Ecology of Microorganisms in Saline Waters (Seas and Oceans)

6

Abstract

The waters of the seas and oceans of the world contain large amounts of solutes; mainly, salt of about 3.5 g/L, occupy about 71% of the earth's surface and have an average depth of 3.8 km. The photic zone of seas and oceans, about 200 m deep, is the region permeated by sunlight where photosynthesis can take place. It has the greatest biodiversity, and all food for the marine population arises from the photic zone; such food includes marine snow which consists of globules of mucopolyssacharides containing dead and living microorganisms floating downward toward the deep ocean. Marine organisms are adapted to the unique conditions found in the marine open sea (pelagic zone) environment: high salinity (3.5 g/L), low temperature (about 4°C), and high barometric pressure of up to 500 bar depending on the depth. Thermophilic organisms grow near the occasional hot thermal vents where hot magma spews out onto the ocean floor.

Using the technique of 16S rRNA, it has been found that over 70% of marine bacteria have not been cultured and hence have no counterparts among known bacteria. Microscopic cyanobacteria (picophytoplankton) make up 15% of all the bacteria. Among them, *Synechoccus* and *Prochlorococcus,* predominate and constitute the most abundant photosynthetic microbes on earth, contributing more than 50% of the total marine photosynthesis. Of the cultivated bacteria, *Roseobacter* spp. form about 15% of the total bacteria, while green non sulfur bacteria make up about 6%.

Keywords

Marine environment • Hydrothermal vents • Pelagic zone • Marine snow • Microbial loop • Redfield ratio • Nitrogen transformations in the ocean • *Pelagibacter ubique* • Marine viruses • Global marine nutrient recycling • Marine organisms and global climate change • Dimethyl sulfide (DMS) • Albedoes • Ammonnox

6.1 The Ocean Environment

Saline waters are waters with high concentrations of dissolved solutes, mostly salt, NaCl. The US Geological Survey classifies saline waters into three: Slightly saline, 1,000–3,000 ppm (1–3 g/L), moderately saline, 3,000–10,000 ppm (3–10 g/L) and highly saline water 10,000–35,000 ppm of solutes (10–35 g/L). Seawater has a salinity of about 35 g/L (Table 6.1).

The seas and oceans constitute planet earth's principal component of the hydrosphere: A major body of saline water that, in totality, covers about 71% of the

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Table 6.1 Concentrations of the 11 most abundant constituents in sea water (From Allaby and Allaby 1990. With permission)

Constituent	Ion symbol	Parts per thousand by weight (g/kg)	Percentage of dissolved material
Chloride	Cl^-	18.980	55.05
Sodium	Na^+	10.556	30.61
Sulfate	SO_4^{2-}	2.649	7.68
Magnesium	Mg^{2+}	1.272	3.69
Calcium	Ca^{2+}	0.400	1.16
Potassium	K^+	0.380	1.10
Bicarbonate	HCO_3^-	0.140	0.41
Bromide	Br^-	0.065	0.19
Borate	$H_3BO_3^-$	0.026	0.07
Strontium	Sr^{2+}	0.008	0.03
Fluoride	F^-	0.001	0.00
Total		34.447	99.99

earth's surface (or an area of some 361 million square kilometers). The average depth of the oceans is 3.8 km, but a number of deep sea trenches exist. The deepest sea trench is Marianas Trench, 11 km deep, in the Pacific Ocean. Though somewhat arbitrarily divided into several "separate" oceans, these waters comprise one global, interconnected body of salt water often referred to as the World Ocean or global ocean. The major oceanic divisions are defined in part by the continents, various archipelagos, and a number of other criteria; these divisions are (in descending order of size) the Pacific Ocean, the Atlantic Ocean, the Indian Ocean, the Southern Ocean (which is sometimes subsumed as the southern portions of the Pacific, Atlantic, and Indian Oceans), and the Arctic Ocean (which is sometimes considered a sea of the Atlantic). Smaller regions of the oceans are called seas, gulfs, bays, and other names (see Fig. 1.6).

There are also some smaller bodies of salt water that are inland and not interconnected with the World Ocean; e.g., the Caspian Sea, the Aral Sea, and the Great Salt Lake. These are not considered to be oceans or parts of oceans, though some are called "seas."

The ocean floor contains large mountain ridges and most, and about 90%, of the earth's volcanic activity take place in these undersea mountains.

The total mass of the hydrosphere is about 1.4×10^{21} kg, which is about 0.023% of the earth's total mass. Less than 2% of the earth's waters or hydrosphere is freshwater; the rest is saltwater, mostly found in the oceans. Some features peculiar to the ocean environment are described below.

1. *Hydrothermal vents* are hot water fountains which occur on the sea floor. They continuously gush out super-hot, mineral-rich water that supports a diverse community of organisms. Although most of the deep sea is sparsely populated, vent sites teem with a wide array of life, including bacteria. Hydrothermal vents were discovered in 1977 in the Pacific Ocean, and have since been found in the Atlantic, the Indian, and the Arctic Oceans. They occur at depths of about 2,100 m in areas of seafloor spreading along the Mid-Ocean Ridge system – the underwater mountain chain that occurs around the globe. They form when the huge plates that form the earth's crust move apart, causing deep cracks in the ocean floor. Seawater seeps into these openings and is heated by the molten rock, or magma, beneath the crust. When the hot springs gush out into the ocean, their temperature may be as high as 360°C, but the water does not boil because it is under so much pressure from the tremendous weight of the ocean above. Hydrothermal vents support the growth of many organisms which live in complete darkness, including many thermophilic bacteria and Archae which grow at temperatures as high as 112°C.
2. *Cold seeps* (also called *cold vents*) are areas of the ocean floor where hydrogen sulfide, methane, and other hydrocarbon-rich fluid seepage occur. Cold seeps are distinct from hydrothermal vents in that their temperature is same as the surrounding sea water. Chemoautotrophic Archae and bacteria, utilize sulfides and methane therein for energy and

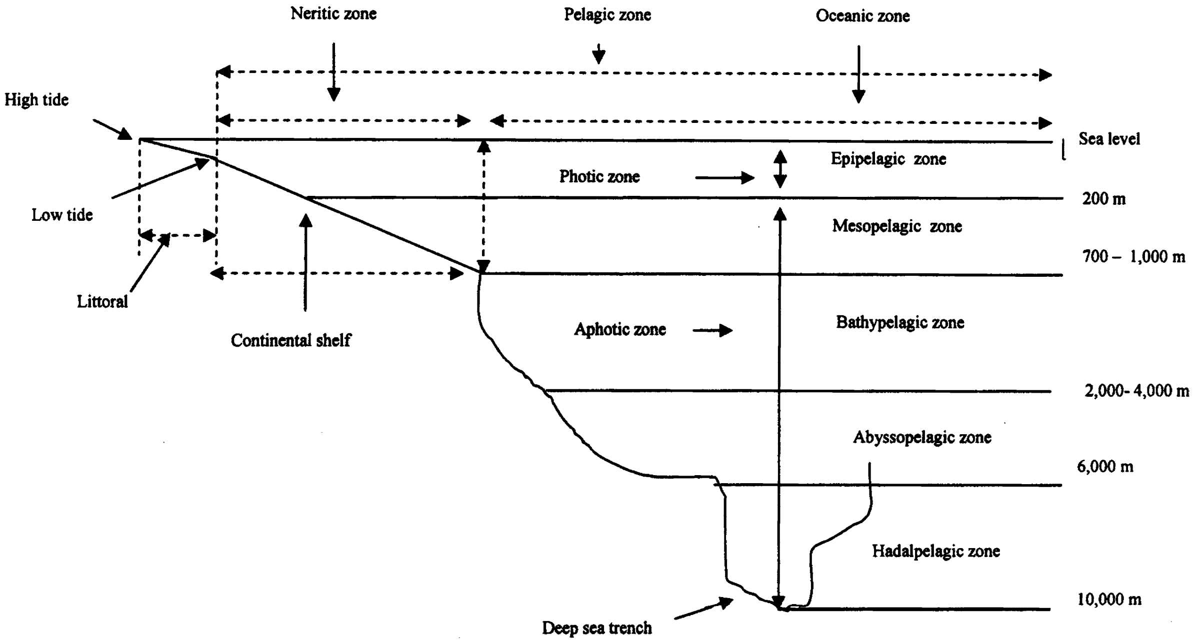

Fig. 6.1 Schematic illustration of ecological zones of the oceans, showing marine microbial habitats (Not drawn to scale)

growth. A unique biological community subsisting in the dark develops through the use of chemosynthesis to produce chemical energy. Higher organisms, namely vesicomyid clams and siboglinid tube worms, which harbor these bacteria, use this energy to power their own life processes, and in exchange provide both safety and a reliable source of food for the bacteria. Other bacteria form mats, blanketing sizable areas in the process.

Unlike hydrothermal vents, which are volatile and ephemeral environments, cold seeps emit at a slow and dependable rate. Perhaps owing to the differing temperatures and stability, cold seep organisms are much longer-lived than those inhabiting hydrothermal vents. Indeed, the seep tubeworm *Lamellibrachia luymesi* is believed to be the longest living noncolonial invertebrate known, with a minimum lifespan of between 170 and 250 years.

Cold seeps were first discovered in 1984 in the Gulf of Mexico at a depth of 3,200 m. Since then, seeps have been discovered in other parts of the world. The deepest seep community known is found in the Japan trench at a depth of 7,326 m.

3. *The continental shelf s*urrounds the continents and is a shallow extension of the landmass of a continent. This shelf is relatively shallow, tens of meters deep compared to the thousands of meters of depth in the open ocean, and extends outward to the continental slope where the deep ocean truly begins. Sediment from the erosion of land surfaces, washed into the sea by rivers and waves, nourishes microscopic plants and animals. Larger animals then feed upon them. These larger animals include the great schools of fish, such as tuna, menhaden, cod, and mackerel, which humans catch for food. The continental shelf regions also contain the highest amount of benthic life (plants and animals that live on the ocean floor). Combined with the sunlight available in shallow waters, the continental shelves teem with life compared to the biotic desert of the oceans' abyssal plain. The pelagic (water column) environment of the continental shelf constitutes the neritic zone, and the benthic (sea floor) province of the shelf is the sublittoral zone (see Fig. 6.1).

   The continental slope connects the continental shelf and the oceanic crust. It begins at the continental shelf break (see Fig. 6.1), or where the bottom sharply drops off into a steep slope. It usually begins at 430 ft (130 m) depth and can be up to 20 km wide. The continental slope, which is still considered part of the continent, together with the continental shelf is called the continental margin.

Beyond the continental slope is the continental rise. As currents flow along the continental shelf and down the continental slope, they pick up and carry sediments along and deposit them just below the continental slope. These sediments accumulate to form the large, gentle slope of the continental rise.

Most commercial exploitation of the sea, such as oil and gas extraction, takes place on the continental shelf. Sovereign rights over their continental shelves were claimed by the marine nations that signed the Convention on the Continental Shelf drawn up by the UN's International Law Commission in 1958 partly superseded by the 1982 United Nations Convention on the Law of the Sea.

4. The *zones of the seas and oceans* are as follows: The *pelagic zone* (see Fig. 6.1) is the part of the open sea or ocean that is not near the coast or sea floor. In contrast, the demersal zone comprises the water that is near to (and is significantly affected by) the coast or the sea floor. The pelagic zone (also known as the open-ocean zone) is further subdivided, creating a number of subzones. These subzones are based on their different ecological characteristics, which roughly depend on their depth and the abundance of light. The subzones of the pelagic zone are as follows:
   - (a) *Epipelagic* (from the surface down to around 200 m) – the illuminated surface zone where there is enough light for photosynthesis. Due to this, marine plants and animals are largely concentrated in this zone. Here, one will typically encounter fish such as tuna and many sharks. This zone is also known as the *photic (sunlight) zone.* This is the region where the photosynthesis most commonly occurs and therefore contains the largest biodiversity in the ocean, including bacteria. Any life found in regions of the sea lower than the photic zone must either rely on material floating down from above known as *marine snow (*see below). Zones of the seas and oceans lower than the photic, or 200 m, are the *aphotic zone*.
   - (b) *Mesopelagic* (from 200 m down to around 1,000 m) – the twilight zone. Although some light penetrates this deep, it is insufficient for photosynthesis. The name stems from Greek for *middle*. Its lowermost boundary has a temperature of about10°C, and, in the tropics generally lies between 700 and 1,000 m.
   - (c) *Bathypelagic,* from the Greek for *deep* (from 1,000 m down to around 4,000 m) – by this depth, the ocean is almost entirely dark (with only the occasional bioluminescent organism). There are no living plants, and most animals survive by consuming the "snow" of detritus falling from the zones above, or (like the marine hatchetfish) by preying upon others. Giant squid live at this depth, and here they are hunted by deep-diving sperm whales. The temperature lies between 10°C and 4°C.
   - (d) *Abyssopelagic* (from 4,000 m down to above the ocean floor) – no light whatsoever penetrates to this depth, and most creatures are blind and colorless. The name is derived from the Greek for *abyss*, meaning bottomless (because the deep ocean was once believed to be bottomless).
   - (e) *Hadopelagic* (the deep water in ocean trenches) – the name is derived from *Hades*, the classical Greek underworld. This lies between 6,000 m and 10,000 m and is the deepest oceanic zone. This zone is relatively unknown and very few species are known to live here (in the open areas). However, many organisms live in hydrothermal vents in this and other zones.

   The bathypelagic, abyssopelagic, and hadopelagic zones are very similar in character, and some marine biologists put them into a single zone or consider the latter two to be the same. Some define the hadopelagic as waters below 6,000 m, whether in a trench or not.

   The pelagic (open sea) zone can also be split into two subregions, the *neritic* zone and the *oceanic* zone. The neritic encompasses the water mass directly above the continental shelves, while the oceanic zone includes all the completely open water. In contrast, the *littoral* zone covers the region between low and high tide and represents the transitional area between marine and terrestrial conditions. It is also known as the *intertidal* zone because it is the area where tide level affects the conditions of the region.

5. *Marine snow* is found in the deep ocean. It is a continuous shower of mostly organic detritus falling from the upper layers of the water column. This continuous shower appeared to deep sea divers like flakes of snow, hence the name. Marine snow is a mucopolysaccharide matrix, extracellular product released marine organisms, especially bacteria and phytoplankton, in which living and dead organisms and their parts are embedded. The origin of marine snow lies in activities within the productive photic (epipelagic) zone. Consequently, the prevalence of

marine snow changes with seasonal fluctuations in photosynthetic activity and ocean currents. Thus marine snow is heavier in the spring, and the reproductive cycles of some deep-sea animals are synchronized to take advantage of this (Anonymous 2010a).

Many marine snow "flakes" are sticky and fibrous like a crumbled spider net, and particles easily adhere to them, forming aggregates. Marine snow is composed of tiny leftovers of animals, plants (plankton), and non-living matter in the ocean's sun-suffused upper zones. Among these particles are chains of diatoms, shreds of protozoan mucous food traps, soot, fecal pellets from upper ocean zooplankton, dust motes, radioactive fallout, sand grains, pollen, and microorganisms which live inside and on top of the flakes. An aggregate begins to sink when it attracts fecal pellets, foraminifera (coats) tests, airborne dust, and other heavier particles. Many zooplankton fecal pellets are covered with a thin coating material. Although individual particles sink very slowly or are even buoyant, when they are bundled into a tight package and ballasted with particles of calcite – one of the densest materials produced in the ocean – they sink as rapidly as 100–200 m a day. As it descends, more suspended particles are added, making the aggregate even heavier and thus faster moving. An aggregate may break apart, spilling its contents into the water, but soon the spilled particles are picked up or "scavenged" by other falling aggregates. Thus aggregates are reorganized constantly with individual particles jumping on and off them before they arrive on the ocean floor. Meanwhile, a large portion of the organic matter in marine snow is recycled by microorganisms and upper and middle water column animals which again generate fecal pellets. Local concentrations of protozoa, principally bacterivorous flagellates and *ciliates*, are found associated with "marine snow."

The "snowflakes" (which are more like clumps or strings) are aggregates of smaller particles held together by a sugary mucus, transparent exopolymer particles (TEPs); natural polymers exuded as waste products by bacteria and phytoplankton. These aggregates grow over time and may reach several centimeters in diameter, traveling for weeks before reaching the ocean floor. Marine snow is everywhere in the ocean, and sometimes, it reaches blizzard proportions, and divers cannot see beyond a few feet

Most organic components of marine snow are consumed by microbes, zooplankton, and other filter-feeding animals within the first 1,000 m of their journey. In this way, marine snow may be considered the foundation of deep-sea mesopelagic and benthic ecosystems. Because sunlight cannot reach them, deep-sea organisms rely heavily on marine snow as an energy source. The small percentage of material not consumed in shallower waters becomes incorporated into the muddy ocean floor, where it is further decomposed through biological activity. Bacteria transported within the flakes may exchange genes with what were previously thought to be isolated populations of bacteria inhabiting the breadth of the ocean floor. The ocean bacteria are also now being exploited as sources of new pharmaceutical bioactive products (Fig. 6.2).

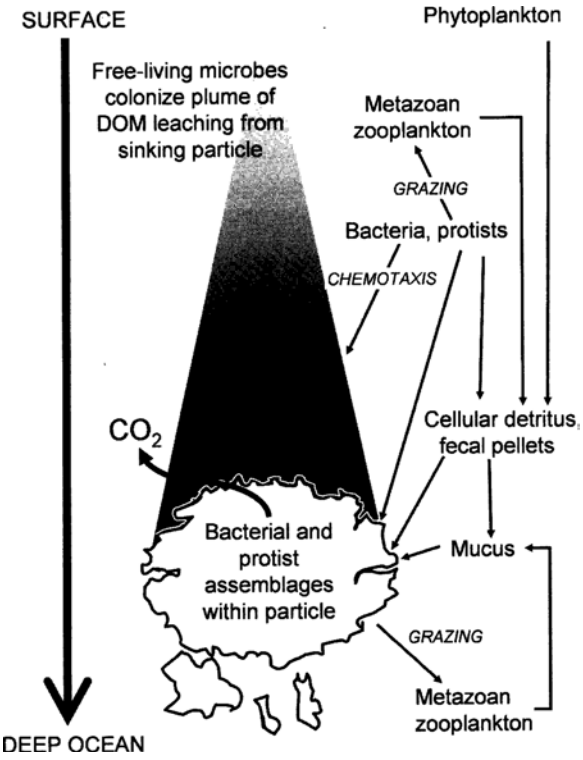

Fig. 6.2 Formation of and fate of marine snow (From Munn 2004. With permission)

6.2 Some Properties of Sea Water

6.2.1 Salinity

Sea water is slightly alkaline (pH 7.5–8.4), with numerous chemicals, organic and inorganic, and gases dissolved in it. The concentration of these varies according to geographic and physical factors and is generally referred to as salinity. Salinity is defined as the mass of materials dissolved in 1 kg of sea water (denoted as salinity per thousand, 0/00). The global average salinity of ocean waters is about 35 g/kg. Oceans in subtropical regions have higher salinity due to higher evaporation, while those in tropical areas are lower due to dilution by higher rainfall. In coastal areas, salinity is diluted by runoffs and rivers. The major ions of sea water are sodium, chloride, magnesium, calcium, and potassium (see Table 6.1).

Salinity, along with temperature, affects the density and thus stability of the water column. In turn, this greatly affects many biological processes in the upper ocean. Saltier water is more dense and thus tends to sink below fresher water. The source of a water mass can be determined from its salinity and temperature. Ocean salinity is measured, either in situ by measuring conductivity or sea water through an instrument lowered from a ship, or by chemical analysis when water is brought to the laboratory.

6.2.2 Temperature

The temperature of deep sea water at 35/00 is −1.9°C. Oxygen and CO_2 are more soluble in cold water and are more abundant at 10–20 m of the sea and this affects the living things in the ocean. The concentration of these gases increases with depth until about 1,000 m when anaerobic conditions set in.

The surface temperatures of sea water in tropical regions can be as high as 25–30°C giving rise to temperature differences in density between surface waters at deep sea waters; the temperature dropping to about 10°C at 150–200 m. In Arctic regions, the water remains cold for most of the year; temperate regions show great variations in the temperature, being warmer in summer and cold in winter

The temperature is fairly uniform at the top layers of the sea, about 20–30°C, depending on the part of the world; this top layer is known as the *mixed layer.* In the deep sea, the temperature is low and fairly uniform. The transition zone between the mixed layer and the deep sea is the thermocline. In the thermocline, the temperature decreases rapidly from the mixed layer temperature to the much colder deep water temperatures, which vary from 0°C to about 3°C. The thermocline varies with latitude and season; it is permanent in the tropics, variable in the temperate climates (strongest during the summer), and weak to nonexistent in the polar regions, where the water column is cold from the surface to the bottom. In the earth's oceans, 90% of the water is below the thermocline (Anonymous 2003) (Fig. 6.3).

As will be seen below, temperature, along with salinity, affects the density and thus the stability of the

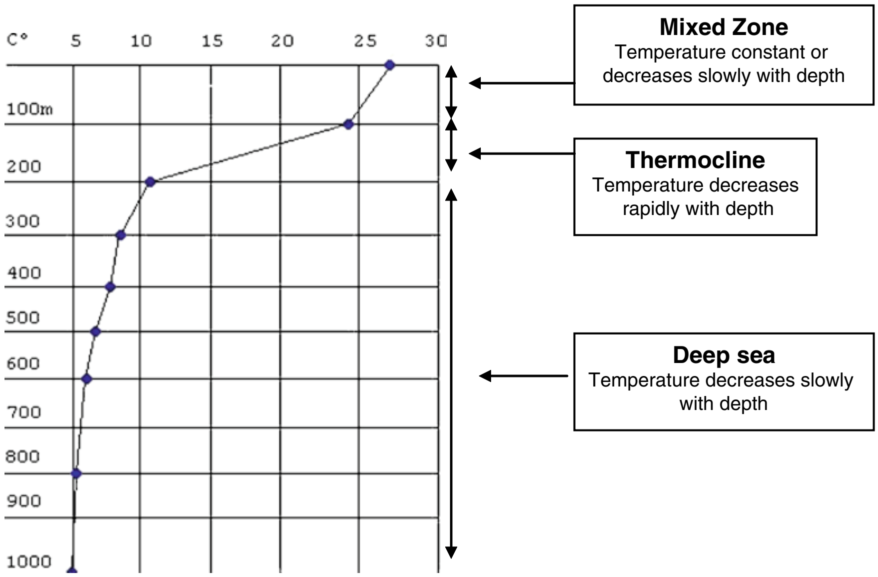

Fig. 6.3 The oceanic temperature profile showing temperatures in the mixed zone, the thermocline and the deep sea (Modified from http://www.windows2universe.org/earth/Water/temp.html; Anonymous 2010b)

water column. Warmer water is less dense and thus tends to stay on top of colder water. During winter, storm winds mix the water column, and the temperature is more uniform in the top – several 100 m. As spring approaches, increasing solar radiation warms the surface waters and this warmer, buoyant water stays on top. This increases the stability of the water column, preventing deeper, nutrient-rich water from being mixed into the surface from below. The stable surface layer keeps the planktonic cyanobacteria and algae near the surface where there is plenty of light. Under this situation, nutrients brought to the surface by winter mixing encourages the rapid growth of the organisms and spring bloom may occur.

Marine organisms are also adapted to live at different temperatures, which can thus determine the diversity or the numbers of organisms at different levels of the water column. As temperature changes with season and location, the diversity and numbers of organisms also change.

Temperature data are recorded in situ with instrumentation lowered from a ship; the temperature is instantaneously recorded at various depths of the water column (Anonymous 2010b).

6.2.3 Light

Light has a major influence on the distribution of photosynthetic organisms. Light is generally limited to the upper 150–200 m or the photic region. Blue light has the deepest penetration in sea water and photosynthetic organisms at the lowest level of the photic region have mechanisms with which they are able to collect blue light. The relationship between light in the ocean with temperature and depth are depicted in Fig. 6.4.

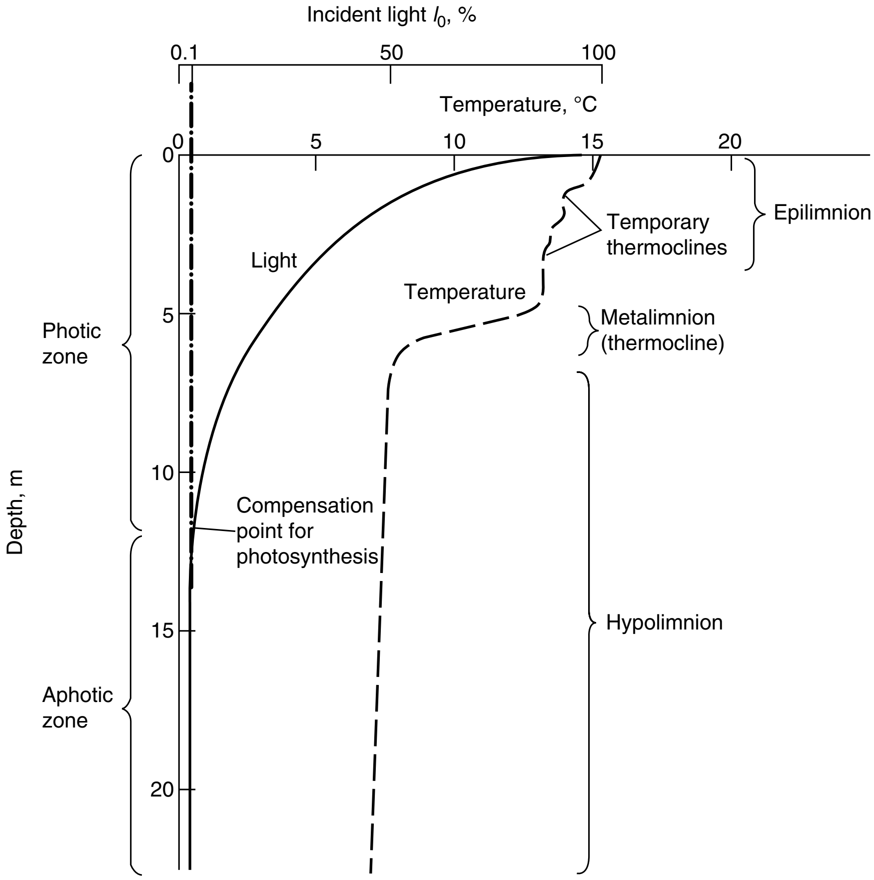

Fig. 6.4 Relationship between light, temperature and increasing depth in the ocean (Modified from http://www.windows2universe.org/earth/Water/temp.html; Anonymous 2010b)

6.2.4 Nutrients

Dissolved organic matter (DOC) is an important source of nutrition for marine bacteria; most of the organic carbon in the sea is in a dissolved form. As can be seen from the microbial loop concept, much of the DOC results from materials released when viruses attack microorganisms (Pomeroy 1974).

In addition to DOC, sea water contains many floating and sinking particles. Collectively, these tiny particles contain large amounts of carbon (particulate organic carbon, POC), and nitrogen (particulate organic nitrogen, PON), which supply nutrients to marine organisms.

Because light only penetrates a few hundred meters into the sea, no photosynthetic organisms occur in the ocean's permanently dark depths. Thus there are no organisms in these regions to remove nutrients from the water, and the ocean's deeper waters tend to be enriched in nutrients compared to its surface waters. Upwelling brings nutrients from the ocean depths to the sunlit surface waters where they can be used by photosynthesis. In some areas of the world's oceans for example, the Sargasso Sea, nutrients are not replenished continually, and phytoplankton can often use them up. These regions become nutrient-poor "ocean deserts" at certain seasons of the year.

6.2.5 Oxygen and CO_2 in the Marine Environment

Oxygen is needed by aerobic living things in the seas and oceans, from bacteria to fish to whales. Oxygen enters the ocean in two main ways: It diffuses into the ocean surface from the atmosphere, and it is produced by photosynthetic marine organisms. The amount of oxygen in the water is controlled by the temperature, as well as by the quantity produced photosynthetically.

Oxygen data are collected by chemical sensors, which work by binding to oxygen molecules. The bound oxygen can be determined by titration.

Carbon dioxide is a greenhouse gas that diffuses into the ocean surface from the atmosphere, and is taken up by marine photosynthetic organisms. The magnitude of the greenhouse effect depends on the amount of carbon dioxide in the atmosphere and how much carbon dioxide the oceans can take up from the atmosphere. Uptake of carbon dioxide by the oceans is affected by the temperature of the water because colder water holds more gas, and by the abundance of photosynthetic organisms.

6.2.6 Sea Sediments

Billions of tons of sediment accumulate in the ocean basins every year. The nature of such sediments may be indicative of climate conditions near the ocean surface or on the adjacent continents. Sediments are composed of both organic and inorganic materials.

The organic component of sea sediment includes the remnants of sea-dwelling microscopic plankton, which provide a record of past climate and oceanic circulation. For example, by studying the chemical composition of plankton shells, we can reveal information about past seawater temperatures, salinity, and nutrient availability. Indeed, such techniques have been used to reconstruct ocean temperatures over the last 100 Ma, and have confirmed continental drift theories of climate change that a long term global cooling has taken place since the extinction of the dinosaurs.

Most inorganic material comes from adjacent landmasses, eroded from rocks and washed down to the coast by river channels, or blown from soils, dusty plains, and deserts. The nature and abundance of inorganic materials provides information about how wet or dry the nearby continents were, and the strengths and directions of winds.

6.3 Microbial Ecology of the Seas and Oceans

In the open ocean, far from the influences of coastal human habitation, sea water still contains huge numbers of microbes: bacteria, archae, protozoa, algae, fungi, and viruses. The presence and significance of these organisms will be discussed below. Coastal areas can contain even greater concentrations.

6.3.1 Bacteria

Using the technique of 16S rRNA it has been found that over 70% of marine bacteria have not been cultured and hence have no counterparts among known bacteria. As shown in Fig. 6.5, SAR11, SAR116,

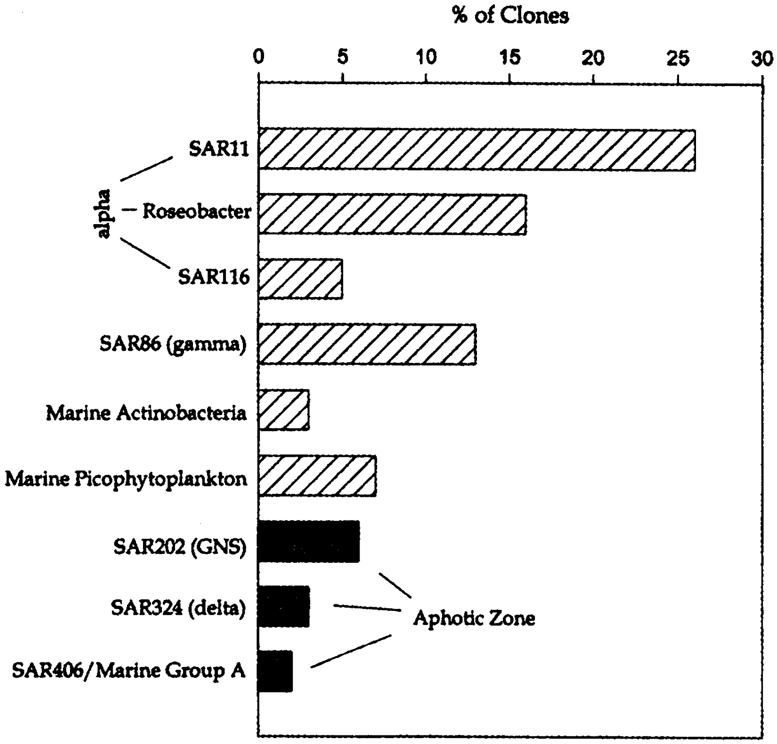

Fig. 6.5 Frequency of the most common marine bacteria based on 16 S rRNA (From Giovannoni and Rappe 2000. With permission)

SAR86, SAR324, and SAR406, all of which do not have known cultivated counterparts make up about 70% of the bacteria. Microscopic cyanobacteria (picophytoplankton) make up 15% of all the bacteria. Of the cultivated bacteria, *Roseobacter* spp. form about 15% of the total bacteria, while green non sulfur bacteria make up about 6%. About 90% of the bacteria are Gram negative; Gram positive Actinobacteria form 3% of the total. Most of the sea bacteria belong to the Proteobacteria: SAR11, Roseobacter, and SAR116 belong to the "α" sub group, while SAR86 and SAR324 belong to "γ" and "δ" sub groups respectively (Irenewagner-D Obler and Biebl 2006).

SAR11 is ubiquitous and widely distributed at all levels of the pelagic zone from the shallow coastal waters to depths of about 3,000 m. SAR116 appears to be confined to the upper portion of the oceans.

SAR-11 was isolated from the Sargasso Sea in 1990 using the r RNA gene. It is said to be so dominant in the sea (about 10^{28}/ml) that its combined weight is more than that of the fishes put together. It was cultivated in 2002 and tentatively designated as a single species, *Pelagibacter ubique.* It belongs to the α-Proteobacteria, and the Order Rickettsiales. It is one of the smallest cells known, being only 0.37–0.89 μm long and 0.12–0.20 μm in diameter. It has very few genes (1,354) while humans have 18,000–25,000. It has no superfluous genes and uses base pairs with less nitrogen, since nitrogen is relatively difficult to obtain by biological objects. All these make the organism very efficient (Fig. 6.5).

Most of the bacteria are in the photic zone, while SAR202 (green non sulfur bacteria), SAR324 and SAR406 are confined to the aphotic zone.

Of the cyanobacteria found in marine environments, two genera, *Synechoccus* and *Prochlorococcus,* predominate and constitute the most abundant photosynthetic microbes on earth, contributing more than 50% of the total marine photosynthesis. *Prochlorococcus* occurs ubiquitously in surface waters between latitudes 40°N and 40°S. *Synechococcus* occurs more widely, but it decreases in abundance beyond 14°C; *prochlorococcus* is about ten times more abundant than *Synechococcus.* Some cyanobacteria encountered in the marine environment are depicted in Fig. 6.6.

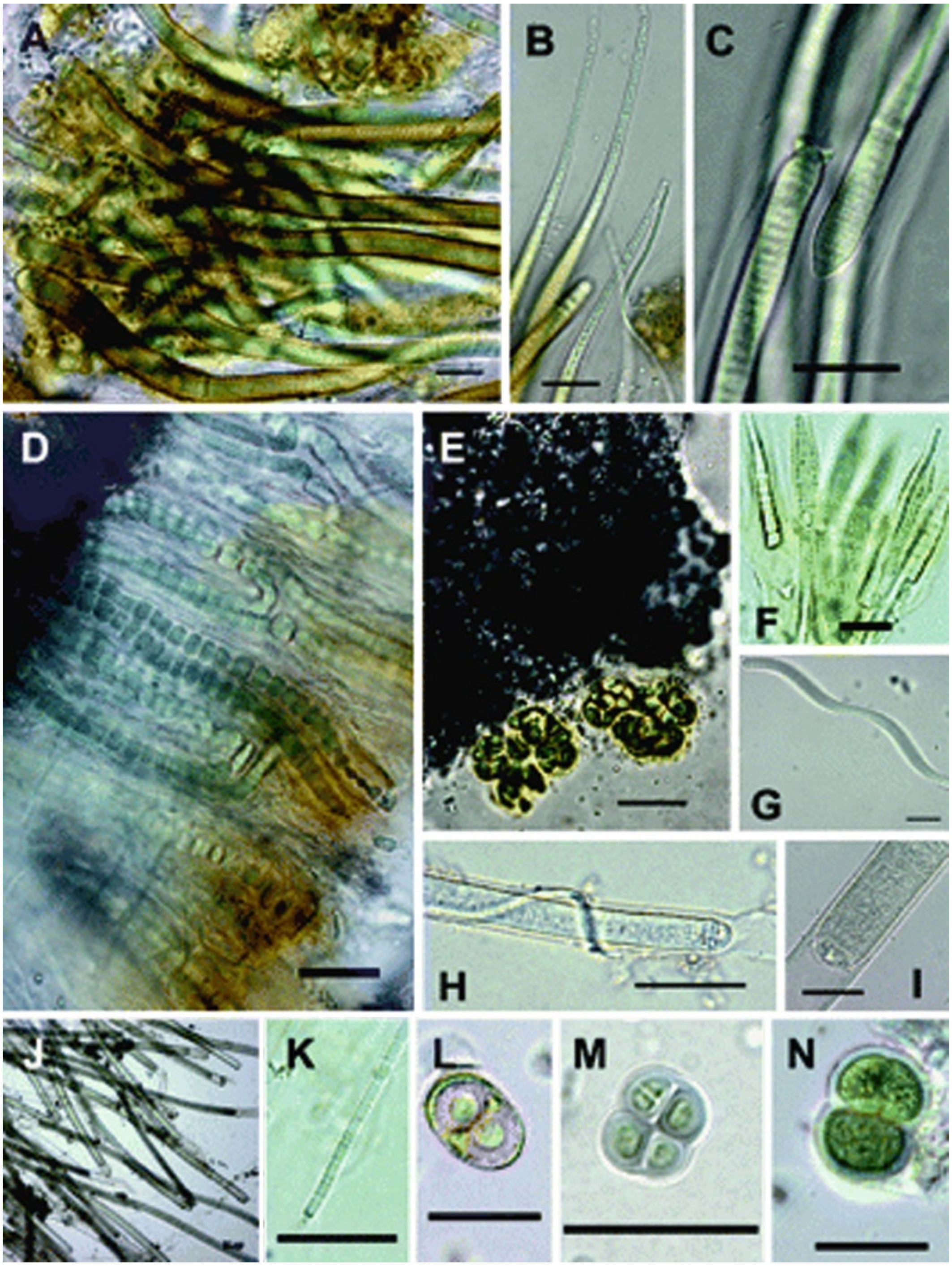

Fig. 6.6 Cyanobacteria found in a tropical marine environment. (**a**) *Calothrix* species 1, (**b**) *Calothrix* species 1, (**c**) *Blennothrix* sp., (**d**) *Kyrtuthrix* sp., (**e**) *Enthophysalis* species 1, (**f**) *Calothrix* species 2, (**g**) *Arthrospira* sp., (**h**) *Lyngbya* species 2, (**i**) *Lyngbya* species 1, (**j**) *Lyngbya* species, (**k**) *Pseudanabaenaceae* family (?), (**l**) *Gloeocapsa* sp., (**m**) *Chroococcidiopsis* sp (?), (**n**) *Chroococcus* sp.
Scale bar = 20 μm. (j) Scale bar = 50 μm (From Díez et al. 2007. With permission)

6.3.2 Archae

Archae are divided into, Euryacheota and Crenarcheota. Several groups of Archae have been found in the sea.

Euryacheota contains methanogens, and hyperthermophilic and hyperhalophilic members.

Methanogens are strict anaerobes and produce methane. Thermophilic methanogens are found in thermophilic vents in the deep sea. *Methanococcus jannaschi* and *Methanococcus pyrus* are found in hydrothermal vents; the latter are among the most thermophilic organisms known, being able to grow at 110°C.

Hyperthermophilc Archae have optimal temperatures of growth of 100°C. They include *Thermococcus celer* and *Pyrococcus furiosus*.

Hyperhalophilic Archae can grow in salt concentrations of more than 9%. Examples are *Halobacterium, Halococcus*, and *Halomegaterium*.

The Crenarcheota are also found in thermophilic vents. *Desulfurococcus* is found in the upper layers of thermophilic vents, where the temperature is highest and is the most thermophilic organism known, being able to grow at 113°C.

6.3.3 Fungi

Fungi of all classes have been encountered in the marine environment, from Phycomycetes through Ascomycetes and Deuteromycetes to Basidiomycetes. In nearly all the cases, they are found attached to dead matter and in some cases, living matter, occasionally as parasites. Thus, the Phycomycete *Atkinsiella dubia,* has been found parasitizing eggs of crabs, while a strain of the plant pathogenic Phycomycete, *Pythium* sp, has been found growing on the marine brown red alga, *Porphyra*. When cultivated in the lab, many marine phycomycetes fail to complete their life history unless sea water or a high (4%) salt concentration is used.

The other three fungal groups Ascomycetes, Fungi Imperfecti, and Basidiomycetes occur in the marine environment in the above order of abundance on live plants or inanimate debris. In the mangrove swamp of *Rhizophora apiculata,* there is vertical distribution of different fungi. Thus some fungi are limited to upper zones of tidal flow, such as *Pyrenographa xylographoides, Julella avicennia,e* and *Aigialus grandis*, while others are found at lower reaches of the tidal ebb such as *Trichocladium achrasporum* and *T. alopallonellum.*

Around the world in both temperate and tropical regions, numerous fungi in the three groups have been found in the order given above on detritus in the intertidal regions of coastal areas on leaves, seaweeds, seagrass, chitinous substrates, even on sand (the *arenicolous* or sand-dwelling fungi), but most frequently on decaying wood. Some of the fungi encountered include *Torpedospora radiate, Antennospora quadricornuta*, *Clavatospora bulbosa*, *Crinigera maritima*, *Periconia prolifica,* and *Torpedospora radiata.*

As has been seen, the most abundant filamentous marine fungi are Ascomycetes. Marine Ascomycetes are peculiar in that their spores show adaptation to the marine ecosystem in the production of appendages, which facilitate buoyancy in water, entrapment, and adherence to substrates. The filamentous ascomycete *Halosphaeria mediosetigera* and the deuteromycete *Culcitalna achraspora* are designated marine and are able to grow in natural and artificial seawater media. Marine fungi are generally able to grow on woody materials in the ocean (see Fig. 6.7).

Fungi are the principal degraders of biomass in most terrestrial ecosystems. Fungi are usually found on drifting wood in the oceans or in the interstitial regions. They decompose the wood making it more available to other inhabitants of the marine ecosystem.

In contrast to surface environments, however, the deep-sea environment (1,500–4,000 m; 146–388 atm) has been shown using fungal-specific 18S rRNA gene analysis to contain very few fungi, which occur mainly as yeasts.

Culturable fungi recovered from sediments and bottom of the deep sea have been found to require salt concentrations of up to 4% and barometric pressures of up to atm 500 bar hydrostatic pressures at 5°C. Among them are strains of the Deuteromycete *Aspergillus sydowii* and the phycomycete *Thraustochytrium globosum.*

6.3.4 Algae

Marine algae vary from tiny microscopic unicellular forms of 3–10 μm (microns) to large macroscopic multicellular forms up to 70 m long and growing at up to 50 cm per day, kwon as seaweeds. Seaweeds include Green algae (Chlorophyta), Brown algae (Phaeophyta), Red algae (Rhodophyta) and some filamentous Blue-green algae (Cyanobacteria). Most of the seaweeds are red (6,000 species) and the rest known are brown (2,000 species) or green (1,200 species). Seaweeds are used in

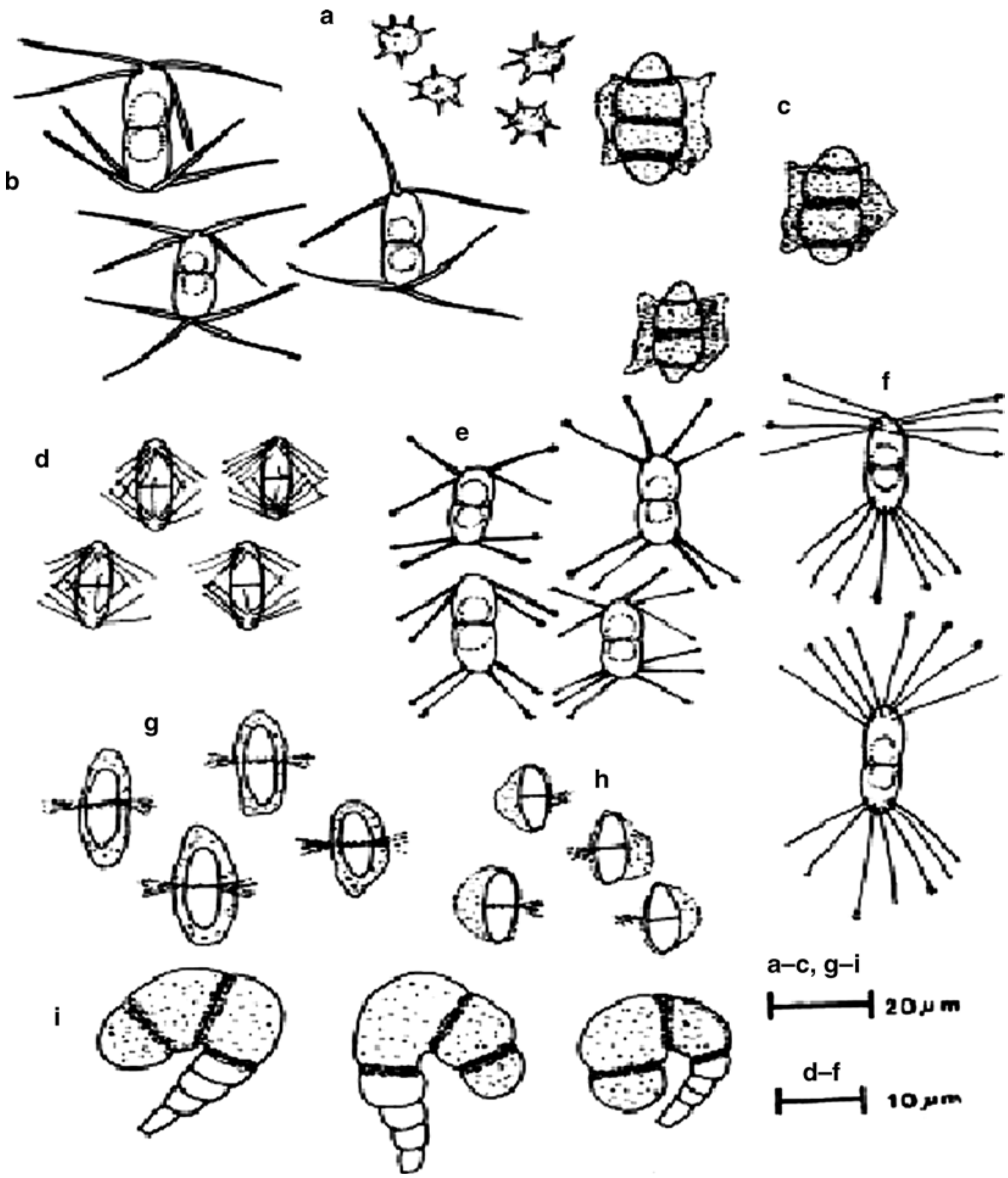

Fig. 6.7 Ascospores of fungi growing on wood in the marine environment. Note the structures for floatation and/or attachment. Ascospores of (**a**) *Amylocarpus encephaloides*, (**b**) *Arenariomyces majusculus*, (**c**) *Carbosphaerella leptosphaerioides*, (**d**) *Crinigera maritima*, (**e**) *Dryosphaera navigans*, (**f**) *Dryosphaera tropicalis*, (**g**) *Nimbospora bipolaris* and (**h**) *Nimbospora effusa*; (**i**) conidia of *Cirrenalia pseudomacrocephala* (From Prasannarai and Sridhar 2001. With permission)

many maritime countries as a source of food, for industrial applications and as a fertilizer. Nori (*Porphyra* spp.), a Japanese red seaweed, is very popular in the Japanese diet, has a high protein content (25–35% of dry weight), vitamins (e.g., vitamin C), and mineral salts, especially iodine. Industrial utilization is at present largely confined to extraction of phycocolloids, industrial gums classified as agars, carrageenans, and alginates. Agars, extracted from red seaweeds such as *Gracilaria* , are used in the food industry and in laboratory media culture. In addition, some tuft-forming blue-green algae (e.g., the poisonous *Lyngbya majusculac*) are sometimes considered as seaweeds.

Seaweeds grow in marine environments, where there is sunlight to enable them carry out photosynthesis. Many of them contain air vacuoles to aid them in

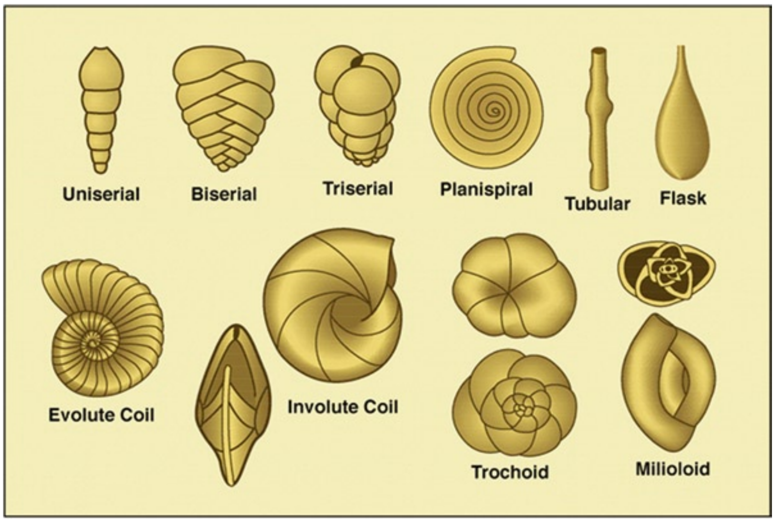

Fig. 6.8 Forminfera testa. (**1**, **2**) *Discorinopsis aguayoi* (Bermudez); (**3**, **4**) *Helenina anderseni* (Warren); (**5**, **6**) *Haplophragmoides wi/berti* Andersen; (**7**) *Miliammina* Fusca; (**8**) *Polysaccammina ipohaiina* Scott (From Javaux and Scott 2003. With permission) Note: The illustrations above are the commoner of the patterns found in foraminifera testa. Some organisms follow a single test construction pattern throughout their life; others can change patterns during their life cycle, switching, for example, from uniserial to biserial chambering or from evolute to involute coiling

floatation. Often, they require a point to which they are attached; some, however, are free floating.

Diatoms are golden brown algae of the group Chrysophyta. They contain chlorophylls "a" and "c," and the carotenoid fucoxanthin. They have a distinctive cell wall with a top and bottom section as in a Petri dish. They are an important part of the primary producers of the colder parts of the world oceans (see Chap. 4).

Coccolithophorids are unicellular flagellated golden brown algae with chlorophylls "a" and "c" and the carotenoids diadinoxanthin and fucoxanthin. They are mostly marine and are found in tropical waters. They sometimes form heavy growths, blooms, during which they may clog the gills of fish. They also produce dimethyl sulfide (DMS), a foul-smelling compound which sometimes turns fish away from their normal migratory routes.

The *phytoflagellates* are algae which are motile with flagella, such as *Euglena. Dinoflagellates* are distinguished by having two flagella, one of which is a transverse flagellum that encircles the body in a groove; the other flagellum is longitudinal and extends to the rear. They also have vesicles under their cell membrane. They are classified as *Pyrrophyta.*

6.3.5 Protozoa

All groups of protozoa, except Sporozoa, (i.e., Sarcodina, Mastigophora, Cilophora, and Suctoria) are found in the marine environment; Sporozoa which are exclusively parasitic are not found (Fig. 6.8).

Sarcodina

Foraminifera: In the deep ocean, a group of Sarcodina which form shells (tests) (Fig. 6.8) and have fine radiating pseudopodia and known as foraminifera, are abound. These shells are made of calcium carbonate ($CaCO_3$). They are usually less than 1 mm in size, but some are much larger. Some have algae as endosymbionts. Foramanifera typically live for about a month.

Flagellates

Flagellates are protozoa which move with flagella and are classified as Mastigophora. Many flagellates are marine (see Fig. 6.9).

Suctoria

The suctoria are exclusively marine. The juvenile stage is a ciliate and moves about. The adult stage is sessile and catches food with tentacles.

Ciliates

Ciliates are protozoa with cilia, and are classified as *Ciliophora* (see Chap. 4). They posses two nuclei. Marine ciliates are large, about 20–80 μm with some as large as 200 μm. Ciliates are important in the marine food web because they ingest (graze) bacteria and other smaller organisms in the marine environment.

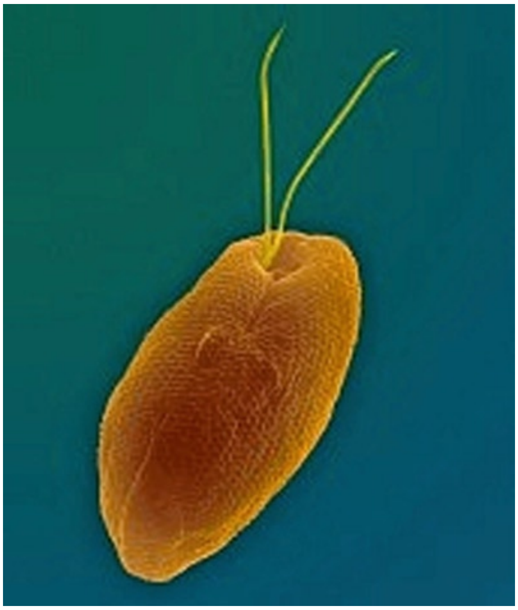

Fig. 6.9 Different flagella types among marine flagellates. A variety of marine flagellates from the various genera (*left* to *right*): *Cryptaulax*, *Abollifer*, *Bodo*, *Rhynchomonas*, *Kittoksia*, *Allas*, and *Metromonas* (From http://www.tolweb.org/notes/?note_id=50. With permission) Note: Marine phytoplankton Cryptomonad (Rhodomonas salina). Cryptomonads are flagellate protists, most of which have chloroplasts,and live in marine, brackish water, and freshwater. Cells are ovoid and flattened in shape with an anterior groove and two flagella used for locomotion. Because some contain chlorophyll, botanists treat them as a division of the Plant Kingdom, Cryptophyta, while zoologists place them in the Animal Kingdom as Cryptomonadida. (Image by Robert Folz, Visuals unlimited Inc. www.visualsunlimited.com reproduced with permission)

Some ciliates contain photosynthetic organisms as endosymbionts; they are able to obtain food by photosynthesis as well as by grazing and are said to be mixotrophic. Some ciliates do selective grazing, ingesting some organisms and leaving others. Freshwater protozoa regulate the water content of their bodies by the expansion and periodic collapse of their contractile vacuole, a vesicle which increases in size as it extracts water from the interior of the cell and collapses to nothing as it expels the extracted water. Because of the high osmotic pressure of the marine environment, contractile vacuoles are not observed in marine protozoa.

6.3.6 Viruses

Viruses are small particles, 20–30 nm long and made of either DNA or RNA, covered with a protein coat and sometimes also with lipid (see Chap. 4). Viruses have no metabolism of their own but use the host mechanism for their metabolism, including reproduction. They attack specific hosts and marine microorganisms seem to have their own peculiar viruses. Three kinds of relationships exist between microbial viruses and their microbial hosts:

(a) *Lytic* infections in which, after attaching to its host, the virus injects its nucleic acid into the host and causes it to produce numerous viruses like itself; the cell bursts and releases the new viruses. Each of the new daughter viruses can start the process again in a new host.

(b) *Lysogeny*, in which on injection of the viral nucleic acid into the host, the host is not lysed. Rather, the viral nucleic acid attaches to and becomes part of the genetic apparatus of the host. It may be induced to become lytic by ultra violet and some chemicals.

(c) *Chronic relationship*, in which the new viruses do not lyse the host, but are released by budding over many generations.

Marine viruses can be both detrimental and beneficial to the ocean's health. Some viruses attack and kill plankton, eliminating the base of the ocean food chain in a particular area. At the same time, the dead plankton can become a source of carbon that is not otherwise readily available to other sea life. It is estimated that up to 25% of all living carbon in the oceans is made available through the action of viruses. When these aspects remain in proper balance, the ocean functions normally.

Until the 1990s, it was believed that since the oceans were then believed to deserts in terms of microorganisms, few viruses would be in the sea. Since then, using the transmission electron microscope and epifluorescence microscopy (see Chap. 2) coupled with uranium stains, viruses have been shown to occur up to 10^{10} per ml in sea water. The distribution of viruses follows the relative abundance of microorganisms along the water column in the ocean. Some viruses affecting marine organisms are shown in Table 6.2.

Viruses are important in the food economy of marine organisms because the materials released when they lyse their hosts contribute to the dissolved organic matter (DOM) and the particulate organic matter (POM) of the oceans. They also contribute to gene transfer among marine organisms (Fuhrman 2000).

6.3.7 Plankton

Plankton are drifting organisms that inhabit the water column of oceans and seas; they also occur in fresh

Table 6.2 Some viruses infecting marine organisms (From Munn 2004. With permission)

Virus family	Nucleic acid	Shape	Size (nm)	Host
Myoviridae	dsDNA	Polygonal with contractile tail	80–200	Bacteria
Podovirrdae, Siphoviridae	dsDNA	Icosahedral with noncontractile tail	60	Bacteria
Microviridae	ssDNA	Icosahedral with spikes	23–30	Bacteria
Leviviridae	ssRNA	Icosahedral	24	Bacteria
Corticoviridae, Tectiviridae	dsDNA	Icosahedral with spikes	60–75	Bacteria
Cystoviridae	dsRNA	Icosahedral with lipid coat	60–75	Bacteria
Lipothrixviridae	dsDNA	Thick rod with lipid coat	400	Archaea
SSV1 group	dsDNA	Lemon shaped with spikes	60–100	Archaea
Parvoviridae	ssDNA	Icosahedral	20	Crustacea
Caliciviridae	ssRNA	Spherical	35–40	Fish, marine mammals
Totiviridae	dsRNN	Icosahedral	30–45	Protozoa
Reoviridae	dsRNA	Icosahedral with spikes	50–80	Crustacea, fish
Birnaviridae	dsRNA	Icosahedral	60	Molluscs, fish
Adenoviridae	dsDNA	Icosahedral with spikes	60–90	Fungi
Orthomyxoviridae	ssRNA	Various, mainly filamentous	20–120	Marine mammals
Baculoviridae	dsDNA	Rods, some with tails	100–400	Crustacea
Phycodnaviridae	dsDNA	Icosahedral	130–200	Algae

Table 6.3 Plankton classification by size and their abundance in the marine environment (Modified from Munn 2004. With permission)

	Size category	Size range (μm)	Microbial group	
Size ↓	Femtoplankton	01–0.2	Viruses	↑ Abundance
	Picoplankton	0.2–2	Bacteria, archae, some flagellates	
	Nanoplankton	2–20	Flagellates, diatoms, dinoflagellates	
	Microplankton	20–200	Ciliates, diatoms, dinoflagellates, other algae	

water. They are important in the food webs of aquatic systems because they provide food for the biotic communities. Organisms which spend their entire life cycle free floating as part of the plankton such as most algae, copepods, salps, and jellyfish are *holoplankton.* Those that are only plankton for part of their lives, usually the larval stage, and later move either to the nekton (free swimming) or a benthic (sea floor) life, are *meroplankton*. Fish, marine crustaceans, starfish, sea urchins belong to this latter group.

The organisms discussed above: Viruses, bacteria, archae, protozoa, algae constitute plankton. Plankton are small and are usually classified by size rather than by their taxonomic composition. Based on size, plankton are grouped into femtoplankton, picoplankton, nanoplankton, and microplankton (see Table 6.3). Some plankton engulf others of about their size. As seen from Table 6.3, the most abundant plankton are the smallest in size, while the largest in size are the fewest.

6.4 Unique Aspects of the Existence of Microorganisms in the Marine Environment

The marine environment has the following peculiarities: The temperature is low, except in the thermophilic vents; the pressure is high; and nutrients are sparse. Microorganisms existing under these conditions have adapted to the conditions

6.4.1 Low Temperature

The differences in temperature between the photic (or sunlit) zones nearer to the surface and the deep sea are dramatic. Temperatures vary more in the waters of the mixed zone and thermocline than the deep sea as shown in Fig 6.3. In most parts of the deep sea, the water temperature is more uniform and constant. With the exception of hydrothermal vent communities where hot water is emitted into the cold waters, the deep sea temperature remains between 2°C and 4°C.

The decreasing temperature of sea water with depth is shown in Fig. 6.3. The temperature in the deep sea is about −1°C. Psychrophiles (bacteria with optimum temperature of 0–5°C, but maximum growth temperature of 15°C) and psychrotolerant (bacteria which can grow at 0°C, but have maximum growth at about 20–25°C) abound in the sea. To enable them to survive and grow in cold environments, psychrophilic bacteria have evolved a complex range of adaptations to all of their cellular components, including their membranes, energy-generating systems, protein synthesis machinery, biodegradative enzymes, and the components responsible for nutrient uptake.

6.4.2 High Pressure

Considering the volume of water above the deepest parts of the ocean, it is not surprising that pressure is one of the most important environmental factors affecting deep sea life. Pressure increases 1 atmosphere (atm) for each 10 m in depth. The deep sea varies in depth from 700 meters to more than 10,000 m; therefore, pressure ranges from 20 atm to more than 1,000 atm. On average, pressure ranges between 200 and 600 atm. Advances in deep sea technology now make it possible for samples under pressure to be collected in such a way that they reach the surface without much damage. Without this technology, the animals would die shortly after being collected and the absence of pressure would cause their organs to expand and possibly explode. Deep sea creatures have adapted to pressure by developing bodies with no excess cavities, such as swim bladders, that would collapse under intense pressure. The flesh and bones of deep sea marine creatures are soft and flabby, which also helps them withstand the pressure. Recent results indicate that the deep-sea strain bacteria express different DNA-binding factors under different pressure conditions.

6.4.3 Oxygen

The dark, cold waters of the deep sea are also oxygen-poor environments. Consequently, deep sea life requires little oxygen. Oxygen is transported to the deep sea from the surface where it sinks to the bottom when surface temperatures decrease. Most of this water comes from arctic regions. Surprisingly, the deep sea is not the most oxygen-poor zone in the ocean. The most oxygen-deficient zone lies between 500 and 1,000 m, where there are more species that require oxygen depleting the oxygen in this zone during respiration. In addition, the bacteria that feed on decaying food particles descending through the water column also require oxygen. Oxygen is never depleted in the deepest parts of the ocean because there are fewer animals to deplete the available oxygen.

6.4.4 Food/Nutrients

Deep sea creatures have developed special feeding mechanisms because of the lack of light and because food is scarce in these zones. Some food comes from the detritus, of decaying plants and animals from the upper zones of the ocean. The corpses of large animals that sink to the bottom provide infrequent feasts for deep sea animals and are consumed rapidly by a variety of species. The deep sea is home to jawless fish such as the lamprey and hagfish, which burrow into the carcass quickly consuming it from the inside out. Deep sea fish also have large and expandable stomachs to hold large quantities of scarce food. They do not expend energy swimming in search of food; rather, they remain in one place and ambush their prey.

6.4.5 Light

The deep sea ocean waters are as black as night. The deep is also known as the twilight zone. The only light is produced by bioluminescence, a chemical reaction in the creature's body that creates a low level light; so, deep sea life must rely on alternatives to sight. Many deep sea fish have adapted large eyes to capture what little light exists. Most often, this light is blue-green, but some creatures have also developed the ability to produce red light to lure curious prey. Lack of light also creates a barrier to reproduction. Bioluminescent light is also used to signal potential mates with a specific light pattern. Deep sea creatures are also often equipped with a powerful sense of smell so that chemicals released into the water can attract potential mates.

6.4.6 High Temperature

Thermophilic bacteria and archae are found near thermal vents, and active underwater volcanoes. The temperature in deep sea vents can be as high as 350°C. A high temperature is created as the hot water mixes with sea water and a variety of bacteria and archae develop in these gradients. Among the hyperthermophilic bacteria found in these regions are *Aquiflex pyrophilus* and *Thermotoga maritama* (bacteria) and *Pyrococcus furiosus* and *Pyrolobus fumarii* (Archae).

6.4.7 Size in Marine Microorganisms

Marine microorganisms are generally small because the marine environment is oligotrophic (low in nutrients). Small cells can absorb nutrients more efficiently (see Table 6.3). The surface area /volume ratio is important. Many microorganisms are 0.6 µm at their widest dimension, and most are less than 0.3 µm, a genetic adaptation due to starvation on account of the scarcity of food in the environment. The spherical shape is inefficient in the absorption of nutrients in the sparse environment of the seas. On account of this, most marine bacteria are elongated. In addition, many marine bacteria have invaginations or buds which increase surface areas leading to greater absorption. There are exceptions and some marine bacteria are large. It is thought that these large bacteria have invaginations in their cell membranes which help increase their surface areas.

6.5 The Place of Microorganisms in the Food Chains of the Oceans and Seas

Until recently, it was thought that microorganisms did not play any role in the ecological hierarchies of the biotic life of the sea and oceans. It was thought that microorganisms were few especially because the open seas and oceans were oligotrophic (i.e., they contain little nutrients); if they played any part at all, it was to breakdown detritus (Azam et al. 1983).

The earlier oceanic (see Fig. 6.10) food chain formulated for such conditions in the photic section of the pelagic region excluded microorganisms and was based on primary producers being photosynthetic plankton, including the following: Diatoms (yellow-brown), single-celled algae typically about 30 µm in diameter and dominant in temperate and polar waters; dinoflagellates, dominant in subtropical and tropical seas and oceans and ranging from 30 to 200 µm (2 mm); coccolithophores dominant in tropical waters, typically 5–10 µm, and cyanobacteria.

The phytoplanktons are eaten by very small floating animals, zooplankton, such as copepods. The zooplankton are eaten by larger zooplankton such as shrimps, fish larvae, and jelly-fish.

The zooplankton are eaten by small fish such as sardines and herrings; these fish are eaten by larger fish. Some of these are birds, fish, and marine mammals.

At the top of the marine food web are the large predators including tuna, seals, and some species of whales.

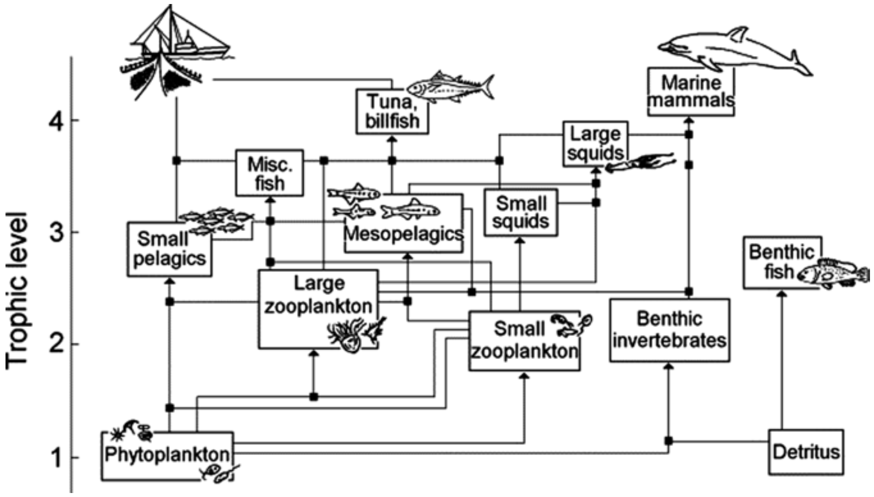

Fig. 6.10 Diagrammatic illustration of the marine food chain without microbial interaction (From Pauly 2007. With permission)

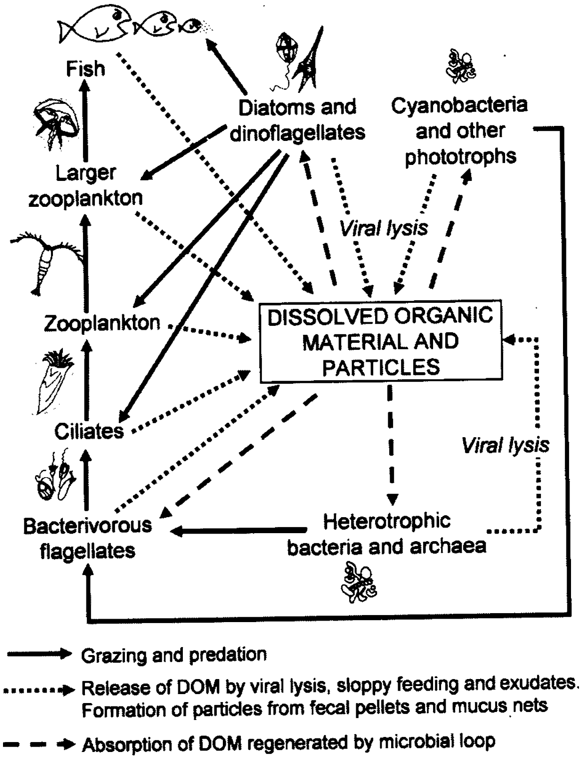

Fig. 6.11 Modern marine food webs. *Arrows* show transfer of organic matter (From Munn 2004. With permission)

In more recent times (see Fig. 6.11) and following the use of newer techniques including epifluorescence light, confocal laser scanning microscopy, flow cytomtery, but especially molecular methods, it has been found that there are far more bacteria than previously known. Furthermore, it is also known that bacteria are central to the biotic activities of oceans and seas.

Modern studies, especially the use of controlled pore-size filters and fluorescent DNA stains, showed that the oceans are rich in very small (picoplanktons, <2 μm) cyanobacteria, to the order of about 10^7 per ml. These methods revealed that two cyanobacterial genera, *Synechoccus* and *Prochlorococcus* constitute the most abundant photosynthetic microbes on earth, contributing more than 50% of the total marine photosynthesis. *Prochlorococcus* occurs ubiquitously in surface waters between latitudes 40°N and 40°S. *Synechococcus* occurs more widely, but it decreases in abundance beyond 14 °C; *Prochlorococcus* is about ten times more abundant than *Synechococcus.*

These methods also show that viruses are more important in the food economy of the oceans than originally recognized in the traditional food chain. Dissolved and particulate organic matter derived from the feces and excreta of fishes and breakdown materials from dead are consumed by bacteria.

Figure 6.11 shows the modern food web of oceans and seas in which the primary producers through photosynthesis are diatoms, dinoflagellates, and cyanobacteria. These are consumed by protozoa (bacterivorous flagellates, ciliates), which are in turn eaten by larger zooplankton (e.g., squids) which are then eaten by fish. Viruses play important parts in the modern food web; they lyse heterotrophic bacteria and Archae, cyanobacteria, and diatoms and flagellates. Dissolved and particulate organic matter which are so important in the nutrition of deep sea organisms are feces of fish and breakdown products from all the members of the community and occur in the sea snow already described (Azam et al. 1983; Stewart 2005).

In particular, modern food chains emphasize the *microbial loop* which illustrates the crucial role of microorganisms in recycling food in the marine environment (Figs. 6.11 and 8.12). The microbial loop is a term coined to describe a trophic pathway in aquatic environments where dissolved organic carbon (DOC) is reintroduced to the food web through the incorporation into bacteria. Bacteria are consumed mostly by flagellates and ciliates. They in turn, are consumed by larger aquatic organisms (for example small crustaceans like copepods).

The dissolved organic carbon (DOC) matter is introduced into aquatic environments from several sources, such as the leakage of fixed carbon from algal cells or the excretion of waste products by aquatic animals and microbes. DOC is also produced by the breakdown and dissolution of organic particles. In inland waters and coastal environments, DOC can originate from terrestrial plants and soils. For the most part, this dissolved carbon is unavailable to aquatic organisms other than bacteria. Thus, the reclamation of this organic carbon into food web results in additional energy available to higher tropic levels (e.g., fish). Because microbes are the base of the food web in most aquatic environments, the tropic efficiency of the microbial loop has a profound impact on important aquatic processes. Such processes include the productivity of fisheries and the amount of carbon exported to the ocean floor (Fig. 6.12).

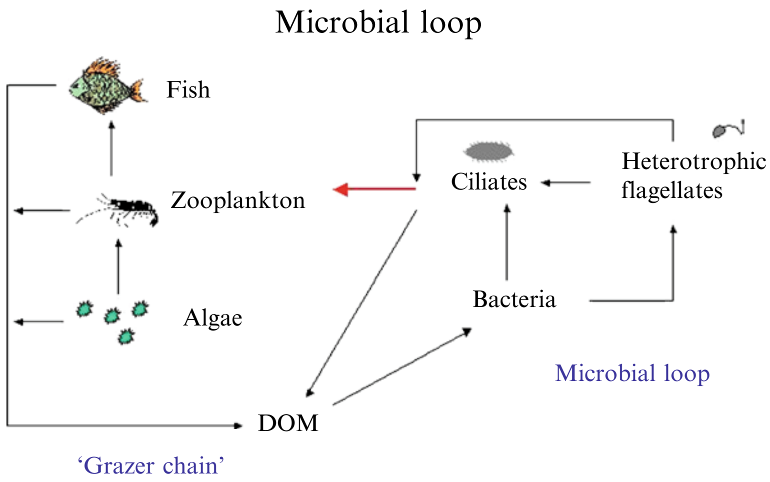

Fig. 6.12 The microbial loop (From Schulz 2006. With permission)

6.6 Marine Microorganisms and Their Influence on Global Climate and Global Nutrient Recycling

The sea and oceans occupy 71% of the earth's surface and 97% of all the waters on earth (i.e., the biosphere). The marine environment contains the greatest biological diversity up to 11 m in ocean waters and up to 400 m in the sediments. At the same time, it has been estimated that the biomass of microorganisms in seas and oceans is more than gigatons, many times more than other marine lives put together. On account of their capacity for rapid growth, and their diverse ability to bring about biochemical transformations, marine microorganisms are major movers of global nutrient cycles. It is not surprising that the activities of marine microorganisms have global effects in the area of global climate as well as the recycling of nutrients on a global scale. This section will discuss these important consequences of marine microbial activities on planet earth (Arrigo 2005).

6.6.1 The Influence of Marine Microorganisms on Global Climate and Global Nutrient Recycling

In microorganisms living in environments such as sea water where the osmotic pressure of the surrounding liquid is higher than that of the cell, the osmoregulation of the organisms is achieved by K^+, especially KCl, as well as one or more of a few low molecular weight organic compounds known as "compatible solutes" due to their compatibility in the cells where they are found. A list of selected compatible solutes is given in Table 6.4.

Apart from their osmoprotectant functions, they also have other uses in the cell. For instance, they act as cell reserves of carbon and nitrogen and are utilized when necessary. They also act to protect the cell against other forms of stress such as high or low temperature,

Table 6.4 Some compatible solutes (Modified from Welsh 2000. With permission)

Microbial group	Compatible solute
Algae	Sucrose
	Glycerol
	Mannitol
	Proline
	Glycine betaine
	Dimethylsulfoniopropionate
Cyanobacteria	Sucrose/trehalose
	Glycine betaine
	Glucosylglycerol
Phototrophic bacteria	Sucrose/trehalose
	Glycine betaine
Sulfate reducing bacteria	Trhalose
	Glycine betaine
Archaebacteria	Glycine betaine
	β-Glutamate

or desiccation. One compound which has been suggested as having general protective capabilities against many types of stress is trehalose. Another important compatible solute is dimethylsulfoniopropionate (DMSP), which is produced by some algae. DMSP is broken down to dimethyl sulfide and acrylate by the enzyme DMSP-lyase which is produced by the algae. It has been suggested that blooms formed by planktonic algae producing DMSP are not grazed by certain protozoa because of the DMS which the protozoa find unpalatable, and that the acrylate inhibits bacterial growth.

6.6.1.1 Global Marine Algal Sulfur Recycling, Dimethylsulfoniopropionate, Dimethyl Sulfide and Climate Change

DMSP is an osmoprotectant in some planktonic algae. One group of planktons, which contains DMSP as an osmoprotectant are the coccolithophorids, which belong to algal group, the Prymnesiophyta which are also known as Haptophyta. Coccolithophores are exclusively marine and are found in large numbers throughout the surface euphotic zone of the ocean. An example of a globally significant coccolithophore is *Emiliania huxleyi.* It is responsible for the release of significant amounts of dimethyl sulfide (DMS) into the atmosphere (Fig. 6.13).

$$\underset{\text{DMSP}}{(CH_3)_2S^{+}CH_2CH_2COO^{-}} \xrightarrow{\text{DMSP-lyase}} \underset{\text{DMS}}{(CH_3)_2S} + \underset{\text{Acrylate}}{CH_2 = CHCOO^{-}} + H^{+}$$

DMSP is synthesized as a compatible solute by many algae as well as by aquatic angiosperms. It is released from plankton by damaged phytoplankton cells due to physical stress (e.g., turbulence, zooplankton grazing, or viral-lysis). It is subsequently transformed by phytoplankton and bacterial enzymes to DMS (see formula above). Many bacteria have DMSP-lyase and are thought to play a significant part in converting the algal DMSP to DMS; some bacteria actually consume the DMSP. Photochemical reactions and ultraviolet radiation can degrade DMS to further break down products, removing DMS. Under aerobic conditions, DMS can be oxidized by chemolithotrophic bacteria such as *Thiobacillus* sp. to CO_2 and sulfate. The various pathways by which DMSP may be metabolized in water are shown in Fig. 6.14, with ultimate release of DMS. Among bacteria which can breakdown DMSP into DMS are members of the *Roseobacter* group and those of the SAR-11 (*Pelagigibacter ubique*) clade. The rate of DMS flux from the ocean to the atmosphere depends on its concentration in sea water (Welsh 2000).

DMS is the most important biologically produced sulfur compound in the marine atmosphere and it is essential in the global sulfur cycle. Gaseous DMS is photo-oxidized to sulfated aerosols in the atmosphere and a relationship has been established between DMS, sulfate aerosols, and cloud condensation nuclei.

The sulfate aerosols function as cloud condensation nuclei and on account of this, DMS has a significant impact on the earth's climate. Plankton production of DMS and its escape to the atmosphere is believed to be one of the mechanisms by which the microorganisms can regulate the climate.

The radiation balance has a fundamental effect on earth's climate. Approximately 33% of the solar radiation that reaches the earth is reflected back into space by clouds and from earth surfaces, such as ice and snow. The atmosphere absorbs some solar energy, but most of the other two thirds is absorbed by the land and oceans, which are warmed by the sunlight. The sun's energy is converted into heat, and the land and oceans then radiate a portion of this energy back as outgoing long-wave radiation (infrared), also known as terrestrial radiation. As this energy is radiated back out, it warms the atmosphere and continues on into space. The amount of solar energy received by the earth, the planetary albedo (the amount reflected back) and the emitted terrestrial radiation, makes up the earth's radiation balance. If the earth receives more energy than it loses, the result is global warming, and if it loses more energy than it receives, the result is global cooling.

The oxidation of DMS by hydroxyl (Fig. 6.14) and nitrate radicals results in the formation of sulfate aerosols, which on advection into water saturated air cause cloud formation. Both increased cloud formation and dry sulfate aerosols increase planetary albedo resulting in a relative cooling effect. Dry deposition of sulfate aerosols and precipitation of sulfate enriched rainwater over the continents couples the marine and terrestrial

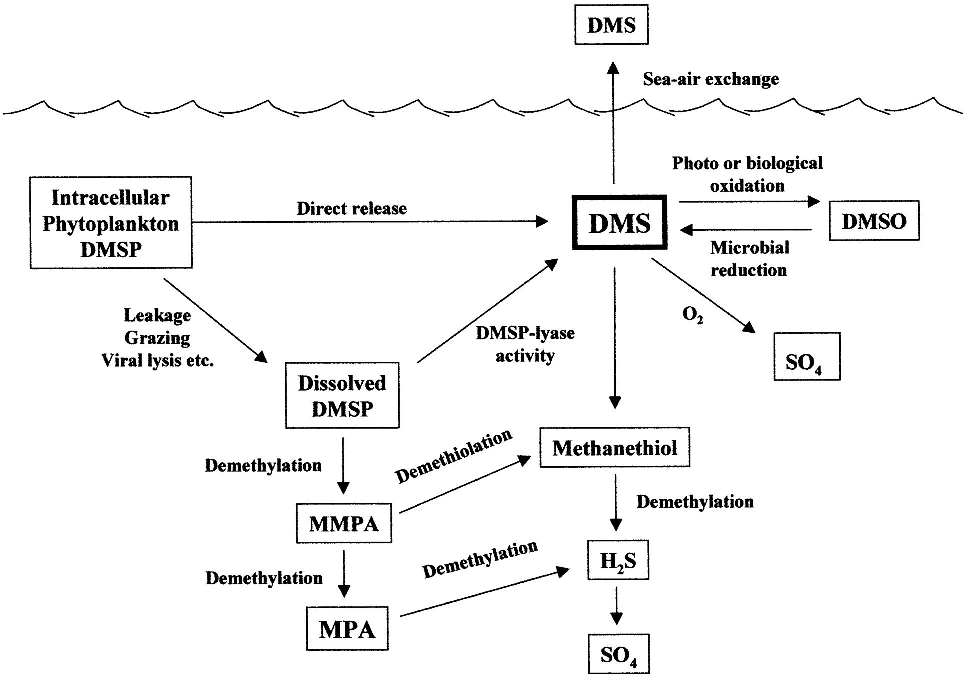

Fig. 6.13 Breakdown of DMSP in water. Microbial transformations involved in the turnover of DMSP and DMS in marine surface waters. Abbreviations: *DMSP* dimethylsulfoniopropionate, *DMS* dimethyl sulfide, *DMSO* dimethylsulfoxide, *MMPA* methylmercaptopropionate, *MPA* mercaptopropionate. DMS is the most important biologically produced sulfur compound in the marine atmosphere (From Welsh 2000. With permission)

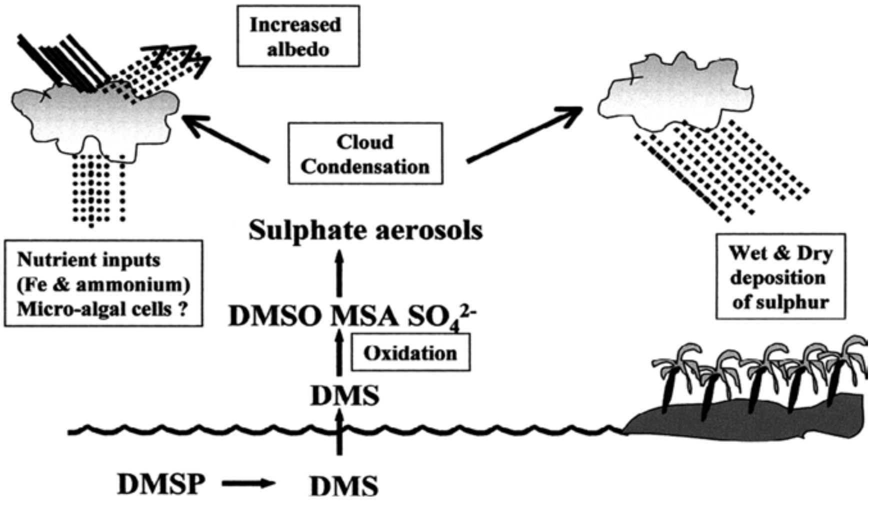

Fig. 6.14 Schematic representation of the processes involved in DMS oxidation, climate regulation, and coupling of the oceanic and terrestrial sulfur cycles. The oxidation of DMS by hydroxyl and nitrate radicals results in the formation of sulfate aerosols, which on advection into water saturated air cause cloud formation. Both increased cloud formation and dry sulfate aerosols increase planetary albedo resulting in a relative cooling effect. Dry deposition of sulfate aerosols and precipitation of sulfate enriched rainwater over the continents couples the marine and terrestrial sulfur cycles. Rainfall over the oceans may provide a feedback between DMS production by micro-algae and their productivity due to increased inputs of dissolved nutrients or by providing a dilute inoculum of micro-algal cells transported within the clouds. (From Welsh 2000. With permission)

Table 6.5 Reflectivity values of various surfaces (From Encyclopedia of Earth; http://www.eoearth.org/article/albedo)

Surface	Description	Albedo
Soil	Dark and wet	0.05–0.40
	Light and dry	0.15–0.45
Grass	Long	0.16
	Short	0.26
Agricultural crops		0.18–0.25
Tundra		0.18–0.25
Fresh asphalt		0.04
Forest	Deciduous	0.15–0.20
	Coniferous	0.05–0.15
Water	Small zenith angle	0.03–0.10
	Large zenith angle	0.10–1.0
Snow	Old	0.40
	Fresh	0.95
Ice	Sea	0.30–0.45
	Glazier	0.20–0.40
Clouds	Thick	0.60–0.90
	Thin	0.30–0.5

sulfur cycles. Rainfall over the oceans may provide a feedback between DMS production by micro-algae and their productivity due to increased inputs of dissolved nutrients or by providing a dilute inoculum of micro-algal cells transported within the clouds.

The word *albedo* comes from the Latin for white. The albedo of an object is the extent to which it reflects light. Typical albedos are given in Table 6.5.

Albedo is an important concept in climatology and astronomy. In climatology, it is sometimes expressed as a percentage. Albedo is an important factor in the radiation balance and clouds have major effect on albedo. The optical properties of a cloud are a key issue to understanding and therefore predicting global climate change. A cloud's optical properties are related to the size distribution and number of its droplets. The more cloud condensation nuclei, the smaller the size of its water droplets and the higher the density of water droplets since the same amount of water vapor is distributed among a greater number of CCN. This affects properties (reflectance, transmittance, and absorbance) of the cloud (Budikova 2010).

Clouds affect both incoming solar and outgoing thermal infrared fluxes; low thick clouds act as shields, blocking and reflecting solar radiation back into space which cools the planet, but high clouds can also trap outgoing heat (longwave radiation), warming the planet. Data indicate that clouds have an overall net cooling effect. The smaller droplet size will likely decrease precipitation, resulting in a longer lifetime for a cloud. Because the models had a poor ability to reproduce the effects of clouds, a priority was set to observe, measure, and learn about clouds' physical properties and radioactive fluxes. DMS may influence both the hydrologic cycle and the global heat budget through its part in cloud formation, and may alter rainfall patterns and temperatures

6.6.1.2 Carbon Recycling by Marine Algae and Reduction of Global Warming

Green house gases are those which stop the heat absorbed by the earth's surface from returning to outer space thus causing the earth's temperature to rise in the "green house effect." Photosynthetic microorganisms in the marine environment, including cyanobacteria fix atmospheric carbon converting it to carbohydrates at the starting point of the food chain, and thus reduce the CO_2 of the atmosphere and its contribution to global warming.

Some of the planktonic organisms, notably micro-algae, such as members of the Prymnesiophyta (Haptophyta) including coccolithophores, convert some of the carbon to calcium carbonate in their shells. This formation of calcareous skeletons by marine planktonic organisms and their subsequent sinking to depth generates a continuous rain of calcium carbonate to the deep ocean and underlying sediments. This is important in regulating marine carbon cycling and ocean-atmosphere CO_2 exchange. A rise in the atmospheric CO_2 levels causes significant changes in surface ocean pH and carbonate chemistry. Such changes have been shown to slow down calcification in corals and coralline macroalgae, but the majority of marine calcification occurs in planktonic organisms.

Another way of reducing the CO_2 of the atmosphere and hence its green house effect is by increasing the photosynthetic activity of marine organisms through increasing their supply of nutrients. Seeding the oceans with iron appears a viable way to permanently lock carbon away from the atmosphere and potentially tackle climate change. In this process, several tons of iron are put into the ocean. Although there is some concern about the long term effect of the action, it is seen as a possible way to slow down global warming. Marine algae and other phytoplankton capture vast quantities of carbon dioxide from the atmosphere as they grow, but this growth is often limited by a lack of essential nutrients such as iron. Artificially adding these nutrients would make algae bloom and, as the

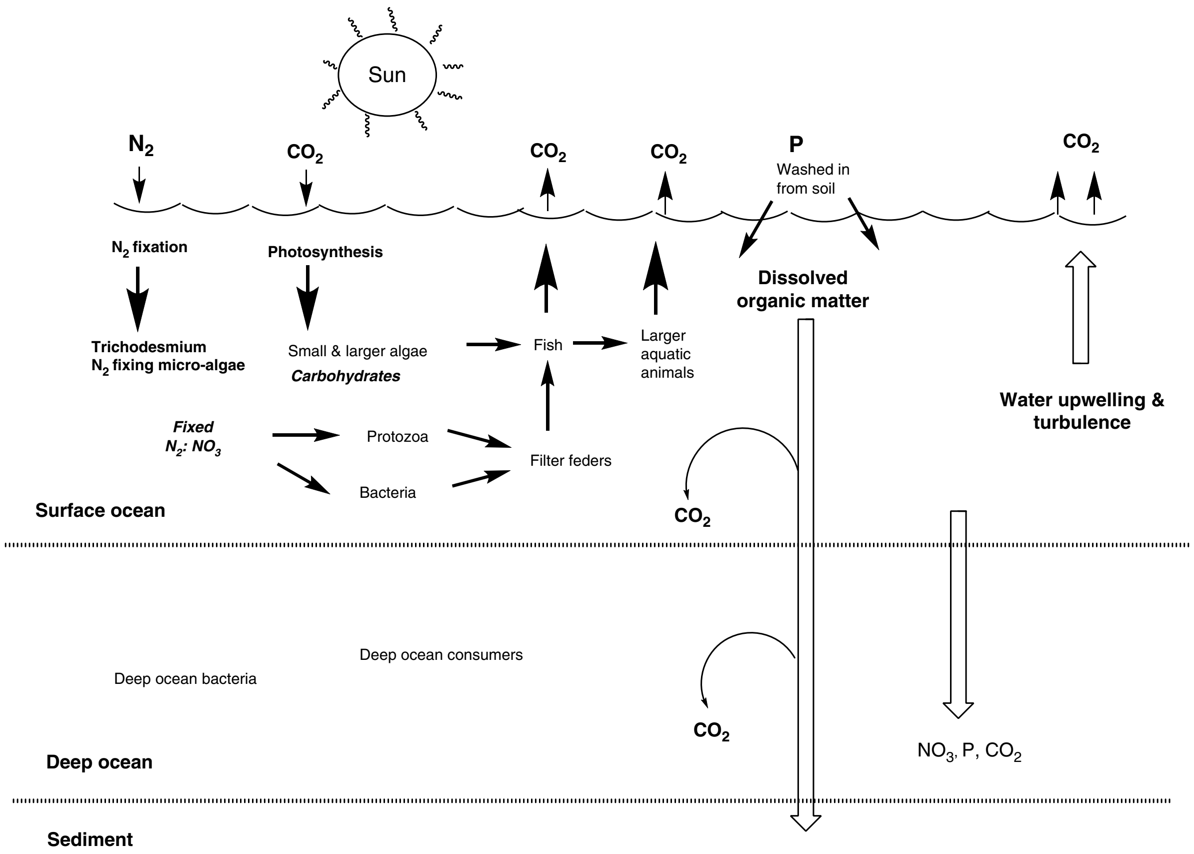

Fig. 6.15 Recycling of carbon, phosphorous and nitrogen in the ocean environment (Modified from Arrigo 2005)

organisms grow, they take up more CO_2. When they die, some of the organisms sink to the bottom of the ocean, taking their carbon with them. Experimentally iron fertilization has been shown to triple the growth of photosynthetic algae and the amount which sink to the ocean's bottom.

Some photosynthetic microorganisms in the marine environment also fix nitrogen. The link between carbon recycling, nitrogen fixation, and phosphorous recycling is further discussed below and shown in Fig. 6.15.

6.6.1.3 Marine Microorganisms and the Nitrogen Economy of Seas and Oceans

Nitrogen Fixation in the Ocean

Oligotrophic oceanic waters of the central ocean sites typically have extremely low dissolved fixed inorganic nitrogen concentrations, and few nitrogen-fixing microorganisms from the oceanic environment have been cultivated. The picture has changed in recent times. Nitrogenase is the enzyme involved in nitrogen fixation. Nitrogenase gene (*nifH*) sequences amplified directly from oceanic waters showed that the open ocean contains more diverse diazotrophic microbial populations and more diverse habitats for nitrogen fixers than previously observed by classical microbiological techniques. Nitrogenase genes derived from unicellular and filamentous cyanobacteria, as well as from the "α" and "γ" subdivisions of the class *Proteobacteria*, have been found in both the Atlantic and Pacific oceans (Zehr et al. 1998).

The current view is that the abundance of the N_2 fixers such as the cyanobacterium, *Trichodesmium*, the most common representative, has been severely underestimated and that N_2 fixation is a more important component of the marine N cycle than previously realized. It was once thought that nitrogen fixation would be more in coastal waters where Fe necessary for full function of nitrogenase would be more abundant. But it is now known that the amount required for the proper functioning of nitrogenase is much less than previously thought and the amount is present in the oceans away from the coast. Apart from *Trichodesmium,* other high N_2 fixers include the diatom genera *Rhizosolenia* and *Hemiaulus* which harbor the endosymbiotic high N_2-fixing cyanobacterium *Richelia intracellularis.* Other nitrogen-fixing cyanobacteria are species of *Synechococcus*, *Prochlorococcus*, *Trichodesmium*, and *Crocosphaera* (Ward 2005).

Unlike other nitrogen fixing bacteria, *Trichodesmium* also called sea sawdust, does not have heterocysts (spore-like structures in which nitrogen is synthesized in many cyanobacteria), nor any other specialized cells for this task. Furthermore, nitrogen fixation peaks at mid-day, i.e., occurs during the same time as photosynthesis.

Photosynthetic fixation of CO_2 in the oceans accounts for approximately half of total global primary production. Cyanobacteria, including species of *Synechococcus*, *Prochlorococcus*, *Trichodesmium*, and *Crocosphaera*, are prominent constituents of the marine biosphere that contribute significantly to this "biological carbon pump." The factors that control the growth of these cyanobacteria directly impact not only the carbon pump, but also the global nitrogen cycles through the activity of nitrogen-fixing organisms (i.e., *Trichodesmium* and *Crocosphaera*). The introduction of this new nitrogen to the euphotic zone is significant since it allows further CO_2 fixation by the remaining non-diazotrophic (i.e., non-nitrogen fixing) phytoplankton community.

Trichodesmium spp. are the most significant cyanobacterial primary producers in tropical and subtropical North Atlantic as well as in the tropical Pacific Ocean. In these regions, *Trichodesmium* introduces the largest fraction of new nitrogen to the euphotic zone, even exceeding the estimated flux of nitrate across the thermocline. In short, cyanobacteria are significant primary producers at the center of the marine food chain, with the genus *Trichodesmium* being particularly important in the tropical and subtropical oceans due to both its high abundance and high N_2-fixation rates.

Anaerobic Oxidations of Ammonium and of Methane

Interest in marine anaerobic ammonium oxidation (anammox), i.e., the microbiological conversion of ammonium and nitrite to dinitrogen gas, is a very recent addition to our understanding of the biological nitrogen cycle. It was discovered in 1986, and so far is the most unexplored part of the cycle. Given its basic features, the anammox process is a viable option for biological wastewater treatment. Very recently, it was discovered that anammox makes a significant (up to 70%) contribution to nitrogen cycling in the World's oceans.

Anaerobic methane oxidation (AMO) and anaerobic ammonium oxidation (Anammox) are two different processes catalyzed by completely unrelated microorganisms. Still, the two processes do have many aspects in common. First, both of them were once deemed biochemically impossible and nonexistent in nature, but have now been identified as major factors in global carbon and nitrogen cycling. Second, the microorganisms responsible for both processes cannot yet be grown in pure culture; their detection and identification were based on molecular ecology, tracer studies, use of lipid biomarkers, and enrichment cultures. Third, these microorganisms grow extremely slowly (doubling time varies from weeks to months). Fourth, both processes have a good potential for application in biotechnology (Strous and Jetten 2004).

The processes can be represented thus:

$$CH_4 + SO_4^{2-} + H^+ = CO_2 + HS^- + 2H_2O \quad (6.1)$$

$$NH_4^+ + NO_2^- = N_2 + 2H_2O \quad (6.2)$$

The anammox and amo bacteria form a monophyletic cluster branching off deep in the order.

Planctomycetales. With 16S rDNA probes based on the sequences derived from enrichment cultures, anammox bacteria were detected in various ecosystems such as the suboxic zone of the water of the Black Sea. Three anammox bacteria has been tentatively named "*Kuenenia stuttgartiensis,*" "*Scalindua sorokinii,*" and "*Brocadia.*" All three genera share the same metabolism. Anammox was found to contribute up to 50% to marine N_2 production.

With regard to the roles of the two processes, current information is that AMO and anammox are responsible for more than 75% of marine methane oxidation and 30–50% of marine ammonium oxidation. Since the marine biosphere is strongly coupled to global climate, AMO and anammox play important parts in this regard.

Anaerobic methane and ammonium oxidation have two properties in common: Slow microbial growth and mutualism. AMO is mediated by syntrophic reversed methanogenic archaea and sulfate-reducing bacteria. The two are always found in close proximity to one another.

The figure shows loss of ammonium and nitrites respectively due to anaerobic ammonium oxidation and anaerobic methane oxidation (AMO). particulate organic nitrogen (PON), including plankton; DON, dissolved organic matter; DNRA, dissimilatory nitrate

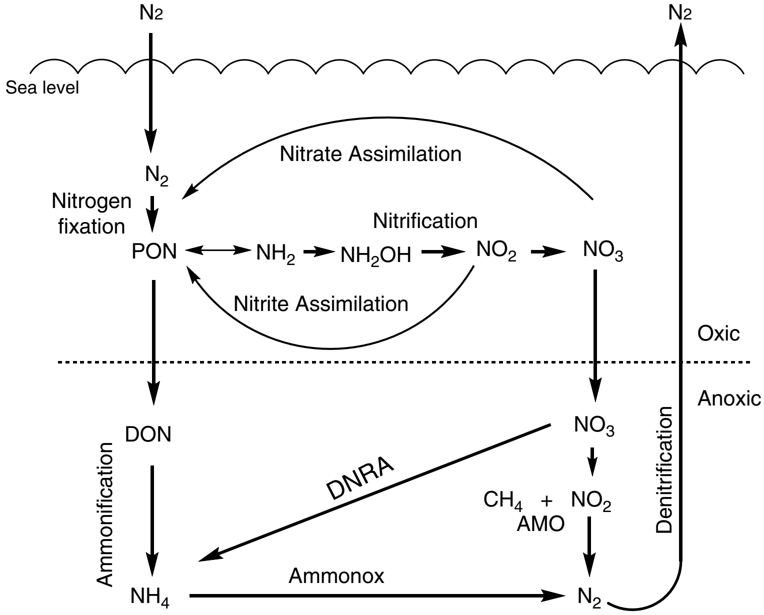

Fig. 6.16 The nitrogen cycle in the marine environment (Modified from Arrigo 2005) The figure shows loss of ammonium and nitrites respectively due to anaerobic ammonium oxidation (AMMONOX) and anaerobic methane oxidation (AMO). *PON* particulate organic nitrogen, including planton; *DON* dissolved organic matter; *DNRA* dissimilatory nitrate reductase to ammonium

reductase to ammonium unknown if these archaea are simply inactive, are capable of AMO without a sulfate-reducing partner, or are doing something completely different. For anammox, the anaerobic ammonium oxidizers always depend on a nearby source of nitrite. Denitrifiers reduce nitrate to nitrite, which is then used by anammox bacteria. The doubling time of anammox bacteria is 2–3 weeks on average, rivaled in their slow growth only by *Mycobacterium leprae* grown in the nine-banded armadillo as a surrogate host.

A possible application is wastewater treatment. The introduction of anammox to nitrogen removal would lead to a reduction of operational costs of up to 90%. Anammox would replace the conventional denitrification step completely and would also save half of the nitrification aeration costs. In feasibility studies with sludge digestor effluents on laboratory scale, the effluents did not negatively affect the anammox activity and anammox biomass could be enriched from activated sludge within 100 days.

6.6.1.4 The Global C:N:P Marine Ratio and Its Maintenance Through Microbial Activity: The Redfield Ratio

The Redfield ratio (named after Alfred Redfield, its discoverer) is that the marine nitrate:phosphate (NO_3:PO_4) ratio of 16:1 in the oceans is controlled by the requirements of phytoplankton, which subsequently release nitrogen (N) and phosphorus (P) to the environment at this ratio as they die, are broken down, and remineralized. Redfield (1934) had analyzed thousands of samples of marine biomass from all ocean regions. He found that globally the elemental composition of marine organic matter (dead and living) was constant. The ratios of carbon to nitrogen to phosphorus remained the same from coastal to open ocean regions. Redfield's initial observations has been extended to include other elements, most notably carbon (C), and it now links these three major biogeochemical cycles through the activities of marine phytoplankton in the ratio of 106:16:1 for phytoplankton and the deep ocean (Redfield 1934).

Under certain conditions, the phytoplankton chemical ratio diverges from the expected Redfield ratio. The change in the ocean ratio could be changes in exogenous nutrient delivery and microbial metabolism (e.g., nitrogen fixation, denitrification and anammox). These changes are reflected as N deficit or excess relative to P for a given water mass.

These biologically mediated cycles modulate, and are themselves modulated by, processes operating at scales ranging from algal photosynthesis to the global climate. The amount of atmospheric carbon dioxide removed by the ocean is very sensitive to the ratio relationships between phytoplankton and nutrients, including inputs by humans of ordinarily limiting elements such as nitrogen, through, for example, fertilizer eutrophication, or by natural nitrogen fixation and losses due to AMO and anammox (see Fig. 6.16).

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