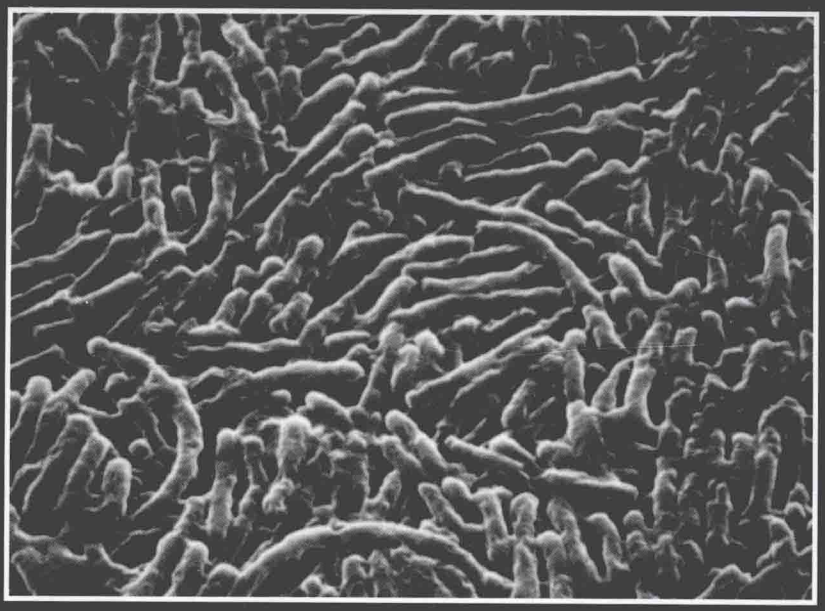
ENVIRONMENTAL MICROBIOLOGY

Second Edition



Edited by
RALPH MITCHELL AND JI-DONG GU

WILEY-BLACKWELL

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PREFACE

It is more than fifteen years since the publication of the last edition of *Environmental Microbiology*. During that time there have been momentous advances in this field both conceptually and experimentally. For example, we have become increasingly aware of the involvement of microbial processes in climate change. New molecular techniques now permit much more accurate identification of the microorganisms and processes involved in both environmental deterioration and remediation.

In this volume we focus on the role of microorganisms in a wide range of ecosystems and deterioration processes. We cover such diverse subjects as the role of microorganisms in the deterioration of cultural heritage materials and the effects of genetically modified crops on microbial processes. In addition to providing historical reviews of their subject, we have asked contributors to speculate on future trends. Our objective in the volume is to further our understanding of the essential role played by microorganisms in both environmental deterioration and the control of pollution. We hope that this book will be helpful to a wide range of scientists and engineers, and will stimulate students to new and original approaches to environmental challenges.

R.M. would like to thank Trinity College, Dublin, Ireland and, particularly, Robin Adams, the director of the college library. Much of the work for this book was carried out in the Trinity College library. Both the help of the librarians and the excellent electronic resources were an enormous help in the production of this book.

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CHAPTER 1

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 CO_2 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 CO_2 fixation into organic matter, thus driving the global carbon cycle (Houghton, 2007). Nearly all of the approximately 50 Pg (1 petagram = 1 Pg = 10^{15} g = 10^9 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

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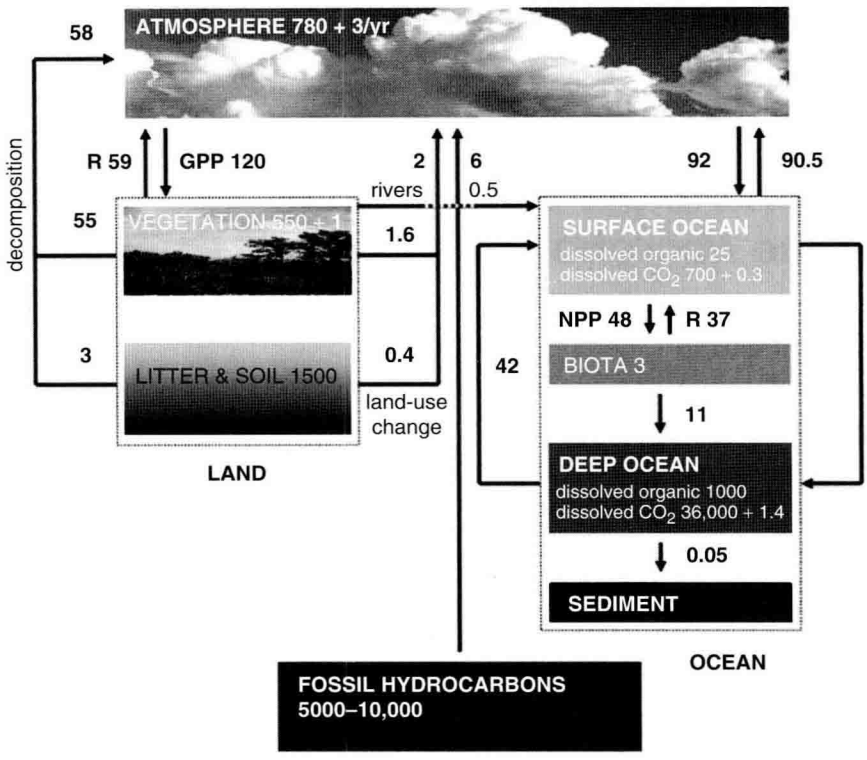

Figure 1.1 The global carbon cycle, including human perturbations in the 1990s. The quantities in the boxes are the size of the carbon reservoir in petagrams (Pg; 10^{15} g), with the annual growth, if any, due to the perturbations. Note that there is direct exchange between the atmosphere and terrestrial 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 CO_2 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 CO_2 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

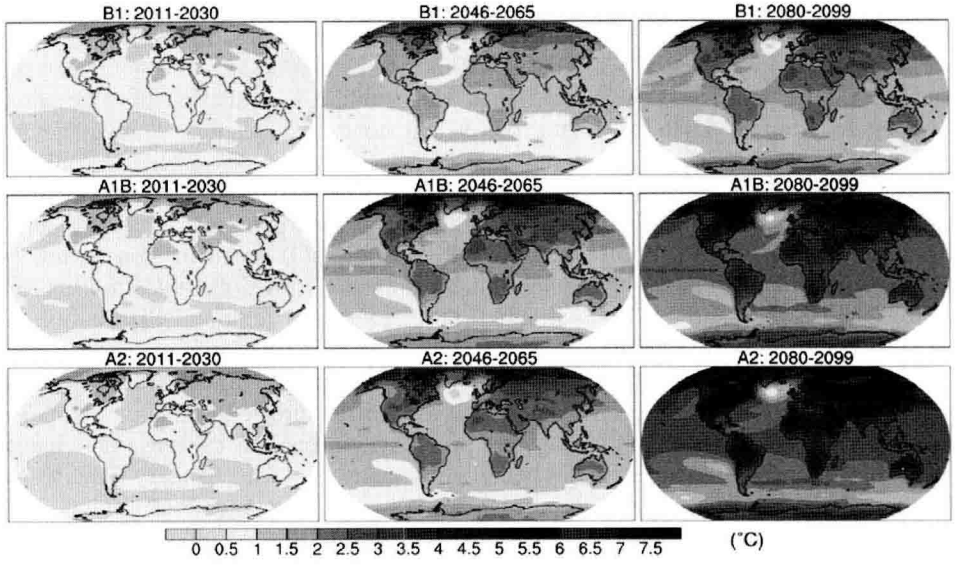

Figure 1.2 Multimodel mean of annual mean surface warming (surface air temperature change,°C) for scenarios B1, A1B, and A2, and three time periods, 2011 to 2030 (left), 2046 to 2065 (middle), and 2080 to 2099 (right). Stippling is omitted for clarity (see the text). Anomalies are relative to the average 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

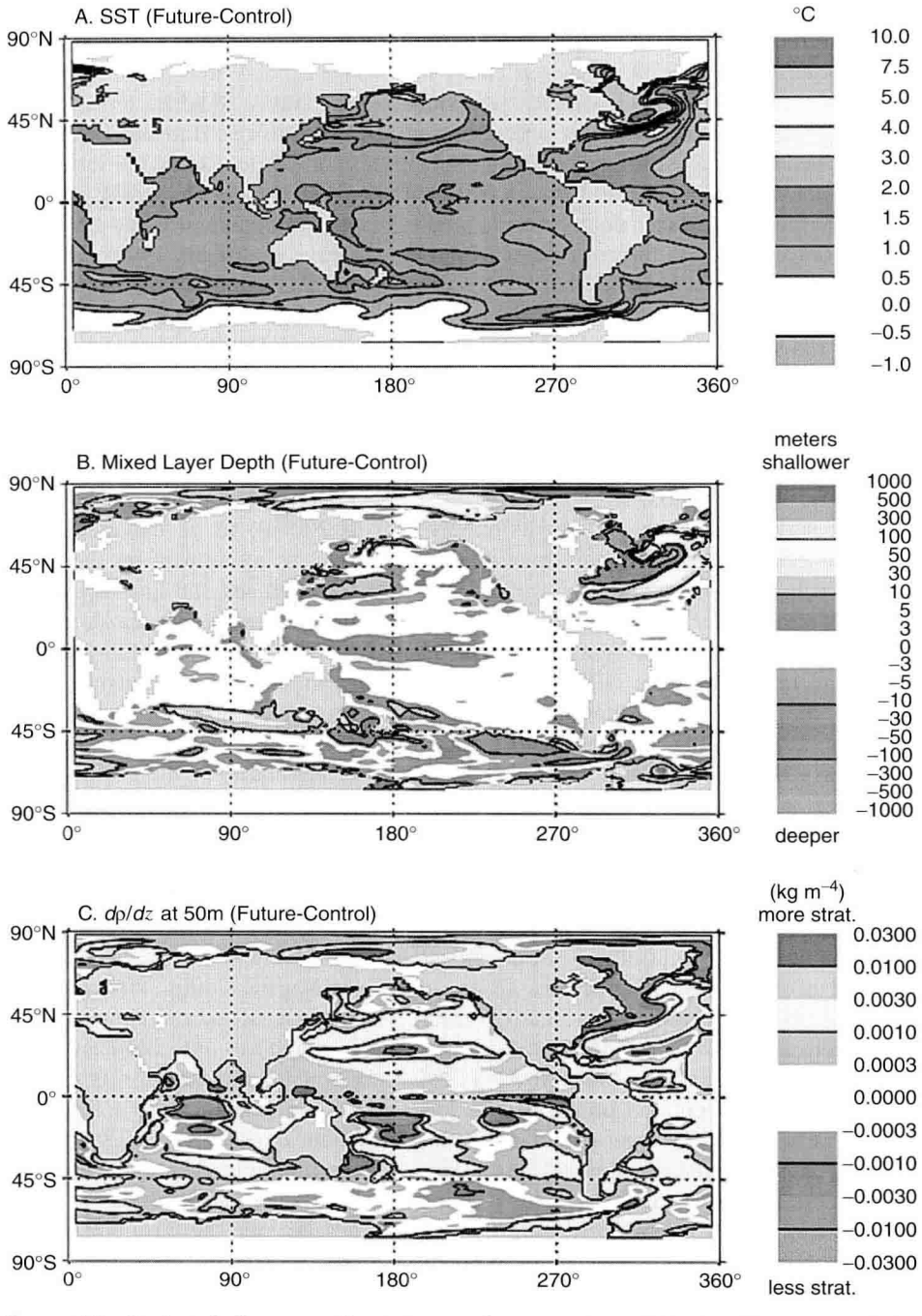

Figure 1.3 Projected climate-mediated changes in ocean physical forcing (future-control, i.e., 2060–2070 minus the present) from the NCAR Community Climate System Model for (A) sea surface temperature, (B) mixed-layer depth, and (C) upper ocean (50 m) stratification. (From Boyd and Doney, 2002, with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

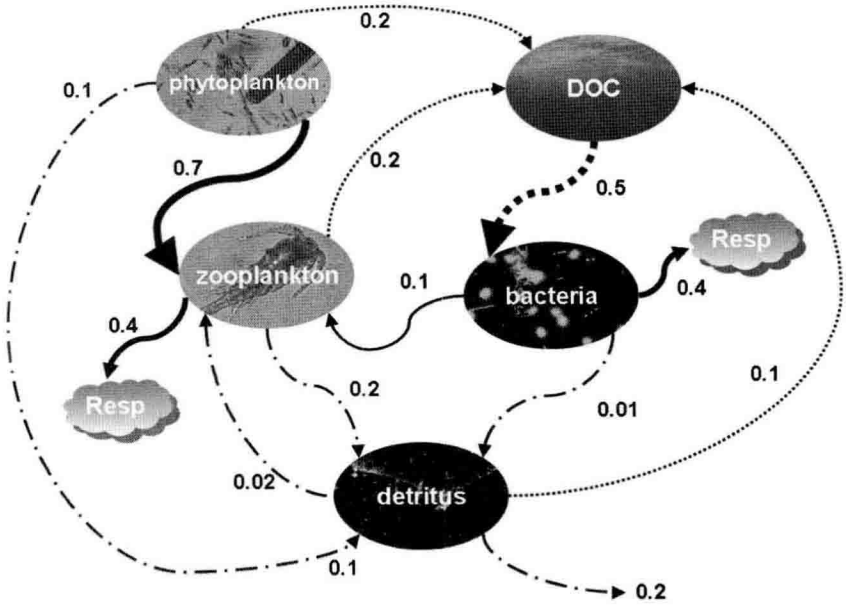

Figure 1.4 Microbial food-web diagram, showing exchanges of carbon in the oceanic surface layer. The flows are normalized to NPP = 1.0. The partitioning of flows among compartments is based on the physiological budget model given in Anderson and Ducklow (2001). Note that the carbon flows are dominated 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 then 20 μm. 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 Bacteriodetes-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 proteorhodpsin 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).