Dillon WP and Paul CK (1983) Marine gas hydrates II. Geophysical evidence. In: Cox JS (ed.) *Natural Gas Hydrate*. London: Buttersworth, pp. 73–90.

Haq BU (1998) Gas hydrates: Greenhouse nightmare? Energy panacea or pipe dream? *GSA Today, Geological Society of America* 8(11): 1–6.

Henriet J-P and Mienert J (eds) (1998) *Gas Hydrates: Relevance to World Margin Stability and Climate Change*, vol. 137. London: Geological Society Special Publications.

Kennett JP, Cannariato KG, Hendy IL and Behl RJ (2000) Carbon isotopic evidence for methane hydrate instability during Quaternary interstadials. *Science* 288: 128–133.

Kvenvolden KA (1998) A primer on the geological occurrence of gas hydrates. In: Henriet J-P and Mienert J (eds) *Gas Hydrates: Relevance to World Margin Stability and Climate Change*, vol. 137, pp. 9–30. London: Geological Society, Special Publications.

Max MD (ed.) (2000) Natural Gas Hydrates: In: *Oceanic and Permafrost Environments*. Dordrecht: Kluwer Academic Press.

Nisbet EG (1990) The end of ice age. *Canadian Journal of Earth Sciences* 27: 148–157.

Paull CK, Ussler W and Dillon WP (1991) Is the extent of glaciation limited by marine gas hydrates. *Geophysical Research Letters* 18(3): 432–434.

Sloan ED Jr (1998) *Clathrate Hydrates of Natural Gases*. New York: Marcel Dekker.

Thorpe RB, Pyle JA and Nisbet EG (1998) What does the ice-core record imply concerning the maximum climatic impact of possible gas hydrate release at Termination 1A? In: Henriet J-P and Mienert J (eds) *Gas Hydrates: Relevance to World Margin Stability and Climate Change*, vol. 137, pp. 319–326. London: Geological Society, Special Publications.

MICROBIAL LOOPS

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doi:10.1006/rwos.2001.0293

Introduction

The oceans contain a vast reservoir of dissolved, organically complex carbon and nutrients. At any given point in time, most of this dissolved organic matter (DOM) is refractory to biological utilization and decomposition. However, a significant flow of material cycles rapidly through a smaller labile pool and supports an important component of the food web based on bacterial production. The recapturing of this otherwise lost dissolved fraction of production by bacteria and its subsequent transfer to higher trophic levels by a chain of small protistan grazers was initially called the microbial loop by Farooq Azam and co-workers in the early 1980s. The following decades have been charecterized by remarkable discoveries of previously unknown life-forms and by major advances in our understanding of trophic pathways and concepts involving the seas' smallest organisms. In modern usage, the term microbial food web incorporates the original notion of the microbial loop within this broader base of microbially mediated processes and interactions.

Perspectives on an Evolving Paradigm

Although early studies date back more than a century, our understanding of the microbial ecology of the seas initially advanced slowly relative to other aspects of biological oceanography largely because of inadequate methods. Prior to the mid-1970s, for example, the simple task of assessing bacterial abundance in sea water was done indirectly, by counting the number of colonies formed when sea water was spread thinly over a nutritionally supplemented agar plate. We know now that about one marine bacterium in a thousand is 'culturable' by such methods. At the time, however, the low counts on media plates, typically tens to hundreds of cells per ml, were consistent with the then held view that sea water would not support a large and active assemblage of free-living bacteria. The role of bacteria was therefore assumed to be that of decomposers of organically rich microhabitats such as fecal pellets or detrital aggregates.

Coincidentally, early deficiencies in phytoplankton production estimates, due to trace metal contaminates and toxic rubber springs in water collection devices, were giving systematic underestimates of primary production, particularly in the low-nutrient central regions of the oceans that we now know to be dominated by microbial communities. For such regions, the low estimates of bacterial

standing stocks and primary production were mutually consistent, reinforcing the notion of the central oceans as severely nutrient-stressed 'biological deserts' with sluggish rates of community growth and activity.

Even so, there were early signs from both coastal and open-ocean studies of much greater microbial potential – one from newly developed sea water analyses of ATP (adenosine triphosphate), the short-lived energy currency of all living organisms; another from respiration (oxygen utilization) measurements of whole and size-fractioned sea water samples. Such measurements implied much larger concentrations of life-forms and metabolic rates than could be explained by the planktonic plants and animals that were being studied intensively in the 1970s. Recently developed methods for measuring bacterial production in the oceans, based on the uptake of radioisotope-labeled thymidine precursor for nucleic acid synthesis, were also giving results inconsistent with conventional wisdom. Thus, by the late 1970s, the stage was set for a revolutionary new paradigm, the microbial loop.

Epifluorescence microscopy was perhaps the tool that most facilitated scientific discovery and general acceptance of the new paradigm. Here, for the first time, one could directly visualize, with the aid of fluorescent stains, the multitude of coccoid, rod, and squiggle-shaped forms that comprised the typical bacterial assemblage of about a million cells per ml. Autoradiography, a technique by which the cellular uptake of radioisotope-labeled substrates is developed on sensitive films, confirmed that most of these cells were living and active.

Epifluorescence microscopy (EPI) also opened the door to discovering and studying other components of the microbial community. *Synechococcus*, a genus of small photosynthetic coccoid cyanobacteria, was soon recognized as a ubiquitous and important component of the marine phytoplankton from its characteristic shape and phycobilin accessory pigments, which glow orange under the EPI standard blue-light excitation. The same excitation wavelength causes the chlorophyll in photosynthetic cells to fluoresce bright red, allowing purely heterotrophic cells to be easily distinguished from chlorophyll-containing cells of similar size and shape. This distinction was critical in demonstrating a clear food web coupling for bacterial production via small phagotrophic (i.e., particle-consuming) colorless flagellates, and it provided an important technique for identifying and quantifying trophic connections using fluorescently labeled beads and cells as tracers to assess grazer uptake rates.

Such studies also had the unintended effect of illustrating the blurry distinction between pure autotrophy and heterotrophy within the microbial assemblage. For example, many of the small photosynthetic flagellates (containing chlorophyll) in the oceans have been observed to consume bacterial-sized particles. Similarly, many, if not most, of the larger pigmented dinoflagellates follow a 'mixed' mode of nutrition involving photosynthesis and phagotrophy. In a phenomena known as kleptoplastidy, common forms of ciliated protozoa have also been shown to retain (literally 'steal') the chlorophyll-containing plastids of their prey and use them as functional photosynthetic units for a day or longer. The widespread occurrence of mixotrophy, in all of its various forms, has consequently emerged as one of the important findings related to the microbial food web.

One notable discovery of the mid-1980s was that of *Prochlorococcus*, a tiny photosynthetic bacterium now known to be one of the most important primary producers in the tropical oceans, and probably on the planet. Although it seems remarkable that such an important organism could have escaped detection for more than a century of oceanographic investigation, this advance was again only made possible by new methods. In this case, the facilitating technology was a laser-based optical instrument, the flow cytometer, developed by medical research for the rapid analysis of individual cells in a narrowly focused fluid stream. The application of this new approach in the ocean sciences was quick to reveal high concentrations of the dimly red-fluorescing (chlorophyll-containing) *Prochlorococcus*, which could not be distinguished from nonpigmented bacteria by standard EPI techniques. Herein lies one of the problems of epifluorescence microscopy, the confounding of significant populations of the autotrophic *Prochlorococcus* cells with heterotrophic bacteria. Some early reports of heterotrophic biomass greatly exceeding autotrophs in surface waters of the tropical oceans were a consequence of this methodological artifact.

Even among the heterotrophic bacteria, there have been discoveries of fundamental importance. For example, kingdom-specific molecular probes have recently shown that a significant fraction of the 'bacteria' from EPI counts are not true Bacteria at all, but lesser-known prokaryotes of the Kingdom Archaea. These organisms have been known to inhabit extreme environments such as hot springs and the interstices of salt crystals, but their presence in more typical oceanic habitats raises many interesting questions about the roles of their unique metabolic systems in ocean biogeochemistry. The

application of powerful molecular methods to the ocean sciences in the 1990s has signaled the beginning a new era in marine microbial ecology with the potential to reveal the full spectrum of microbial population and physiological and metabolic diversity.

As a natural extension of new methods to visualize and characterize community components of decreasing size, the 1990s have also seen a growing recognition of the importance of viruses in marine microbial communities. Based on a combination of fluorescent staining methods and electron microscopy, viruses are now clearly the most numerous component of the microbial community, exceeding bacteria in most cases by an order of magnitude. While not technically 'real' organisms, in the sense of having independent metabolic or reproductive capabilities, viruses can be significant vectors of bacterial and algal mortality and therefore have important implications for the functioning and energy flows in marine microbial communities. Recent studies have shown rates of microbe infection and viral turnover that would account for the loss of about half of bacterial production. The typical host-specificity of viruses and their spread by density-dependent encounter frequency suggest that they also have a major role in maintaining bacterial diversity, by selectively punishing the most successful competitors.

Organization of the Microbial Food Web

For the sake of representing diagrammatically the trophic connections among marine microbes, and indeed as a practical strategy for most ecological studies, it is necessary to compress the known complexities of microbial communities into a few functional categories (**Figure 1**). There is no clear cut-off between particulate and dissolved organic matter in the oceans, for example, but rather a spectrum of material ranging from low molecular weight (low-MW) amino acids and sugars to large complex molecules, to colloids, viruses and submicrometer remnants of previously consumed biota, and to wispy strands that link a fragile gelatinous matrix of living and dead material. Labeled simply as DOM in **Figure 1**, this material can cycle between refractory and labile pools by slow physical winnowing and leaching, extracellular enzymatic cleavage, or accelerated photochemical oxidation, the latter principally from enhanced ultraviolet radiation in near-surface waters. Although the relative magnitudes are debatable and likely to vary seasonally and regionally, inputs to the DOM box come from virtually all components of the marine plankton. Phytoplankton leak low-MW compounds across porous membranes, and they also produce the sugary products of photosynthesis in excess when nutrients are insufficient for cell growth. Many larger consumers feed sloppily, producing DOM and particulate fragments as they grind and rip their food with silica-tipped teeth. Both large and small consumers excrete low-MW organics, often as a significant fraction of their total metabolism, and release organics in the form of incompletely digested material. Lastly, whole cells are fragmented into numerous components in the operationally defined DOM size range during the final stages of the viral lytic cycle. DOM from all of these various sources provides the substrate that fuels the growth of marine heterotrophic bacteria.

The original microbial loop was patterned on the notion that consumers typically feed on prey organisms that are a factor of 10 less in cell size (length or equivalent spherical diameter), a view that fitted nicely with the traditional decadal size classifications of marine plankton. Accordingly, picoplankton (0.2–2 μm cells, including most prokaryotes) would be fed upon by nano-sized protists (2–20 μm cells, typically flagellates), and they, in turn, by microheterotrophs (20–200 μm cells, typically ciliates). From laboratory feeding experiments as well as from size-fraction manipulations of natural communities, however, it has become increasingly clear that many protists feed optimally on prey much closer to their own body size. The most common bacterivores in the oceans, small naked flagellates, are typically only 3–6 times the size of their average bacterial prey. Heterotrophic and mixotrophic dinoflagellates generally prey on cells of even larger relative size, some using extracellular capture and digestion to handle preferred prey larger than their own body size. Compared to the original microbial loop paradigm, the effect of compacting mean predator–prey size relationships for flagellates can add at least one more level of intermediate consumer between bacteria and the largest protozoa in the grazing chain.

As will be presented in more detail below, complex relationships and feedbacks among bacteria and protists and their different degrees of availability to higher-order consumers argue for a broad view of the microbial food web, rather than a narrow focus on a single loop element. This brings us to the matter of definition. Are all single-celled organisms to be included in this web, or are there size or functional reasons to exclude some? **Figure 1** is organized from the perspective of organisms described in the original microbial loop paradigm,

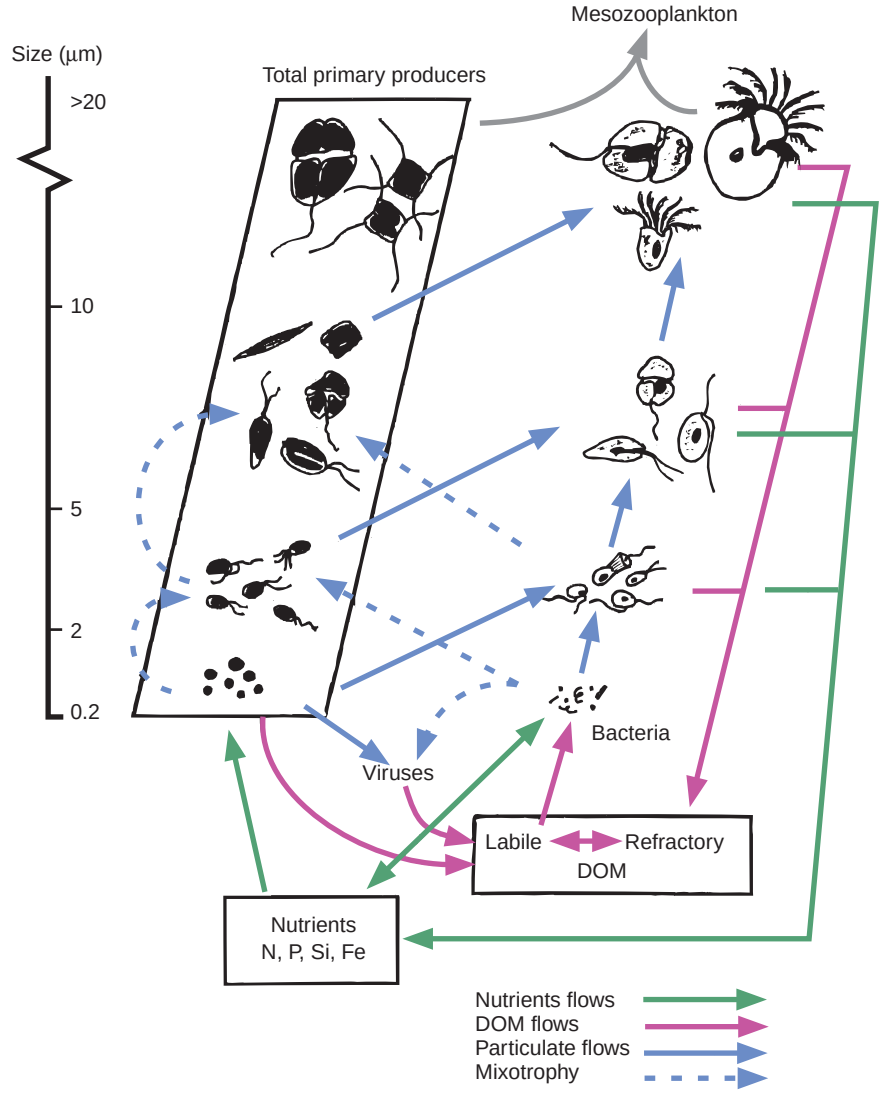

Figure 1 Conceptual representation of the microbial food web showing flows of nutrients and dissolved organics and interactions among various size classes of bacteria and protists. Primary producers (left side) are shown as chlorophyll-containing cells and heterotrophic (right side) cells are drawn without pigments. Mixotrophy is shown as feeding of some of the pigmented cells on smaller prey organisms.

the bacteria and the grazer chain. It therefore includes the autotrophic organisms that would constitute the main food items of some protistan grazers. Notably absent are the very large phytoplankton, principally large solitary cells or long diatom chains that figure so prominently in classical descriptions of the seasonal bloom cycles of temperate and boreal oceans. Such cells would not be readily available to protistan grazers because of their size, spines or other defensive strategies. They also function differently from smaller primary producers, being more intimately related to export flux from the euphotic zone by aggregate formation and direct cell sinking or by incorporation into the fast-sinking fecal pellets of large metazoan consumers. Thus, while all planktonic organisms are related in a sense by trophic linkages and feedbacks to dissolved organics and nutrients, we specifically exclude these larger primary producers from the microbial assemblage. The division is functional and roughly follows size, distinguishing the direct flow of primary production to a network of metazoan consumers as opposed to that going primarily to protists. It is important to observe that the division is only loosely related to taxonomic groupings. For example, the dominant diatoms in many open ocean regions are tiny ($< 10\,\mu m$) pennate cells and well within the size range that can be grazed efficiently by ciliates and large flagellates. By the same token, large clump-forming filaments of the nitrogen-fixing

cyano-bacteria *Trichodesmium* spp. appear to be directly utilized only by certain harpacticoid copepods.

Food Web Transfers

The original descriptions of the microbial loop by Williams and Azam and co-workers carefully observed that the transfer of bacterial production to higher trophic levels by a chain of protistan consumers was likely to be inefficient. Nonetheless, there was early speculation that this newly discovered pathway could represent a significant link or energy bonus to higher levels as opposed to a metabolic sink. This view was bolstered by evidence of high gross growth efficiencies (e.g., carbon growth = 50–70% of carbon substrate uptake) for bacteria under optimal laboratory conditions and observations that the growth efficiencies of small protists were also much higher and less sensitive to food concentration that those of metazoan consumers, like copepods.

There is little support these days for significant transfer of DOM uptake by bacteria through the protistan grazing chain. For one, experimental studies, now available from many marine ecosystems, suggest an average bacterial growth efficiency of about 20% on naturally occurring organic substrates. In other words, 5 moles of dissolved organic carbon are needed to produce 1 mole C of bacteria, the remainder being metabolized to inorganic carbon. Virus-induced cell lysis, the so-called viral shunt to DOM, represents a further loss of potential production to trophic transfer. Lastly, each step in the grazing chain, operating at about 30% efficiency, takes its toll. Assuming half of bacterial mortality goes to viral lysis and half to small bacterivorous flagellates, less than 0.3% ($0.2 \times 0.5 \times 0.3 \times 0.3 \times 0.3 = 0.0027$) of the DOM carbon uptake would be transferred past the largest protistan consumers in **Figure 1**.

While such calculations can diminish one's expectations for supporting significant fish production from bacteria *per se*, we must take a broader view of microbial contributions to plankton energy flows. In **Figure 1**, for example, bacteria do not constitute the single source of materials to large heterotrophic protists and the animals that ultimately feed on them. At each step along the grazing chain, production of flagellates and ciliates is well supplemented by consumption of appropriate sizes of photosynthetic organisms. Two-way flows between autotrophic and heterotrophic compartments due to mixotrophs further complicate these interactions, making it difficult to view the contribution of individual components and loops in isolation of the others.

To make matters even more complex, metazoan consumers do not as a rule wait patiently to siphon off only those resources that make it to the largest size categories of the microbial grazing chain. Mucus-net feeding pelagic tunicates, like appendicularians and salps, short-circuit the grazing chain by efficiently exploiting bacterial-sized particles, or at least the smallest size categories of nanoplankton. Somewhat less appreciated, the early developmental stages of planktonic crustaceans like copepods and euphausiids, as well as the larvae of benthic invertebrates in coastal areas, typically feed efficiently on the smallest size fractions of the microbial assemblage, graduating to larger prey as they grow. Regardless of the feeding habits of the adults, therefore, the developmental success of these organisms may depend on interactions with the smallest microbial size fractions.

Nutrient Cycling

The lack of efficient transfer of bacterial production through the long protistan grazing chain suggests that the microbial loop must be extremely important in remineralization and nutrient cycling. This has clearly emerged as one of the primary functions of the microbial food web and has brought particularly a new understanding to the ecology of the open oceans where microbial interactions predominate. Such systems are often limited by primary nutrients such as nitrogen or phosphorus, and in some cases trace elements like iron. Their common characteristic is the relatively high turnover rate of small primary producers supported by the efficient recycling of nutrients. Without this positive feedback of nutrient recycling, the available resources would rapidly be locked into the standing biomass of plankton, and new growth and production would stop.

Even though bacteria grow inefficiently on naturally available DOM and help to solubilize and degrade particulate organics with extracellular enzymes, they are typically not the major remineralizers in the seas. In fact, they often compete significantly with phytoplankton for the uptake of dissolved nutrients. Their superior competitive ability comes, of course, from the high surface area to volume ratios of bacterial cells. Their demand derives from their relatively high nutrient requirements for cell growth compared to phytoplankton. For example, while phytoplankton grow optimally with a carbon to nitrogen ratio (C:N) of about 7, the typical ratio for bacteria is 5. Compared to phytoplankton, bacteria also seem to require iron at about twice the concentration relative to carbon.

We can appreciate the interplay among growth efficiencies, nutrient richness of available substrates, and bacteria as a source or sink for recycled nutrients from **Figure 2**. High growth efficiency allows bacteria to use more nutrients for growth, with less recycled. Reducing the nutrient content (increasing C:N) of available DOM has a similar effect. Where the dissolved substrates are nutritionally rich, growth efficiency is likely to be high, so nutrient release will be positive but depressed. On the other hand, when the C:N ratio of DOM is too high to satisfy nutrient needs for growth, bacteria will seek limiting elements in inorganic pools.

It is precisely in this latter case that we run across an interesting paradox of microbial interrelationships. Phytoplankton respond to nutrient-limited conditions by producing photosynthate sugars in excess of their growth needs and excreting them to the external environment. Since these sugars are easily assimilated by bacteria but are devoid of associated nutrients (i.e., high C:N), the effect is to enhance bacterial demand for inorganic nutrients and hence their competition for limiting substrate with phytoplankton. According to some analyses, if one considers the many indirect consequences of this enhancement effect on the microbial network, phytoplankton could 'win' in the end by stimulating grazing on bacteria and subsequent nutrient remineralization. However, bacterivorous mixotrophs have an inherent advantage under such conditions since they benefit both from direct consumption of nutrient-rich bacteria and by the stimulation of bacterial growth and nutrient cycling from the DOM released by true autotrophs. At the same time, photosynthetic carbon production allows mixotrophs to utilize ingested nutrients for growth at very high efficiency, releasing little back to the environment compared to pure heterotrophs. As one might imagine, bacterivorous mixotrophs become more important and can even dominate over pure autotrophic or heterotrophic flagellates in systems of increasing oligotrophy.

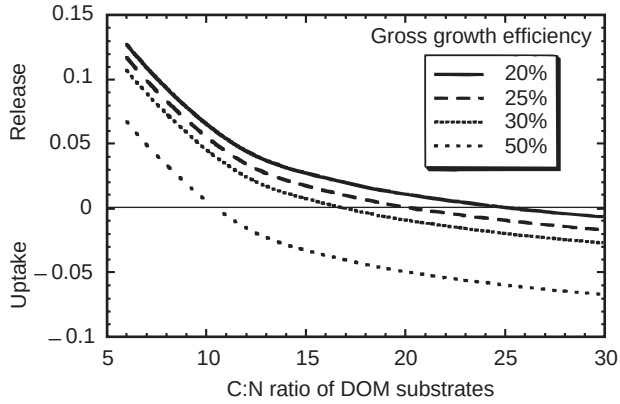

Figure 2 Uptake or release of dissolved inorganic nitrogen (DIN) by bacteria as a function of gross growth efficiency (GGE) and the carbon:nitrogen ratio (C:N) of dissolved organic substrates. Figure shows that bacteria can act as decomposers (releasing nutrients) when substrates are nutrient rich (low C:N). With increasing C:N or increasing carbon growth efficiency, bacteria will show a deficit (negative) in nutrients from DOM and will compete with phytoplankton in nutrient uptake. In comparision, bacterivorous flagellates feeding on relatively nutrient-rich bacteria should always serve as significant decomposers, recycling about 75% of ingested N as DIN or small particulates at GGE = 30%.

Regional Patterns and Variations

Bacterial abundance and biomass vary in the oceans, within and between regions, but the range of variability is generally less than that observed for larger components of the food web. This is because bacteria and small algae in the microbial food web can be contained within certain limits by fast-growing protistan predators. In contrast, larger phytoplankton, such as diatoms, enjoy a substantial growth rate advantage over slow-responding mesozooplankton consumers, allowing them to increase explosively when light and nutrient conditions become optimal. Such cells give many regions of the oceans their characteristic seasonal blooms.

Plankton blooms are generally short-lived phenomena because the larger components of the food web are not good at retaining nutrients in the surface waters once the water column is seasonally stratified. Large cells aggregate and sink when nutrients are exhausted, and mesozooplankton export nutrient-rich material from surface waters as compact, fast-sinking fecal pellets. Increasing nutrient stress naturally favors smaller competitors for the limiting resource and the smaller consumers that feed on them. Therefore, a declining bloom will evolve through various successional states toward a microbially dominated community in which production, grazing, and nutrient remineralization are more tightly coupled. One such transitional state is likely to be a period in which the bacterial carbon demand overshoots the concurrent production of phytoplankton. This occurs during the declining stages of the bloom, when senescent phytoplankton produce carbohydrates in excess, when sick phytoplankton cells lyse, or when diminished antibacterial chemical defenses of phytoplankton allow bacteria to more effectively exploit the DOM accumulated during the bloom. Reduced carbon supply and enhanced mortality to bacterivorous protists and viruses will rapidly bring the bacteria back into balance.

Table 1 Representative estimates of bacterial cell abundances, carbon biomass, and percentage heterotrophic cell biomass for several regions of the open oceans according to recent studies

Region	*Abundance (10^3 cells ml^{-1})*				*Biomass (μg C l^{-1})*	*% Hetero*	*Chla (μg l^{-1})*	*BP/PP*
	T (°C)	*Hbact*	*PRO*	*SYN*				
Central Equatorial Pacific, 1°S–1°N	28	670	140	7	14	59	0.26	0.17
Subtropical Pacific, 23°N	25	550	210	1	14	47	0.06	
Arabian Sea, NE Monsoon	27	850	70	90	22	47	0.40	0.22
Tropical Atlantic, 5–20°N	27	750	210	12	18	51	0.41	
Subtropical Atlantic, 30°N	22	500	70	7	9	66	0.07	0.05
Subarctic Atlantic, 50–60°N	12	1500	20	40	23	79	0.87	0.15
Southern Ocean bloom, 47°S, 6°W	4	2000	ND	ND	24	–	3.0	0.16
Southern Ocean, 60°S, 170°W	0	300	0	0	4	100	0.4	

T (°C) and Chl*a* are mean environmental temperature and total phytoplanton chlorophyll *a*. BP/PP is the ratio of bacterial (heterotrophic) production to total primary production. Total bacterial biomass is for combined populations of heterotrophic cells (Hbact), *Prochlorococcus* (PRO) and *Synechococcus* (SYN) determined from cell counts and mean carbon contents of 12, 35 and 100×10^{-15} g C per cell.

ND, not determined.

If we consider the full range of variability in the oceans, it is possible to find very rich coastal ecosystems or events with chlorophyll concentrations of $30\,\mu g\,l^{-1}$ or more and bacterial abundances exceeding 10^7 cells ml^{-1}. However, such extremes are relatively rare. Average concentrations are about two orders of magnitude lower for phytoplankton chlorophyll and 10-fold lower for bacteria. Particularly in the open oceans, many regions share similar characteristics with regard to general low levels of bacterial and phytoplankton standing stocks.

If one looks, for example, at mean levels of bacterial abundance and biomass in tropical and subtropical seas, they vary quite little, regardless of whether the regions are relatively rich and productive (Arabian Sea), iron-limited (equatorial Pacific), or extremely oligotrophic (subtropical Pacific) (**Table 1**). As an indication of the selective pressures for small primary producers in such systems, photosynthetic bacteria (*Prochlorococcus* and *Synechococcus*) usually account for 40–50% of total bacterial biomass, with the relative abundance shifting toward *Synechococcus* in richer more-productive systems or seasons. As we move toward higher latitudes, photosynthetic bacteria decline in importance relative to eukaryotic phytoplankton, and bacteria as a group become increasingly more heterotrophic. *Prochlorococcus* are largely absent from the plankton at water temperatures below 12°C, while *Synechococcus* are rare in polar waters.

The importance of the microbial communities in the ecology of the oceans derives from the flow of nutrients and fixed carbon through them. This is in addition to the many roles that bacteria have with respect to chemical transformations and ocean geochemistry. When one takes into account the low growth efficiencies of bacteria and the deficiencies of the carbon-14 method, typical bacterial production estimates on the order of 5–20% of ^{14}C-bicarbonate uptake (**Table 1**) are consistent with a carbon demand of about 50% of primary production. In addition, protistan grazers directly consume 50–90% of phytoplankton cellular growth in the open oceans, and often half or more in coastal waters. Through these two routes, most of the organic production of the oceans is dissipated in the microbial food web.

Conclusion

The last 20–30 years have been a period of unprecedented discovery relating to the microbial ecology of the oceans. Largely ignored only a short while ago, microbial food web interactions are now central to our understanding of energy and nutrient flows in the oceans. The ubiquitous and self-regulating microbial community provides the foundation upon which the rest of the food web operates. Though sometimes overridden by the dynamics of larger bloom-forming organisms, it emerges as the dominant trophic pathway in most open-ocean regions and the end point of community succession when nutrients become limiting. In contrast to the ecology of larger organisms in the seas, we know little about the dynamics and unique contributions of microbes at the species level. This remains an exciting area of research for the future.

Glossary

Autotrophs Primary producers, organisms that utilize only inorganic carbon for metabolic synthesis.

Bacterivory Consumption of bacteria.

DOM Dissolved organic matter; operationally, all organic matter that can pass through a filter with 0.2 μm pores.

Gross growth efficiency For a given organism, the efficiency of conversion of carbon intake into new carbon growth.

Heterotrophs Organisms that utilize organic sources of carbon (particulate or dissolved) for metabolic synthesis.

Microplankton Planktonic organisms in the size range 20–200 μm; includes single-celled as well as multicellular organisms.

Mixotrophic Organisms with a mixed mode of nutrition, typically combining the ability to derive significant nutrition from photosynthesis as well as feeding directly on other organisms (or dissolved substrates).

Nanoplankton Planktonic singled-celled organisms in the size range 2–20 μm.

Oligotrophic System characterized by low concentrations of nutrients and plankton biomass.

Picoplankton Planktonic singled-celled organisms in the size range 0.2–2 μm.

See also

Bacterioplankton. Photochemical Processes. Phytoplankton Blooms. Primary Production Distribution. Primary Production Methods. Primary Production Processes.

Further Reading

Azam F, Fenchel T, Gray JG, Meyer-Reil LA and Thingstad T (1983) The ecological role of water-column microbes in the sea. *Marine Ecology Progress Series* 10: 257–263.

Fenchel T (1987) *Ecology of Protozoa. The Biology of Free-living Phagotrophic Protists*. Madison, WI: Brock/Springer Science Tech.

Fuhrman JA (1999) Marine viruses and their biogeochemical and ecological effects. *Nature* 399: 541–548.

Hobbie JE and Williams PJ leB (eds) (1984) *Heterotrophic Activity in the Sea*, NATO Conference Series. IV, vol. 15. New York: Plenum Press.

Partensky F, Hess WR and Vaulot D (1999) *Prochlorococcus*, a marine photosynthetic prokaryote of global significance. *Microbiology and Molecular Biology Reviews* 63: 106–127.

Raven JA (1997) Phagotrophy in phototrophs. *Limnology and Oceanography* 42: 198–205.

Thingstad FT (1998) A theoretical approach to structuring mechanisms in the pelagic food web. *Hydrobiologia* 363: 59–72.

Williams PJ leB (1981) Incorporation of microheterotrophic processes into the classical paradigm of the planktonic food web. *Kieler Meeresforsch. Sondh.* 5: 1–28.

MICROPHYTOBENTHOS

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doi:10.1006/rwos.2001.0213

Introduction

Microphytobenthos is a descriptive term for the diverse assemblages of photosynthetic diatoms, cyanobacteria, flagellates, and green algae that inhabit the surface layer of sediments in marine systems. Microphytobenthos occur wherever light penetrates to the sediment's surface, and are abundant on intertidal mud and sandflats and in shallow subtidal regions. Microphytobenthic primary production may be high, matching that of phytoplankton in the overlying water column, yet this activity is compressed into a biofilm only a few millimeters thick. The relationship between irradiance and rates of microphytobenthic photosynthesis is fairly well understood, but new methods are revealing fine-scale effects of microspatial distribution within the vertical light profile and migration of cells throughout the diel illumination period. Patterns of biomass distribution and seasonal and spatial changes in species composition are well described, but studies differ on the relative importance of the factors influencing microphytobenthic biomass (irradiance, resuspension, nutrients, grazing, exposure, desiccation, etc.). Microphytobenthic biofilms play an important role in mediating the exchange of nutrients across the sediment–water interface, and microphytobenthos both stimulate and compete with various bacterial sediment processes. The presence of biofilms rich in extracellular polysaccharides alters the erosional properties of sediments, termed biostabilization.

Types of Microphytobenthos

Sediment properties play a major role in determining the type of microphytobenthic assemblage present in a particular environment. Sediments consisting of fine silts and clays (less that 63 μm) are termed cohesive sediments. The fine nature of such material and the lack of suitable attachment points result in assemblages dominated by motile micro-