

A sea of microbes: the diversity and activity of marine microorganisms



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Covering 70% of the earth's surface, with an average depth of 3.6 km, the ocean's total volume of 1.3 billion cubic kilometres represents perhaps the largest inhabitable space in the biosphere. Within this vast ecosystem, 90% of all living biomass is microbial. Indeed, seawater from all marine environments, ranging from the warm and sunlit upper ocean to the cold, dark and anoxic deep sea floor, and from the tropics to the arctic, is teeming with microbial life. A single teaspoon of seawater typically contains over 50 million viruses, 5 million *Bacteria*, 100,000 *Archaea* and 50,000 eukaryotic microbes. The numerical importance of these microbes is matched only by their ecological and biogeochemical significance. By performing the bulk of oceanic primary production and mediating key chemical transformation processes, planktonic microbes form the base of the marine food-web and are the engines that drive the ocean's major biogeochemical cycles (Figure 1). While marine microbes are the dominant biological feature throughout the entire water column and within ocean sediments, as well as being important symbionts and pathogens of marine animals and plants, this review will focus on the activity and diversity of microbes inhabiting seawater in the upper sun-lit depths of the global ocean.

'Keystone microbes' in a sea of diversity

The ecological and biogeochemical importance of marine microbes is underpinned by the staggering diversity of microbial communities within the ocean. This has only become apparent relatively recently, as the advent of molecular microbiological and genomic approaches has revolutionised the field of marine microbiology. Deep 16S rRNA amplicon sequencing approaches have led to estimates that a single

litre of seawater can contain tens of thousands of microbial 'species'¹. More recent approaches using single cell genomics have revealed that even a single marine bacterial species is comprised of hundreds of discrete co-existing sub-populations, which differ in flexible gene content and exhibit different ecological characteristics and environmental tolerances and preferences². These and other observations of the adaptive divergence of distinct ecotypes among marine bacterial species³ indicate that there is likely to be a microbe to exploit every niche in the ocean. However, embedded within this striking biodiversity are some star players that can be considered 'keystone organisms' among the ocean's microbiota.

Between 25–50% of all prokaryotic cells in the ocean belong to a single clade of *Alphaproteobacteria*, known as SAR11⁴. Originally named after clone 11 from a clone library derived from seawater collected in the Sargasso Sea⁵, the SAR11 clade is now recognised as perhaps the most abundant group of closely related organisms on earth. While SAR11 dominates microbial assemblages in ocean surface water across the globe⁴, bacteria belonging to this clade are classic oligotrophs and are most successful in the open ocean, which from a microbe's perspective is akin to a desert, where organic resources are significantly below the levels required by most other heterotrophic bacteria. SAR11 can thrive under these conditions with the aid of genome streamlining, whereby their extremely small genomes lack many of the cellular functions thought to be required by free-living bacteria⁶. As a consequence, SAR11 bacteria utilise atypical nutrient acquisition strategies that appear to minimise the cells' requirements for organic substrates and allow replication in the most nutrient deplete conditions⁶.

Not all important marine bacteria are oligotrophs like SAR11. Several copiotrophic species, which prefer the nutrient rich waters found near to the coast or in association with phytoplankton blooms, also often represent a significant fraction of marine bacterial assemblages. Genera including the *Roseobacters* and *Flavobacteria* are ecologically important groups that commonly occur in high numbers in seawater^{7–9}. Unlike the highly streamlined genome of the specialist oligotroph SAR11, the genomes of these organisms are often large, providing the cells with significant metabolic flexibility underpinned by a diverse repertoire of energy and carbon acquisition strategies, which allows them to exploit a wide variety of marine niches and thrive under a range of environmental conditions⁹.

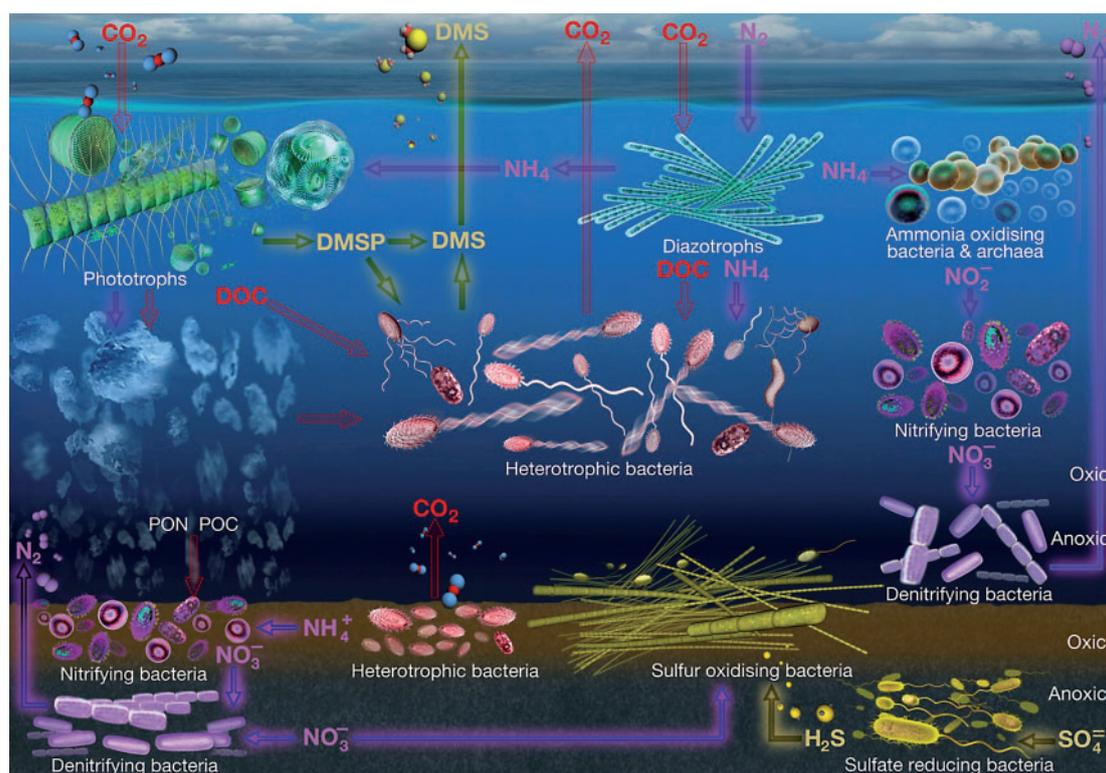


Figure 1. Diverse populations of marine microorganisms are responsible for the chemical transformations that underpin key features of ocean biogeochemistry, including the carbon (red arrows), nitrogen (purple arrows) and sulphur (yellow arrows) cycles shown here. The surface sunlit and oxic layers of the ocean occur within the navy blue region of the diagram, while the deep and anoxic ocean is characterised by the dark blue-black region. The oxic layer of the ocean sediments is denoted by the orange-brown layer, while the bottom grey layer denotes the anoxic sediments. POC=particulate organic carbon; DOC=dissolved organic carbon; PON=particulate organic nitrogen; DMSP = dimethylsulfoniopropionate; DMS = dimethylsulfide.

While spatial partitioning of the key oligotrophic and copiotrophic bacteria occurs across geographic boundaries¹⁰, within a given location ocean microbial communities also undergo constant substrate controlled successional shifts. During periods of low seawater nutrient concentrations and reduced primary production, oligotrophs such as SAR11 dominate the microbial community. However, following nutrient input events, like those that occur during and immediately after the spring phytoplankton bloom, bacterial communities rapidly shift to become dominated by copiotrophic organisms, including the *Roseobacters* and *Flavobacteria*, which can efficiently degrade phytoplankton derived carbohydrates¹¹. These successional processes are often repeatable and predictable, with highly synchronous seasonal shifts in the composition of microbial communities observed over multiple years¹², indicating the presence of well-defined microbial niches and unique functional properties of the organisms that inhabit them¹³.

Other important marine bacteria include members of the cyanobacteria. Two particularly numerically and ecologically important genera are *Prochlorococcus* and *Synechococcus*, which often comprise a significant fraction of the total bacterial community in the sunlit ocean surface waters¹⁴. Commonly occurring in concentrations of 10^5 cells/mL, *Prochlorococcus* is the most abundant

phototrophic organism on earth and is responsible for a significant fraction of global photosynthesis¹⁵. While occurring in latitudes as high as 40° , *Prochlorococcus* dominates in tropical oligotrophic regions¹⁴. On the other hand, the closely related genus *Synechococcus* is more cosmopolitan, occurring in high abundances in temperate coastal waters as well as in the open ocean¹⁴. In some coastal environments *Synechococcus* can represent the most abundant bacterial genus¹⁶.

Once thought to be primarily extremophiles inhabiting only harsh environments like the extremely hot and anoxic waters surrounding deep sea hydrothermal vents, the *Archaea* are now recognised as another ubiquitous and important group of marine microbes¹⁷. The two main groups of marine *Archaea*, the Marine Group I *Thaumarchaeota* and Marine Group II *Euryarchaeota*, are in fact estimated to account for more than 20% of all prokaryotic cells in the global ocean¹⁸. Indeed, below depths of 100 m, the Group I *Thaumarchaeota* are often the dominant group of microbes in seawater. A significant representative from this group, *Nitrosopumilus maritimus* is globally abundant and due to its unique mechanisms for nitrification and autotrophy is believed to play an important role in marine carbon and nitrogen biogeochemical cycling¹⁹.

The most abundant and diverse of all marine microbes are viruses. There are 10^{31} viruses in the global ocean and it has been estimated that every second 10^{23} viral infections occur in the sea²⁰. Marine viruses are known to infect most marine organisms from seaweeds to whales, but as a simple consequence of available host density, most viruses in seawater are bacteriophages²⁰. By manipulating community composition through the selective killing of dominant organisms and facilitating the exchange of genetic material via horizontal gene transfer, marine viruses are a fundamental structuring agent within marine microbial foodwebs²¹. Moreover, by lysing microbial cells, viruses can strongly alter marine chemical cycling pathways, which has a substantial impact on ocean biogeochemistry²².

Marine microbial activities and their influence on ocean biogeochemistry

Marine biogeochemical cycling processes, driven by the activities of microbes, control the rates and directions of ocean-atmosphere gas exchange, which strongly influences global climate²³. However, marine microbial activities and growth rates are highly variable in space and time and across species. On average, marine bacterial growth rates are relatively low, with cells in the open ocean dividing only 0.2 times per day²⁴. However, under optimum conditions, some marine bacteria have the capacity for staggering metabolic rates. For instance, *Pseudomonas natrigens* is capable of dividing once every 10 minutes²⁴, a likely adaptation for the opportunistic exploitation of intermittent and ephemeral substrate pulses in a dynamic ocean environment. The sum of this heterogeneous pool of marine microbial activities controls the turnover of labile organic substrates and inorganic nutrients in seawater, which ultimately regulates the ocean's major biogeochemical cycles²³ (Figure 1).

Within the ocean's carbon cycle, phototrophic microbes including cyanobacteria like *Prochlorococcus* and *Synechococcus* and a diverse assemblage of eukaryotic phytoplankton use sunlight to fix CO_2 into living biomass. Approximately 60 billion tonnes of carbon are fixed each year by these phototrophic microbes²⁵. For perspective, this equates to 40% of total global carbon fixation, yet the biomass of marine microbial phototrophs is equivalent to only about 1% of terrestrial plant biomass²⁵. The carbon fixed by marine photosynthetic microbes has several fates, which are largely determined by the activities of other microbes within seawater, and the balance of these processes profoundly influences global carbon budgets.

Some of the photosynthetically fixed carbon is transferred from phototrophic microbial biomass directly into the marine foodweb via zooplankton grazing. In addition, up to 50% of fixed carbon is

exuded by phytoplankton back into the surrounding seawater in the form of dissolved organic carbon (DOC)²⁶. This carbon is ultimately transferred to the higher food-web via a trophic pathway called the 'Microbial Loop', whereby heterotrophic bacteria rapidly assimilate DOC from the water column and are subsequently consumed by bacterivorous protists, which are then eaten by larger zooplankton²⁷.

In addition to the fixed carbon that is channeled into the foodweb either by zooplankton grazing or the microbial loop, another significant fraction of C sinks out of the photic zone as dead or senescent phytoplankton biomass, in the form of Particulate Organic Carbon (POC). This POC is transported to the deep ocean sediments and effectively removed from the carbon cycle for millennia, via a process known as the 'Biological Carbon Pump'. This downward flux of POC leads to the sequestration of up to 300 million tonnes of C to the deep sea each year. However, before all sinking POC is sequestered to the deep sea floor, a significant amount is metabolised by heterotrophic bacteria in the water column, leading to the return of the sinking C to the food web and its subsequent conversion to CO_2 through respiration²⁸. Importantly though, recent evidence indicates that not all of the sinking POC that is metabolised by bacteria is respired back as CO_2 . A potentially large proportion is instead converted into refractory (non-bioavailable) DOC, or RDOC, which remains in the water column. This process, known as the Microbial Carbon Pump, leads to the sequestration of biologically unavailable RDOC in the water column, where it may be stored for thousands of years²⁹.

The balance of these microbiologically mediated carbon cycling processes ultimately determines whether regions of the ocean act as sources or sinks of CO_2 ³⁰. Indeed, given that marine carbon cycling processes are so tightly coupled to microbiological activity within seawater, and the oceanic pools and fluxes of carbon are among the largest on earth, even seemingly subtle changes in the composition and activity of microbial assemblages have the potential to profoundly influence the global carbon cycle.

The role of planktonic microbes in the marine sulphur cycle is largely tied to the production and transformation of an organic sulphur compound called dimethylsulphoniopropionate, or DMSP, which is produced by several species of phytoplankton. DMSP is believed to act as an antioxidant, cryoprotectant or osmolyte for phytoplankton³¹, but also represents an important microbial growth resource, contributing to up to 10% of the carbon demand and over 40% of the sulphur requirements for heterotrophic bacteria in ocean environments³². However, not all marine bacteria use, and cycle, DMSP in the same way, and this has important implications for marine sulphur cycling.

Many marine bacteria demethylate DMSP and subsequently assimilate the sulphur into proteins³³. However, others cleave DMSP in a manner that liberates the volatile compound dimethyl sulphide, or DMS³⁴. This is significant because DMS is the major vehicle for ocean to atmosphere sulphur efflux and once in the atmosphere, DMS is rapidly oxidised into aerosol sulphates, which act as cloud condensation nuclei (CCN)³⁵. The balance between the competing demethylation and cleavage pathways of DMSP degradation, which is determined by the composition and activities of marine bacterial populations, influences the amount of DMS that is released from the ocean into the atmosphere and subsequently influences regional climate.

Nitrogen is a key limiting nutrient in many parts of the ocean, so its input and cycling by microbial activity fundamentally shapes the fertility and biology of the global ocean. Diverse populations of bacteria, archaea and eukaryotic phytoplankton are responsible for performing and mediating the key nitrogen cycling steps of fixation, assimilation, nitrification and denitrification³⁶. Analogous to soil environments, where discrete nitrogen cycling microbes and transformation processes are vertically partitioned across oxic niches, different depths of the ocean water column play host to specific microbiological modules of the marine nitrogen cycle³⁷. Additionally, there is strong geographic partitioning of some key nitrogen cycling microbes and processes across the global ocean, with, for instance, much of cyanobacterial nitrogen fixation concentrated within the warm, well-lit oligotrophic regions of the ocean³⁸. Among all of the ocean's biogeochemical cycles, our understanding of the nitrogen cycle has perhaps been most radically re-shaped with the advent of molecular microbiological approaches³⁶. The resultant discoveries of new groups of nitrogen cycling microbes, including unicellular nitrogen fixing cyanobacteria and large populations of ammonia oxidising archaea, have fundamentally shifted our understanding of marine nitrogen cycling and the microbiological processes that regulate global nitrogen budgets.

New directions: dynamic microbial networks control ocean function

Our view of the identities and roles of microbes in the ocean continues to rapidly expand. Microbial oceanography is currently transitioning from a fruitful era of discovery where molecular tools allowed us to uncover the diversity of marine microbial communities and their functions, to an exciting new phase where this information is feeding sophisticated new ecological questions and concepts. For instance, recent evidence suggests that rather than consisting of a soup of loosely associated populations, the microbial communities in seawater are comprised of highly interconnected

ecological units that function in tight synchrony^{12,13,39,40}. It is becoming apparent that networks of key groups of marine microbes consistently co-occur non-randomly, indicating the existence of community assembly rules among the microbial plankton⁴¹, while the occurrence of multi-species timing of gene regulation in seawater^{40,42} likely permits coordination of complex metabolic processes. With the aid of a suite of new automated sampling technologies⁴² and rapidly advancing ecogenomic approaches², exploration of these new ecological concepts promises to deliver unprecedented insights into the lives of the ocean's smallest, but arguably most important inhabitants.

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Biography

Justin Seymour is an ARC Future Fellow, based at the University of Technology, Sydney and his research interests incorporate aquatic microbial ecology and biological oceanography. His research involves examinations of the ecology of microbes across a range of marine environments, spanning tropical coral reefs to Antarctica, and a continuum of spatiotemporal scales. At the ocean-basin scale he is interested in how large-scale oceanographic processes influence microbial community dynamics and functionality, while at the scale of individual drops of seawater he studies the foraging behaviours of individual marine microbes living within a patchy chemical seascape.



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