *Proc. Nat. Acad. Sci. U.S.A.*, 103, 12115–12120.
- Steinberg, D. K., Carlson, C. A., Bates, N. R., et al. (2001) Overview of the US JGOFS Bermuda Atlantic time-series study (BATS): a decade-scale look at ocean biology and biogeochemistry. *Deep-Sea Res. II*, 48, 1405–1447.
- Strom, S. L. (2000) Bacterivory: interactions between bacteria and their grazers. In Kirchman, D. L. (ed.), *Microbial Ecology of the Oceans*. Wiley, New York, pp. 351–386.
- Strom, S. L. (2008) Microbial ecology of ocean biogeochemistry: a community perspective. *Science*, 320, 1043–1045.
- Suttle, C. A. (2007) Marine viruses: major players in the global ecosystem. *Nat. Rev. Microbiol.*, 5, 801–812.
- Teira, E., Pazó, M. J., Serret, P., and Fernández, E. (2001) Dissolved organic carbon production by microbial populations in the Atlantic Ocean. *Limnol. Oceanogr.*, 46, 1370–77.
- Teira, E., Lebaron, P., van Aken, H., and Herndl, G. J. (2006) Distribution and activity of bacteria and archaea in the deep water masses of the North Atlantic. *Limnol. Oceanogr.*, 51, 2131–2144.
- Thingstad, T. F., and Lignell, R. (1997) Theoretical models for the control of bacterial growth rate, abundance, diversity and carbon demand. *Aquat. Microb. Ecol.*, 13, 19–27.
- Thingstad, T. F., Krom, M. D., Mantoura, R. F. C., et al. (2005) Nature of phosphorus limitation in the ultraoligotrophic eastern mediterranean. *Science*, 309, 1068–1071.
- Tréguer, P., and Jacques, G. (1992) Dynamics of nutrients and phytoplankton and fluxes of carbon, nitrogen and silicon in the Antarctic Ocean. *Polar Biol.*, 12, 149–162.
- Vaughan, D. G., Marshall, G. J., Connolley, W. M., et al. (2003) Recent rapid regional climate warming on the Antarctic Peninsula. *Clim. Change*, 60, 243–274.
- Vázquez-Domínguez, E., Vaqué, D., and Gasol, J. M. (2007) Ocean warming enhances respiration and carbon demand of coastal microbial plankton. *Glob. Change Biol.*, 13, 1327–1334.
- Venter, J. C. (2004) Environmental genome shotgun sequencing of the Sargasso Sea. *Science*, 304, 66–74.
- Ver, L. M. B., Mackenzie, F. T., and Lerman, A. (1999) Carbon cycle in the coastal zone: effects of global perturbations and change in the past three centuries. *Chem. Geol.*, 159, 283–304.
- Weinbauer, M. G., and Rassoulzadegan, F. (2004) Are viruses driving microbial diversification and diversity? *Environ. Microbiol.*, 6, 1–11.
- Wiebe, W. J., Sheldon, W. M., Jr., and Pomeroy, L. R. (1992) Bacterial growth in the cold: evidence for an enhanced substrate requirement. *Appl. Environ. Microbiol.*, 58, 359–364.
- Williams, P. J. L. (1981) Incorporation of microheterotrophic processes into the classical paradigm of the planktonic food web. *Kiel. Meeresforsch.*, 5, 1–28.
- Wright, R. T., and Coffin, R. B. (1984) Factors affecting bacterioplankton density and productivity in saltmarsh estuaries. In Reddy, C. A., and Klug, M. J. (eds.), *Current Perspectives in Microbial Ecology*. American Society of Microbiology, Washington, DC, pp. 485–494.
- Wuchter, C., Abbas, B., Coolen, M. J. L., et al. (2006) Archaeal nitrification in the ocean. *Proc. Natl. Acad. Sci. U.S.A.*, 103, 12317–12322.
- Yager, P. L., and Deming, J. W. (1999) Pelagic microbial activity in an arctic polynya: testing for temperature and substrate interactions using a kinetic approach. *Limnol. Oceanogr.*, 44, 1882–1893.

