Chapter 1

Microbes in the Marine Environment

Viewed from space, it is clear why our planet would be better named “Ocean” than “Earth.” More than 70% of the planet’s surface is covered by interconnected bodies of water. Life originated in the oceans about 3.5 billion years ago and microbes were the only form of life for two thirds of the planet’s existence. The development and maintenance of all other forms of life depend absolutely on the past and present activities of marine microbes. Yet the vast majority of humans—including many marine scientists—live their lives completely unaware of the diversity and importance of marine microbes. Such understanding is vital as we now live in a period of rapid global change. This chapter introduces the scope of marine microbiology, the different types of marine microbe (viruses, bacteria, archaea, fungi, and protists), and their place in the living world. The role of microbes in the many diverse habitats found in the marine environment is explored.

Key Concepts

- Modern methods have led to new ideas about the evolution of microbial life.
- Marine microbes exist in huge numbers and form a major component of biomass on Earth.
- Although there is a wide range of sizes, most marine microbes are exceptionally small.
- A wide range of physical and chemical conditions provide diverse specialized habitats.
- Microbes are major components of plankton and marine snow.
- Microbes are important in sediment formation and there is abundant life below the seafloor.
- Microbes colonize the surfaces of inanimate objects and other living organisms by the formation of biofilms.

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Marine microbiology is one of the most exciting and important areas of modern science

Ever since a detailed study of the microbial world began at the end of the nineteenth century, microbiologists have asked questions about the diversity of microbial life in the sea, its role in ocean processes, its interactions with other marine life, and its importance to humans. However, despite excellent work by pioneering scientists, progress in understanding these issues was often slow and most microbiologists remained unaware of this field of study until recently. Toward the end of the twentieth century, a number of factors conspired to propel marine microbiology to the forefront of “mainstream” science, and the subsequent application of new technology means that it is now one of the most exciting and fast-moving areas of investigation. Powerful new tools in molecular biology, remote sensing, and deep-sea exploration have led to astonishing discoveries of the abundance and diversity of marine microbial life and its role in global ecology. Continuing new discoveries in marine microbiology necessitate radical rethinking of our understanding of ocean processes. We now realize the vital role that marine microbes play in the maintenance of our planet, a fact that will have great bearing on our ability to respond to problems such as the increase in human population, overexploitation of fisheries, climate change, ocean acidification, and marine pollution. Study of the interactions of marine microbes with other organisms is providing intriguing insights into the phenomena of food webs, symbiosis, and pathogenicity. Since some marine microbes produce disease or damage, we need to study these processes and develop ways to overcome them. Finally, marine microbes have beneficial properties such as the manufacture of new products and development of new processes in the growing field of marine biotechnology. This chapter sets the scene for the discussion of all these topics in this book.

Marine microbiology encompasses all microscopic organisms and viruses

Defining the terms “microbiology” and “microorganism” is surprisingly difficult! Microbiology is the study of very small organisms that are too small to be seen clearly with the naked eye (i.e., less than about 1 mm diameter), but most microbiologists are concerned with the activities or molecular properties of microbial communities rather than viewing individual cells with a microscope. The term “microorganism” simply refers to a form of life that falls within the microscopic size range, but there is a huge spectrum of diversity concealed by this all-encompassing term. Indeed, some “microorganisms” are large enough to see without using a microscope, so this is not entirely satisfactory either. Some scientists would argue that the distinguishing features of microorganisms are small size, unicellular organization, and osmotrophy (feeding by absorption of nutrients). The osmotrophic characteristic is important because diffusion processes are a major limitation to cell size, as discussed in the next section. However, this characteristic would exclude many microscopic unicellular protists (a loose grouping of simple eukaryotes), many of which feed by phagotrophy (engulfment of particles). These “plant-like” or “animal-like” groups are most commonly studied by specialists who traditionally have a background in botany or zoology. Indeed, the study of marine protists and recognition that they are microbes with a major role in ocean processes has lagged behind the study of bacteria. Many marine protists are mixotrophic and can switch from photosynthesis to phagotrophic feeding, so the plant or animal similarity is meaningless. Additionally, viruses are microscopic and are obviously included in the remit of microbiologists, but they are not cellular and it can be argued that they are not living organisms either (this question is explored in depth in Chapter 7). There is a huge diversity of interconnected microbial life forms in the marine environment, and worrying about such artificial divisions is not going to be helpful; so in this book I use the term...
“microbe” as a generic descriptor for all microscopic organisms (i.e. the bacteria, archaea, fungi, and unicellular protists), together with the viruses.

**Marine microbes are found in all three domains of cellular life**

Biologists usually rely on the study of morphology and physiological properties to classify living organisms, but these characteristics have always proved frustratingly unhelpful when dealing with microbes. Phylogenetic systems of classification depend on comparisons of the information content of their macromolecules, especially nucleic acids and proteins. If two organisms are very closely related, we expect the sequence of the individual units in a macromolecule to be more similar than they would be in two unrelated organisms. In the 1970s, Carl Woese and colleagues pioneered the use of ribosomal RNA (rRNA) sequencing in order to develop a better view of microbial diversity. Our view of the living world has since been revolutionized by advances in this approach, made possible because of the parallel advances in molecular biological techniques and computer processing of the large amounts of information generated. Because the secondary structure of rRNA is so important in the ribosome and the vital cell function of protein synthesis, base sequence changes in the rRNA molecule occur quite slowly in evolution. In fact, some parts of rRNA are highly conserved and sequence comparisons can be used to ascertain the similarity of organisms on a broad basis. The methods and applications of this major technique are described in Chapter 2.

Woese identified three distinct lineages of cellular life, referred to as the domains *Archaea*, *Bacteria*, and *Eukarya*. A phylogenetic “tree of life” based on rRNA sequences envisaged divergence of the three domains from an original “universal ancestor” (Figure 1.1A). The three-domain system of classification is used by most microbiologists, although it has never been universally adopted by other biologists and remains a topic of fierce controversy. Apart from our preference for a phylogenetic system, it allows microbiologists to say that we study two entire domains of life, and a significant proportion of the third! The most important consequence of the three-domain tree of life is that we now realize that the *Archaea* are not a peculiar, specialized group of bacteria as originally thought (for many years they were called the archaebacteria), but are in fact a completely separate group with closer phylogenetic relationships to the *Eukarya* than to the *Bacteria*.

![Figure 1.1](image-url) Representations of the three domains of life. (A) Simple tree based on ribosomal RNA sequencing. In this model, the root of the tree is envisaged as a hypothetical universal ancestor from which all life evolved. (Adapted from Martin and Embley [2004] by permission of Macmillan Publishers Ltd.) (B) A three-domain tree based on evidence of extensive lateral gene transfer, revealed by studies of other genes. (Image courtesy of Gary J. Olsen, University of Illinois; based on concept of W. Ford Doolittle.)
Eukaryotes are distinguished by a membrane-bound nucleus and organelles with specific functions. Mitochondria occur in all eukaryotic cells, with the exception of a few anaerobic protozoa, and carry out the processes of respiratory electron transport. In photosynthetic eukaryotes, chloroplasts carry out reactions for the transfer of light energy for cellular metabolism. Various lines of evidence (especially the molecular analysis of the nucleic acids and proteins) support the hypothesis that the organelles of eukaryotic cells have evolved by a process of endosymbiosis, in which one cell lives inside another cell for mutual benefit. This hypothesis proposes that the original source of mitochondria in eukaryotic cells occurred when primitive cells acquired respiratory bacteria (most closely related to proteobacteria) and that the chloroplasts evolved from endosymbiosis with cyanobacteria. Such interactions between different types of cell have continued throughout evolution, and Chapter 10 contains many examples of endosymbiosis involving microbes.

**Horizontal gene transfer confounds our understanding of evolution**

Since it became possible to study the whole genome sequences of organisms, we have found increasing evidence of extensive lateral gene transfer (LGT; also known as horizontal gene transfer, HGT) between microbes. Such transfer occurs most commonly between related organisms, but transfer across bigger genetic distances also occurs—even between domains. Members of the **Bacteria** and **Archaea** contain some genes with very similar sequences, and members of the **Eukarya** contain genes from both of the other domains. Some members of the domain **Bacteria** have even been shown to contain eukaryotic genes. Previously, evolution was explained only by the processes of mutation and sexual recombination, but we now know that the pace of evolution is accelerated by the transfer and acquisition of modules of genetic information. This phenomenon is widespread in modern members of the **Bacteria** and **Archaea** and can occur via three processes. During the process known as transformation, cells may take up and express naked DNA; whilst conjugation relies on cell–cell contact mediated by pili. The most important source of LGT is the process of transduction by phages (viruses infecting bacteria); this is explored in detail in Chapter 7. The enormous diversity of marine viruses and the identification of a viral origin of genes in many marine organisms indicate how important this process has been throughout evolution.

**Viruses are noncellular entities with great importance in marine ecosystems**

Virus particles (virions) consist of a protein capsid containing the viral genome composed of either RNA or DNA. Because they only contain one type of nucleic acid, viruses must infect living cells and take over the host’s cellular machinery in order to replicate. It is often thought that viruses could have evolved (perhaps from bacteria) as obligate parasites that have progressively lost genetic information until they consist of only a few genes, or that they represent fragments of host-cell RNA or DNA that have gained independence from cellular control. New ideas about the evolution of viruses are discussed in Research Focus Box 7.2. The genome of viruses often contains sequences that are equivalent to specific sequences in the host cell. Viruses exist for every major group of cellular organisms (**Bacteria**, **Archaea**, **Fungi**, protists, plants, and animals), but at present we have knowledge of only a tiny proportion of the viruses infecting marine life. As discussed in Chapter 7, recognition of the abundance and diversity of marine viruses, and the role that they play in biogeochemical cycles and control of diversity in marine microbial communities, has been one of the most important discoveries of recent years.
Microbial processes shape the living world

Probably the most important overriding features of microbes are their exceptional diversity and ability to occupy every conceivable habitat for life. Indeed, what we consider “conceivable” is challenged constantly by the discovery of new microbial communities in habitats previously thought of as inhospitable, or carrying out processes that we had no idea were microbial in nature. Bacteria and archaea have shaped the subsequent development of life on Earth ever since their first appearance—the metabolic processes that they carry out in the transformation of elements, degradation of organic matter, and recycling of nutrients play a central role in innumerable activities that affect the support and maintenance of all other forms of life. Microbial life and the Earth have evolved together and the activities of microbes have affected the physical and geochemical properties of the planet. Indeed, they are actually the driving forces responsible for major planetary processes like changes in the composition of the atmosphere, oceans, soil, and rocks. This is especially relevant to our consideration of the marine environment, in view of the huge proportion of the biosphere that this constitutes. Despite the preponderance of microbes and the importance of their activities, they are unseen in everyday human experience. Microbes live and grow almost everywhere, using a huge range of resources, whereas plants and animals occupy only a small subset of possible environments and have a comparatively narrow range of lifestyles.

Marine microbes show great variation in size

Table 1.1 shows the range of dimensions and volumes of some representative marine microbes. Even by the usual standards of microbiology, the most abundant microbes found in seawater are exceptionally small. Their very small size is the main reason appreciation of their abundance eluded us until quite recently. As described in Chapter 2, recognition of the abundance of marine microbes depended on the development of fine-pore filters and direct counting methods using epifluorescence microscopy and flow cytometry. Small cell size has great significance in terms of the physical processes that affect life. At the microscale, the rate of molecular diffusion becomes the most important mechanism for transport of substances into and out of the cell. Small cells feeding by absorption (osmotrophy) can take up nutrients more efficiently than larger cells. The surface area:volume ratio (SA/V) is the critical factor because as cell size increases, volume (V) increases more quickly than surface area (SA), as shown in Figure 1.2.

The most abundant ocean bacteria and archaea have very small cell volumes and large SA/V ratios. The majority are smaller than about 0.6 μm in their largest dimension, and many are less than 0.3 μm, with cell volumes as low as 0.003 μm³. If nutrients are severely limiting, as they are in most of the oceans, selection will favor small cells. Since the first description of such small cells, termed “ultramicrobacteria,” their size has provoked considerable controversy. Such extremely small cells could result from a genetically fixed phenotype maintained throughout the cell cycle or because of physiological changes associated with starvation. The latter explanation is supported by the fact that some cultured bacteria become much smaller when starved. Most naturally occurring bacteria have been impossible to grow in culture—this is a central problem in marine microbiology, which we shall return to on several occasions in future chapters. Because of this, it has been difficult to determine whether small size is a genotypically determined condition for marine bacteria. However, studies with some recently cultured marine bacteria from low-nutrient (oligotrophic) ocean environments show that addition of nutrients does not cause an increase in cell size. Small cell size also has important implications for mechanisms of active motility and chemotaxis, because of the microscale effects of Brownian movement (bombardment by water molecules) and shear forces. Small marine bacteria have
mechanisms of motility and chemotaxis quite unlike those with which we are familiar in “conventional” microbiology. Cells use various strategies to increase the SA/V ratio and thus improve efficiency of diffusion and transport. In fact, spherical cells are the least efficient shape for nutrient uptake, and many marine bacteria and archaea are thin rods or filaments or may have appendages such as stalks or buds. Figure 1.3 shows examples of the diverse morphology of marine bacteria. Many of the larger organisms overcome the problems of diffusion by having extensive invaginations of the cytoplasmic membrane or large intracellular vacuoles, increasing the SA.

As shown in Table 1.1, marine eukaryotic microbes also show a considerable variation in size. Many flagellates are in the 1–2 μm range, cellular dimensions that are more typical of many familiar bacteria. The smallest known eukaryote is *Ostreococcus tauri*, which is only about 0.8 μm diameter (Figure 1.4B). Again, the realization that such small cells (now referred to as “picoeukaryotes”) play a key role in ocean processes escaped attention until quite recently. Many small protists seem capable of engulfing bacteria of almost the same size as themselves or can prey on much larger organisms. Many groups of the flagellates, ciliates, diatoms, and dinoflagellates are somewhat larger, reaching sizes up to 200 μm, and

![Diagram of SA/V ratios for spherical cells](image)
amoeboid types (radiolarians and foraminifera) can be even larger and visible to the naked eye. Finally, a few types of bacteria are bigger than many protists, the largest of which is *Thiomargarita namibiensis* (Figure 1.4C).

**The world's oceans and seas form an interconnected water system**

The oceans cover $3.6 \times 10^8$ km$^2$ (71% of the Earth’s surface) and contain $1.4 \times 10^{21}$ liters of water (97% of the total on Earth). The average depth of the oceans is 3.8 km, with a number of deep-sea trenches, the deepest of which is the Marianas Trench in the Pacific (11 km). The ocean floor contains large mountain ranges and is the site of almost all the volcanic activity on Earth. More than 80% of the area and 90% of the volume of the oceans constitutes the deep sea, most of which remains unexplored. It is usual to recognize five major ocean basins, although they actually form one interconnected water system, as illustrated in Figure 1.5.
The Pacific is the deepest and largest ocean, almost as large as all the others combined. This single body of water has an area of $1.6 \times 10^8$ km$^2$ and covers about 28% of the Earth’s surface, more than the total land area. The ocean floor in the eastern Pacific is dominated by the East Pacific Rise, while the western Pacific is dissected by deep trenches. The Atlantic Ocean is the second largest with an area of $7.7 \times 10^7$ km$^2$ lying between Africa, Europe, the Southern Ocean, and the Americas. The mid-Atlantic Ridge is an underwater mountain range stretching down the entire Atlantic basin. The deepest point is the Puerto Rico Trench (8.1 km). The Indian Ocean has an area of $6.9 \times 10^7$ km$^2$ and lies between Africa, the Southern Ocean, Asia, and Australia. A series of ocean ridges cross the basin, and the deepest point is the Java Trench (7.3 km). The Southern Ocean is the body of water between 60°S and Antarctica. It covers $2.0 \times 10^7$ km$^2$ and has a fairly constant depth of 4–5 km, with a continual eastward water movement called the Atlantic Circumpolar Current. The Arctic Ocean, lying north of the Arctic Circle, is the smallest ocean, with an area of $1.4 \times 10^7$ km$^2$. About half of the ocean floor is continental shelf, with the remainder being a central basin interrupted by three submarine ridges. As well as the major oceans, there are marginal seas, including the Mediterranean, Caribbean, Baltic, Bering, South China Seas, and many others.

At the margins of major landmasses, the ocean is shallow and lies over an extension of the land called the continental shelf. This extends offshore for a distance ranging from a few kilometers to several hundred kilometers and slopes gently to a depth of about 100–200 m, before there is a steep drop-off to become the continental slope. The abyssal plain covers much of the ocean floor; this is a mostly flat surface with few features, but is broken in various places by ocean ridges, deep-sea trenches, undersea mountains, and volcanic sites.
The upper surface of the ocean is in constant motion owing to winds

Wind belts created by differential heating of air masses generate the major surface current systems, shown in Figure 1.6. Rotation of the Earth deflects moving water in a phenomenon known as the Coriolis Effect, which results in boundary currents between large water masses. This leads to large circular gyres that move clockwise in the northern hemisphere and anticlockwise in the southern hemisphere. Such gyres and currents affect the distribution of nutrients and marine organisms. On the basis of surface ocean temperatures, the marine ecosystem
Chapter 1

can be divided into four major biogeographical zones, namely polar, cold temperate, warm temperate (subtropical), and tropical (equatorial). The boundaries between these zones are not absolute and vary with season.

Deep-water circulation systems transport water between the ocean basins

Below a depth of about 200 m, ocean water is not affected by mixing and wind-generated currents. However, a system of vast undersea rivers transports water around the globe and has a major influence on the distribution of nutrients and classic processes (Figures 1.7 and 8.1). This thermohaline circulation system—often referred to as the “global conveyor belt”—is formed by the effects of temperature and salinity causing differences in the density of water. Surface water in the North Atlantic flows toward the pole as the Gulf Stream. Water is removed to the atmosphere as it cools through evaporation, resulting in higher salinity. Water is also removed during the formation of sea ice. Thus, the water becomes denser and sinks to form a deep pool, which then flows toward Antarctica, where more cold, dense water is added. The current then splits, with one branch going toward the Indian Ocean and the other to the Pacific Ocean. As the current nears the equator it warms and becomes less dense, so upwelling occurs. The warmer waters loop back to the Atlantic Ocean, where they start the cycle again.

Seawater is a complex mixture of inorganic and organic compounds

Seawater is a slightly alkaline (pH 7.5–8.4) aqueous solution—a complex mixture of more than 80 solid elements, gases, and dissolved organic substances. The concentration of these varies considerably according to geographic and physical factors, and it is customary to refer to the salinity of seawater in parts per thousand (‰) to indicate the concentration of dissolved substances. The open ocean has a constant salinity in the range 34–37‰, with differences due to dilution by rainfall and evaporation. Oceans in subtropical latitudes have the highest salinity as a result of higher temperatures, whilst temperate oceans have lower salinity as a result of less evaporation. In coastal regions, seawater is diluted considerably.

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by freshwater from rivers and terrestrial runoff and is in the range 10–32‰. Conversely, in enclosed areas such as the Red Sea and Arabian Gulf, the salinity may be as high as 44‰. In polar areas, the removal of freshwater by the formation of ice also leads to increased salinity. The major ionic components of seawater are sodium (55% w/v), chloride (31%), sulfate (8%), magnesium (4%), calcium (1%), and potassium (1%). Together, these constitute more than 99% of the weight of salts. There are four minor ions—namely bicarbonate, bromide, borate, and strontium—which together make up just less than 1% of seawater. Many other elements are present in trace amounts (<0.01%), including key nutrients such as nitrate, phosphate, silicate and iron. The concentration of these is crucial in determining the growth of marine microbes and the net productivity of marine systems, as discussed in Chapter 9.

The concentration of salts has a marked effect on the physical properties of seawater. The freezing point of seawater at 35‰ is −1.9°C, and seawater increases in density up to this point. As noted above, this results in the formation of masses of cold, dense water in polar regions, which sink to the bottom of the ocean basins and are dispersed by deep-water circulation currents. Differences in the density of seawater create a discontinuity called the pycnocline, which separates the top few hundred meters of the water column from deeper water. This has great significance, because the gases oxygen and carbon dioxide are more soluble in cold water.

Oxygen is at its highest concentrations in the top 10–20 m of water, owing to exchange with the atmosphere and production of oxygen by photosynthesis. Concentration decreases with distance from the surface until it reaches a minimum between 200 and 1000 m, and bacterial decomposition of organic matter may create conditions that are almost anoxic. Below this, the oxygen content increases again as a result of the presence of dense water (with increased solubility at lower temperature) that has sunk from polar regions and been transported on the thermohaline circulation system. This oxygen gradient varies greatly in different regions, and there are several regions where large bodies of hypoxic water occur at relatively shallow depths—these are the oxygen minimum zones (see Plate 9.1).

The solubility of carbon dioxide is an important factor in controlling the exchange of carbon between the atmosphere and the oceans and therefore is of huge significance in understanding climatic processes, as discussed in Chapter 8. Only a very small proportion of dissolved inorganic carbon (DIC) is present in the form of dissolved CO₂ gas. Carbon dioxide reacts with water to form carbonic acid, which rapidly dissociates to form bicarbonate, hydrogen ions, and carbonate in the reactions:

\[
\text{CO}_2 (\text{gas}) + \text{H}_2\text{O} \rightleftharpoons \text{H}_2\text{CO}_3 \rightleftharpoons \text{H}^+ + \text{HCO}_3^- \rightleftharpoons 2\text{H}^+ + \text{CO}_3^{2-}
\]

These reactions tend to stay in equilibrium, buffering the pH of seawater within a narrow range and constraining the amount of CO₂ taken up from the atmosphere. However, the accelerating atmospheric concentration of high levels of CO₂ since the industrial revolution is shifting the equilibrium and causing the pH to fall because of increased levels of H⁺ ions. This phenomenon is called ocean acidification and some of its possible consequences for microbial life are discussed in Research Focus Box 3.1.

**Light and temperature have important effects on microbial processes**

Light is of fundamental importance in the ecology of microbes that use light energy for photosynthesis and other functions (see Research Focus Box 3.1), thus affecting primary productivity. The extent to which light of different wavelengths
The effects of high levels of CO₂ (together with other gases such as methane and nitrous oxide) in promoting global warming via the “greenhouse effect” are well known and a major topic of current sociopolitical concern. However, a less well-known effect of atmospheric CO₂ is the process of ocean acidification (OA), which has been termed “the other CO₂ problem” to bring it to the attention of the public (see Mitchell, 2009). When CO₂ is absorbed from the atmosphere, it leads to an increase in the concentration of hydrogen ions and hence a fall in pH (see equation on p. 11). Approximately half of the CO₂ produced by human activities in the past 200 years has been absorbed by the oceans, leading to a fall in the average pH of ocean surface water from about 8.21 to 8.10. Although this seems small, it represents a 30% increase in the hydrogen ion concentration because pH is a logarithmic scale. Some models predict that the average ocean pH of the oceans could fall to pH 7.9 by 2100—at which point hydrogen ions will be three times the current levels—unless CO₂ emissions are drastically reduced. This level is lower than has occurred for hundreds of millions of years; more importantly, this rate of change has probably never occurred in the history of the planet (Royal Society, 2005). Even if the world succeeds in controlling CO₂ emissions, much of this change will be irreversible, because of the long time needed for mixing of deep waters and natural buffering processes to take effect.

One of the main effects of the altered seawater chemistry as a result of OA is likely to be on calcifying organisms that use calcium carbonate (CaCO₃) to construct a skeleton or shell. As well as animals such as corals, crustaceans and mollusks, there are some very important planktonic microbes that carry out calcification, especially the coccolithophores (see Chapter 6). Orr et al. (2005) concluded that such calcifying organisms could begin to experience difficulties in maintaining their CaCO₃ skeletons as early as 2050, especially in polar oceans, where the state of CaCO₃ saturation is lower. When considering the effect of OA on microbes, some examples of recent research given here illustrate how difficult it is to reach clear conclusions about the effect of OA on microbial processes.

When coccolithophores make the plates of calcite that surround the cell (see Figure 6.5B), they release CO₂, but they also fix CO₂ during photosynthesis. Thus, the balance between these processes is very important in the global carbon cycle. Research has indicated that there is great variation in the responses of different species (and strains within species) to changes in ocean pH and CO₂ levels. Riebesell (2004) concluded that increased CO₂ levels enhance photosynthetic carbon fixation of some phytoplankton groups and predicted that calcifying plankton might benefit at the expense of some other groups. Mesocosm studies (see Figure 2.2) of the response of blooms of the coccolithophore Emiliania huxleyi showed a reduction in calcification rates when CO₂ levels simulating end of the century conditions were applied (Delille et al., 2005; Engel et al., 2005). However, Iglesias-Rodriguez et al. (2008a) developed observations from sediment cores from a site in the North Atlantic, indicating that coccolithophores have increased their calcification rates in response to rising CO₂ levels—the average coccolith mass has increased by ~40% over the past 220 years. In laboratory cultures, a strain of E. huxleyi increased photosynthesis and calcification rates by 100–150% at high CO₂ levels, a level much higher than that observed in previous studies. This paper has attracted a lot of interest because of the important conclusion that coccolithophores are adapting to a high CO₂ ocean and the impact that this will have on predicting future trends. Following publication, Riebesell et al. (2007) were highly critical of the experimental setup, but Iglesias-Rodriguez et al. (2008b) have defended their conclusions. In another mesocosm study, Riebesell et al. (2007) showed that CO₂ uptake by phytoplankton was 27% and 39% higher, respectively, when CO₂ was at two or three times present-day levels. These authors also found that the ratio of carbon to nitrogen uptake increased at higher CO₂ concentrations, whereas the carbon–nitrogen ratio within the cells of the phytoplankton was unaltered. It seems that extra carbon incorporated through photosynthesis was rapidly lost from the cells to form transparent exopolymer particles that contribute to the formation of marine snow and the flux of organic carbon from the surface to the deep sea (see Figure 1.9). Thus, increased productivity might provide a partial negative feedback mechanism by which some of the increased CO₂ dissolved in seawater is removed. Further evidence for a possible negative feedback mechanism comes from the observation by Ramos et al. (2007) that the cyanobacterium Trichodesmium increases its rate of nitrogen fixation very markedly at high CO₂ levels. The authors suggest that this could enhance the productivity of oligotrophic oceans that are currently limited by nitrogen limitation and increase the flux of carbon in the biological pump.

From the few examples of conflicting results presented here, it is clear that our knowledge of the effects of OA on the physiology and diversity of marine microbes is very poorly understood. Experts have recently been coordinating efforts to highlight the challenges for future research in this area and the need for coordinated methodological approaches (C-MORE, 2009; EPOCA, 2009). Microbes have adapted to previous changes in ocean chemistry that have occurred periodically over the past 3 billion years. How will they adapt to the extreme changes currently occurring?

**Ocean acidification—“the other CO₂ problem”**

How will microbes respond to rapid changes in ocean chemistry?

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penetrates seawater depends on a number of factors, notably cloud cover, the polar ice caps, dust in the atmosphere, and variation of the incident angle of solar radiation according to season and location on the Earth's surface. Light is absorbed or scattered by organisms and suspended particles. Even in the clearest ocean water, photosynthesis is restricted by the availability of light of sufficient intensity to the upper 150–200 m. This is termed the photic or euphotic zone (from the Greek, "well lit"). Blue light has the deepest penetration, and photosynthetic microbes at the lower part of the photic zone have light-harvesting systems that are tuned to collect blue light most efficiently (see p. 114). In turbid coastal waters, during seasonal plankton blooms, the euphotic zone may be only a few meters deep.

Solar radiation also leads to thermal stratification of seawater. In tropical seas, the continual input of energy from sunlight leads to warming of the surface waters to 25–30°C, causing a considerable difference in density from that of deeper waters. Thus, throughout the year, there is a marked thermocline at about 100–150 m, below which there is a sudden reduction in temperature to 10°C or less. Little mixing occurs between these layers. In polar seas, the water is permanently cold except for a brief period in the summer, when a slight thermocline results. Apart from this period, turbulence created by surface winds generates mixing of the water to considerable depths. Temperate seas show the greatest seasonal variation in the thermocline, with strong winds and low temperatures leading to extensive mixing in the winter. The thermocline develops in the spring, leading to a marked shallow surface layer of warmer water in summer. As the sea cools and wind increases, the thermocline breaks down again in the autumn. Combined with seasonal variations in light intensity, these temperature stratification effects and vertical mixing have a great impact on rates of photosynthesis and other microbial activities.

**Marine microbes form a major component of the plankton**

Microbes occur in all the varied habitats found in the oceans, shown in [Figure 1.8](#). The surface interface (neuston) between water and atmosphere is rich in organic matter and often contains high numbers of diverse microbes. From the limited studies conducted in coastal environments, there does not seem to be much evidence of a stable and unique neuston community, although it might be expected that there are some specialized bacteria that are permanent members of this interface, adapted to high levels of solar radiation.

![Figure 1.8](#) Schematic representation of the major ecological zones of the oceans and marine microbial habitats. (Not to scale.)
Plankton is a general term in marine biology referring to organisms suspended in the water column that do not have sufficient power of locomotion to resist large-scale water currents (in contrast to the nekton, which are strong-swimming animals). Traditionally, biologists refer to the phytoplankton (plants) and zooplankton (animals). Using this approach, we could add the terms bacterioplankton for bacteria and virioplankton for viruses. Traditional concepts of “plant” and “animal” are unsatisfactory, and the term phytoplankton now refers to all photosynthetic microbes, including cyanobacteria as well as eukaryotic protists. Another approach to classifying the plankton is in terms of size classes, for which a logarithmic scale ranging from megaplankton (>20 mm) to nanoplankton (<0.2 μm) has been devised. Table 1.2 shows the size classes that encompass marine microbes. Thus, the viruses constitute the femtoplankton, bacteria mainly occur in the picoplankton, whilst protists occur in the picoplankton, nanoplankton, and microplankton.

**Table 1.2 Classification of plankton by size**

<table>
<thead>
<tr>
<th>Size category</th>
<th>Size range (μm)</th>
<th>Microbial groups</th>
</tr>
</thead>
<tbody>
<tr>
<td>Femtoplankton</td>
<td>0.01–0.2</td>
<td>Viruses</td>
</tr>
<tr>
<td>Picoplankton</td>
<td>0.2–2</td>
<td><em>Bacteria</em>, <em>Archaea</em>, some flagellates</td>
</tr>
<tr>
<td>Nanoplankton</td>
<td>2–20</td>
<td>Flagellates, diatoms, dinoflagellates</td>
</tr>
<tr>
<td>Microplankton</td>
<td>20–200</td>
<td>Ciliates, diatoms, dinoflagellates, other algae</td>
</tr>
</tbody>
</table>

aSome filamentous cyanobacteria and sulfur-oxidizing bacteria occur in larger size classes (see Table 1.1).

**What does “dissolved organic matter” really mean?**

Oceanographers have traditionally talked about “dissolved” and “particulate” organic matter (DOM and POM, respectively). Measurements of concentrations and fluxes of DOM and its constituent elements carbon (DOC), nitrogen (DON) and phosphorus (DOP) are among the most important factors in the study of ocean processes. It is important to remember that the difference between “dissolved” and “particulate” is a purely empirical distinction and simply reflects the size of filters used in sample preparation. There is no absolute definition, but most filters used in studies of DOM and POM have pore sizes from about 0.45 to 1.0 μm. Many bacteria and almost all viruses would pass through such filters and therefore appear in the DOM fraction. Colloidal material and polymers aggregate to form particles, and it is only low-molecular-weight compounds like sugars and amino acids that are truly dissolved. Thus, DOM and POM form a continuum, with microbes spanning both fractions.
diatoms, at the end of a bloom, often precipitate large-scale snow formation owing to the production of large amounts of mucopolysaccharides in their cell walls. The generation of water currents during feeding by flagellates and ciliates colonizing the aggregate also collects particles from the surrounding water and leads to growth of the snow particle.

Marine snow is mainly produced in the upper 100–200 m of the water column, and large particles can sink up to 100 m per day, allowing them to travel from the surface to the ocean deep within a matter of days. This is the main mechanism by which a proportion of the photosynthetically fixed carbon is transported from the surface layers of the ocean to deeper waters and the seafloor. However, aggregates also contain active complex assemblages of bacteria and protists that graze on them. Levels of microorganisms in marine snow are typically $10^8$–$10^9$ ml$^{-1}$, which are about 100–10000-fold higher than in the bulk water column. As particles sink, organic material is degraded by extracellular enzymes produced by the resident microbial population. Microbial respiration creates anoxic conditions, so that diverse aerobic and anaerobic microbes colonize different niches within the snow particle. The rate of solubilization exceeds the rate of remineralization, so dissolved material leaks from snow particles, leaving a plume of nutrients in its wake as it spreads by diffusion and advection. This may send chemical signals that attract small zooplankton to consume the particle as food. The trailing plume also provides a concentrated nutrient source for suspended planktonic bacteria, which may show chemotactic behavior in order to remain within favorable concentrations. Thus, much of the carbon is recycled during its descent, but some material reaches the ocean bottom, where it is consumed by benthic organisms or leads to the formation of sediments. Photosynthesis by algae and bacteria leads to the formation of organic material through CO$_2$ fixation, but viruses, heterotrophic bacteria, and protists all play a part in the fate of this fixed carbon. The balance of their activities throughout the water column determines the

Figure 1.9 Schematic diagram showing the microbial processes occurring in the formation and fate of a marine snow particle as it falls through the water column. The action of extracellular enzymes and viral lysis leads to the release of dissolved organic material (DOM).

HOW DID CHERNOBYL FALLOUT HELP IN THE STUDY OF MARINE SNOW?

In 1986, a major environmental catastrophe occurred when the nuclear reactor in Chernobyl, Ukraine, exploded, releasing hundreds of tons of radioactive particles. These were carried by winds to many distant regions and settled with rain on land and sea. Fowler et al. (1987) were able to extract some benefit from this tragedy. They had already set up time-series sediment traps to measure vertical transport in the Mediterranean Sea. Following the deposition of Chernobyl fallout, they found that the pulse of radioactivity—in particular the rare earth nuclides $^{141}$Ce and $^{144}$Ce—was rapidly removed from surface waters and transported to depths of over 200 m within a few days at an average settling rate of 29 m per day. Physical processes alone could not account for such rapid settlement. Fowler and colleagues identified the fecal pellets of zooplankton, leading to the conclusion that zooplankton were ingesting particles adsorbed to their food source and repackaging them as larger, denser particles that aggregated with marine snow to sink at a high rate. Subsequent studies have shown that the fecal pellets of different zooplankton species vary greatly in their density and sinking rate, and this is affected by many factors.
Proportions of fixed carbon that are remineralized to CO₂, transferred to higher trophic levels, or reach the sea floor. The discovery of this mechanism, termed the microbial loop, was one of the most important conceptual advances in biological oceanography, and its significance is considered further in Chapter 8.

**Microbes play a key role in the formation of sediments**

Much of the continental shelf and slope is covered with terrigenous or lithogenous sediments derived from erosion of the continents and transported into the ocean as particles of mud, sand, or gravel. The mineral composition reflects the nature of the rocks and the type of weathering. Large rivers such as the Amazon, Orinoco or Ganges transfer millions of tons of fine sediments to the ocean each year. Most of this mud settles along the continental margins or is funneled by submarine currents as dilute suspensions.

In the deep ocean, about 75% of the deep ocean floor is covered by abyssal clays and oozes. Abyssal clays are formed by the deposition of wind-blown terrestrial dust from the continents, mixed with volcanic ash and cosmogenic dust from meteor impact. These accumulate very slowly—less than 1 mm per 1000 years—whilst oozes accumulate at up to 4 cm per 1000 years. Biogenous oozes contain over 30% of material of biological origin, mainly shells of protistan plankton, mixed with clay. Oozes are usually insignificant in the shallow waters near continents. Calcareous oozes or muds cover nearly 50% of the ocean floor, especially in the Indian and Atlantic Oceans. They are formed by the deposition of the calcium carbonate shells (tests) of two main types of protist: the coccolithophorids and the foraminifera (see Chapter 6). Siliceous oozes are formed from the shells (frustules) of diatoms and radiolarians, which are composed of opaline silica (SiO₂·nH₂O). The rate of accumulation of biogenous oozes depends on the rate of production of organisms in the plankton, the rate of destruction during descent to the seafloor, and the extent to which they are diluted by mixing with other sediments. In the case of coccolithophorids and foraminifera, depth has an important effect on dissolution of the tests. At relatively high temperatures near the surface, seawater is saturated with CaCO₃. As calcareous shells sink, CaCO₃ becomes more soluble as a result of the increased content of CO₂ in water at lower temperatures and higher pressures. The carbonate compensation depth is the depth at which carbonate input from the surface waters is balanced by dissolution in deep waters; this varies between 3000 m in polar waters and 5000 m in tropical waters. For this reason, calcareous oozes tend not to form in waters more than 5000 m deep. Similarly, not all of the silica in the frustules of diatoms reaches the ocean floor because bacterial action has been shown to play a large part in the dissolution of diatom shells during their descent (see p. 145). The rate of deposition of protist remains to the seabed is much more rapid than would be assumed from their small size. This is because they are aggregated into larger particles through egestion as fecal pellets after grazing by zooplankton and through the formation of marine snow as described above. In shallower waters near the continental shelf, the high input of terrigenous sediments mixes with and dilutes sediments of biogenous origin.

Remineralization of readily degradable organic matter in the water column through microbial action means that only a small fraction of fixed carbon—probably less than 1% of primary production—reaches the deep ocean floor. Oxygen only penetrates the top few millimeters of sediments, and below this the sediments are anoxic. Indeed, the overlying water column may be completely anoxic in some regions where high nutrient concentrations promote high oxygen consumption by microbes. For example, the Black Sea contains no free oxygen from a depth of 150 m to the bottom, at 2000 m, owing to sulfate reduction. There are also large anoxic basins off the coasts of Venezuela and Mexico and in the Eastern
Mediterranean (see Research Focus Box 1.2). As organic material settles deeper into anoxic sediments, it accumulates more rapidly than it is degraded and thus joins the geological cycle, reemerging millions of years later when uplifted in continental rocks through tectonic processes.

There is increasing recognition of the importance of microbial activities in the sediment–water interface (SWI) and deep-sea benthic boundary layer (BBL), which is a layer of homogeneous water 10 m or more thick, adjacent to the sediment surface. The SWI includes high concentrations of particulate organic debris and dissolved organic compounds that become absorbed onto mineral particles. The structure and composition of the microbial habitat is modified by benthic “storms” and the action of animals such as worms and burrowing shrimps, which move and resuspend sediments, transporting oxygen into deeper layers.

As well as the constant “snowfall” of plankton-derived material, concentrated nutrient inputs reach the seabed in the form of large animal carcasses. For example, time-lapse photography has shown how quickly fallen whale carcasses attract colonies of animals, and microbiological studies accompanying these investigations have yielded novel bacteria, some with biotechnological applications (see p. 308). The microbial communities and symbioses that develop are similar to those found at hydrothermal vents and cold seeps. Other types of sediment that provide special habitats for microbes include those in salt marshes, mangroves, and coral reefs.

Studies of the extent to which carbon fixed in the photic zone finds its way to the seabed, and its fate in sediments, are important in understanding the role of the oceans in the planetary carbon cycle. Microbial processes such as production and oxidation of methane and oxidation and reduction of sulfur compounds are of special interest. Studies of the diversity and activity of microbial life in the various types of sediment are yielding many new insights, mainly because of the application of molecular techniques, and are described in subsequent chapters.

**Microbes colonize surfaces through formation of biofilms**

In the last two decades, the special phenomena that govern the colonization of surfaces by microbes have come under intense scrutiny, with the growing recognition that such biofilm formation involves complex physicochemical processes and community interactions. Biofilms consist of a collection of microbes bound to a solid surface by their extracellular products, which trap organic and inorganic components. In the marine environment, all kinds of surfaces including other microbes, plants, animals, rocks, and fabricated structures may be colonized by biofilms. As a result of metabolic processes, ecological succession results in the development of microenvironments and colonization by mixed communities of bacteria and protists to form layered structures known as microbial mats, which can be several millimeters thick. These are particularly important in shallow and intertidal waters. The composition of microbial mats is affected by physical factors such as light, temperature, water content, and flow rate; and by chemical factors such as pH, redox potential, the concentration of molecular oxygen and other chemicals (especially sulfide, nitrate, and iron), and dissolved organic compounds. Phototrophic bacteria and diatoms are major components of stratified microbial mats, and the species composition and zonation are determined by the intensity and wavelength of light penetration into the mat. Light normally only penetrates about 1 mm into the mat and anoxic conditions develop below this. The formation and diurnal variations of oxygen and sulfide gradients has a major effect on the distribution of organisms in the mat. Biofilm formation is considered in more detail in Chapter 3, and the economic importance in biofouling is discussed in Chapter 13.
An international consortium of scientists is studying the microbiology of deep hypersaline anoxic basins (DHABs) as part of the European Commission Biodeep project. There are at least four known DHABs (called Bannock, L’Atalante, Discovery, Urania), occurring at depths of 3.2–3.6 km in the Eastern Mediterranean. It is thought that they were formed when the Mediterranean Sea evaporated about 250 million years ago, leaving a layer of rock salt, which then became covered by sediments. Movement of the tectonic plates has exposed the salt deposits in a few areas. Here, the salts have dissolved to form dense pockets of highly concentrated salt solutions, separated from the overlying seawater by extremely sharp environmental interfaces (chemoclines). These undersea brine lakes have extreme physical and chemical conditions, notably the complete lack of oxygen and near-saturated solutions of salts (up to 10 times the salinity of seawater).

The interface is just a few meters thick, and accurate sampling within this chemocline at such a great depth requires great ingenuity. Conventional remotely operated vehicles (ROVs) and manned submersibles cannot be used because of the damaging properties of the brines. Daffonchio et al. (2006) describe the use of a specially adapted sampling module with a CTD probe (see p. 28) containing a sensor to record the exact pressure at which sampling bottles are closed. Operators on the research vessel can observe entry into the narrow band of water at the interface with a camera. Daffonchio and colleagues found that the interface at the Bannock basin contained about 10^6 cells ml^-1, compared with about 10^4 cells ml^-1 in both the overlying water and underlying brine. As in previous studies of the deep sea (Karner et al., 2001), the proportion of organisms belonging to the *Bacteria* and *Archaea* in overlying seawater was about the same, but within the interface the proportion of *Bacteria* was much higher. The interface also showed significantly higher metabolic activity than the overlying or underlying layers. By careful fractionation of the samples from different depths, Daffonchio et al. (2006) found two peaks in biomass and biodiversity, occurring at about 8% and 15–22% salinity. Because salt creates a high osmotic potential, organisms growing in such habitats require special adaptations, and it might be expected that the diversity of bacterial types would be low. However, through the use of DNA-based identification methods, many previously unknown groups of *Bacteria* were identified, occupying narrow niches in the highly stratified interface.

Boring et al. (2009) also used the fine-scale sampling to study microbial processes in the Urania basin, which has lower salt concentrations but exceptionally high levels of sulfide. Two chemoclines occurred, indicating two overlying lakes of brine with very little mixing. The first interface (about 2 m thick), is a very sharp barrier between oxic and anoxic conditions, with differences in temperature and salinity and the presence of different electron acceptors. Again, bacterial abundance and diversity was higher along the chemoclines than in the seawater or in the uniform brines. The main group of *Bacteria* found belonged to the *Delta-proteobacteria* (sulfate reducers) and *Epsilonproteobacteria* (sulfide oxidizers), whilst the deepest, most saline parts of the basin were dominated by archaea responsible for very high levels of methane production. What sustains this dense microbial community? At such a depth, photosynthesis is obviously impossible, and the chemocline acts as a powerful density barrier to nutrient particles settling through the water column. Could chemosynthesis be responsible? Yakhmova et al. (2007) measured carbon fixation through uptake of radioactively labeled bicarbonate and showed that this was much higher within the brine lake than in the overlying water. By using gene probes to detect genes involved in the anaerobic oxidation of ammonia (*anammox*, see p. 69), it was shown that *Crenarchaeota* dominate the brine lake.

In the Discovery Basin, the brine is an almost saturated solution of MgCl₂ rather than NaCl. There is a steep gradient of MgCl₂ from 55 mM at the seawater face to 5.05 M at the lower face. Although Mg is essential in low concentrations, life would be inhibited by such high levels of MgCl₂ because it is a highly chaotropic salt (i.e., it weakens electrostatic interactions that help to stabilize biological molecules). Hallsworth et al. (2007) isolated and cultured some bacteria from the upper parts of the interface, but laboratory tests showed that these would not grow—even after 18 months—above 1.26 M MgCl₂. DNA corresponding to sulfate-reducing bacteria and methanogenic archaea was found throughout the interface, but mRNA (a reliable indicator of active microbes because it only has a short life) was only found in the uppermost layer, with MgCl₂ concentrations below 2.3 M, suggesting that this is the limit for life.

As well as *Bacteria* and *Archaea*, Edgcomb et al. (2009) recently showed that the interface in Bannock and Discovery Basins harbors an astonishing diversity of protists. They obtained more than 1500 protistan gene sequences, most of which have never been described before.

Clearly, microbes thrive in environments that we previously thought completely inhospitable to life. Such studies are important for our understanding of life and biogeochemical processes in the deep sea, as well as having technological potential through discovery of new genes and compounds. They will also inform the search for life on other planets or moons, for example in the planned missions to Mars and Europa.
**Microbes in sea ice form an important part of the food chain in polar regions**

At the poles, the temperature is so low during the winter that large areas of seawater freeze to form sea ice, some of which forms adjacent to the coastal shoreline and some of which forms floating masses of pack ice. Sea ice forms when the temperature is less than −1.8°C, the freezing point of water at 35‰ salinity. The first stage in sea-ice formation is the accumulation of minute crystals of frazil ice on the surface, which are driven by wind and wave action into aggregated clumps called grease ice. These turn into pancake-shaped ice floes that freeze together and form a solid ice cover. At the winter maxima, the combined coverage by sea ice at the north and south polar regions is almost 10% of the Earth’s surface (1.8 × 10^7 km² in the Antarctic and 1.5 × 10^7 km² in the Arctic). During the formation of frazil ice, planktonic microbes become trapped between the ice crystals and wave motion transports more organisms into the grease ice during its formation. Near the ice–air interface, temperatures may be as low as −20°C during the depths of the polar winter, whilst the temperature at the ice–water interface remains fairly constant at about −2°C. When seawater freezes, it forms a crystalline lattice of pure water, excluding salts from the crystal structure. The salinity of the liquid phase increases and its freezing point drops still further. This very cold, high-density, high-salinity (up to 150‰) water forms brine pockets or channels within the ice, which can remain liquid to −35°C. The ice becomes less dense than seawater and rises above sea level, with the channels draining brine through the ice to the underlying seawater. Thus, sea ice is very different from freshwater glacial ice.

The structure of sea ice provides a labyrinth of different microhabitats for microbes, with variations in temperature, salinity, nutrient concentration, and light penetration. This enables colonization and active metabolism by distinctive mixed communities of cold-adapted (psychrophilic) photosynthetic and heterotrophic protists and bacteria, as well as viruses. Microbial activities also alter the physicochemical conditions, mainly owing to the production of large amounts of cryoprotectant compounds and extracellular polymers, leading to the creation of additional microenvironments. The dominant photosynthetic organisms near the ice–sea interface are pennate diatoms and small dinoflagellates. The density of diatoms in sea ice may be up to 1000 times that in surface waters. Through photosynthesis, the microalgae make a small, but significant, contribution to primary productivity in the polar regions. For example, the contribution of sea ice to primary productivity in the Southern Ocean is only about 5% of the total, but it extends the short summer period of primary production and provides a concentrated food source that sustains the food web during the winter. During the Antarctic winter, microalgae on the undersurface of sea ice are the main source of food for grazing krill, shrimp-like crustaceans that are the main diet of fish, birds, and mammals in the Southern Ocean. A wide range of protists and heterotrophic bacteria have been found in sea ice, including new species with biotechnological potential. Some microbes remain active—albeit at a much reduced metabolic rate—even in the coldest parts of the ice and in “frost flowers” formed on the surface of the ice, where they are trapped in pockets of very low temperatures and high salinity.

**Microbial activity at hydrothermal vents provides an oasis of life in the deep sea**

Hydrothermal vents form a specialized and highly significant habitat for microbes. They occur mainly at the mid-ocean ridges at the boundary of the Earth’s tectonic plates, where seafloor spreading and formation of new ocean crust is occurring. Numerous such sites have been studied in the Pacific and Atlantic Oceans. Seawater permeates through cracks and fissures in the crust and interacts with the
heated underlying rocks, thereby changing the chemical and physical characteristics of both the seawater and the rock. The permeability structure of the ocean crust and the location of the heat source determine the circulation patterns of hydrothermal fluids. As cold seawater penetrates into the ocean crust, it is gradually heated along its flow path, leading to the removal of magnesium from the fluid into the rock, with production of acid during the process. This leads to the leaching of other major elements and transition metals from the rock into the hydrothermal fluid, and sulfate in the seawater is removed by precipitation and reduction to hydrogen sulfide. As the percolating fluids reach the proximity of the magma heat source, extensive chemical reactions occur within the rock and the pressurized fluids are heated to over 350°C, becoming buoyant and rising toward the ocean floor. As they rise, decompression causes the fluids to cool slightly, and precipitation of metal sulfides and other compounds occurs en route. The hydrothermal fluid is injected into the ocean as plumes of mineral-rich superheated water. The hottest plumes (up to 350°C) are generally black, because of the high content of metal sulfide and sulfate particles, and precipitation occurs as the hot plume mixes with the cold seawater. Some of these precipitates form chimney structures called “black smokers,” while others are dispersed through the water and form sediments in the vicinity. In other parts of the vent field, the circulation of hydrothermal fluid may be shallower, leading to diffuse plumes of water heated to 6–23°C (Figure 1.10). The gradients of temperature and nutrients that exist at hydrothermal systems provide a great diversity of habitats for microbes suspended in the surrounding heated waters, in sediments, and attached to surfaces of the chimneys. Many of these are hyperthermophilic bacteria and archaea, which can grow at temperatures up to 121°C, whilst others grow at lower temperatures further from the fluid emissions. Molecular studies are revealing an astonishing diversity of such organisms, many of which have biotechnological applications. The microbiology of the deep subsurface rocks beneath vents is also now under investigation, and many novel microbes and metabolic processes are being discovered. Microbial activity in the deep subsurface contributes to the chemical changes in composition during circulation of the hydrothermal fluids.

Hydrothermal vent systems were first described in 1977, when scientists aboard the submersible Alvin, from Woods Hole Oceanographic Institution, were exploring the seafloor about 2500 m deep near the Galapagos Islands. The discovery of life around the vents was totally unexpected. The Alvin scientists observed dense communities of previously unknown animals, including tube worms, clams, anemones, crabs, and many others (see Plate 10.3). Subsequent research showed that the warm waters near hydrothermal vents contain large populations of chemo-synthetic bacteria and archaea, which fix CO2 using energy from the oxidation of sulfides in the vent fluids. This metabolism supports a food chain with many trophic levels that is independent of photosynthesis. We now know that many of the animals at vent sites contain chemosynthetic bacteria as symbionts within their tissues or on their surfaces—these relationships are discussed in Chapter 10. In addition, bacterial populations directly support the growth of filter-feeding animals, such as clams and mussels, or shrimps, which graze on microbial mats. Thus, hydrothermal vents are an oasis of life in the deep sea. Previously, life was thought always to rely ultimately on the fixation of CO2 by photosynthesis, but the vent communities function without the input of material derived from the use of light energy. However, note that sulfide oxidation depends on dissolved oxygen in the water, and the origin of this is photosynthetic.

**Cold seeps also support diverse life**

Cold seeps are abundant along the continental shelf and slope, where the upwards percolation of fluids through the sediments is influenced by plate tectonics and other geological processes. At these sites, high concentrations of methane and sulfide support prolific chemosynthetic communities consisting of free-living
bacteria and archaea, as well as those living symbiotically with invertebrates (Chapter 10). Extensive populations of foraminifera also occur at cold seeps. Some sites are associated with seeps of hypersaline brines or hydrocarbons.

**Living organisms are the habitats of many microbes**

Microbial biofilms also form on the surfaces of all kinds of animals, algae, and coastal plants, which provide a highly nutritive environment through secretion or leaching of organic compounds. Many organisms seem selectively to enhance surface colonization by certain microbes and discourage colonization by others. This may occur by the production of specific compounds that inhibit microbial growth or interfere with microbial attachment processes. Once established, particular microbes may themselves influence colonization by other types. These processes offer obvious applications in the control of biofouling (see p. 282). As well as surface (epibiotic) associations, microorganisms can form endosymbiotic associations within the body cavities, tissue, or cells of living organisms.

Many microalgae such as diatoms and dinoflagellates harbor bacteria on their surfaces, or as endosymbionts within their cells. Intimate associations between bacterial and archaeal cells are also being revealed by new imaging techniques (see Plate 5.1). Seaweeds and seagrasses have dense populations of bacteria (up to $10^6$ per cm$^2$) on their surfaces, although this varies considerably with species, geographic location and climatic conditions.

The external surfaces and intestinal content of animals provide a variety of habitats to a wide diversity of microbes. Such associations may be neutral in their effects, but commonly lead to some mutual benefit for host and microbe (symbiosis). Examples of symbiotic interactions between animals and microbes are considered in Chapter 10, whilst diseases of marine organisms are discussed in Chapter 11.
Conclusions

This chapter has introduced the marine environment and the various types of marine microbes that are found. The adaptations of marine microbes to the different physical, chemical, and biological conditions encountered in the wide range of marine habitats have led to the evolution of highly diverse microbes. The discovery that these tiny microbes are present in such large numbers and are largely responsible for the biogeochemical processes that shape our planet can be viewed as one of the most important advances of modern science. Subsequent chapters build on this introduction by exploring the mechanisms underlying this diversity of form and function.

References


Microbes in the Marine Environment


Further reading

Historical perspectives

Microbial diversity and evolution

Microscale processes, marine snow, and dissolved organic matter


Sea-ice microbiology and polar oceans

Sediments and subsurface microbiology

Hydrothermal vents