Cyanobacteria

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Introduction

Cyanobacteria are photosynthetic prokaryotes that capture sunlight for energy using chlorophyll *a* and various accessory pigments. They are common in lakes, ponds, springs, wetlands, streams, and rivers, and they play a major role in the nitrogen, carbon, and oxygen dynamics of many aquatic environments. The exact timing of appearance of the first cyanobacteria-like microbes on Earth is still unclear because of controversy over the interpretation of Precambrian fossils; however, much of their present diversity was achieved more than 2 billion years ago, and they likely played a major role in the accumulation of oxygen in the Earth's early atmosphere. In addition to their remarkably long persistence as free-living organisms, cyanobacteria also form symbiotic associations with more complex biota; for example, the nitrogen-fixing species *Anabaena* (or *Nostoc*) *azollae* forms a symbiotic association with the floating fern *Azolla*, which is widely distributed in ponds and flooded soils. The chloroplasts in plants and algae appear to be originally derived from an endosymbiosis in which a cyanobacterium was engulfed and retained within a colorless eukaryotic cell.

Modern-day cyanobacteria include some 2000 species in 150 genera and 5 orders (Table 1), with a great variety of shapes and sizes. Ecologically, there are three major groups in the aquatic environment: mat-forming species, which form periphytic biofilms over rocks, sediments, and submerged plants; bloom-formers, which create a wide range of water quality problems and that are most common in nutrient-rich (eutrophic) lakes; and picocyanobacteria, which are extremely small cells (<3 μm in diameter) that are often abundant in clear water lakes. Additional groups include colonial non-bloom-formers, which are common in a variety of aquatic habitats, including mesotrophic lakes, wetlands, and saline waters; metaphytic species that form aggregates that are loosely associated with emergent macrophytes (water plants such as rushes and reeds that extend out of the water into the air above); certain species that grow as periphyton but that can also enter the plankton; and various symbiotic associations.

Cellular Characteristics

Cyanobacteria were formerly classified as blue-green algae (*les algues bleues* in French, *las algas azules* in Spanish) because of their algal-like appearance, their possession of chlorophyll rather than bacteriochlorophyll, and their photosynthetic production of oxygen by a two-photosystem process as in algae and higher plants. The most widely used taxonomic schemes for these organisms are largely based on the International Botanical Code, with separation according to classic morphological criteria. Ultrastructural studies, however, clearly show that the Cyanobacteria are prokaryotic; that is, they lack nuclei and other organelles and they have a peptidoglycan cell wall that is typical of gram-negative Eubacteria. They also possess several features that set them apart from other bacteria, especially their photosynthetic apparatus and oxygen production. The term 'blue-green algae' is still widely used by the media and in the water quality management area. The current taxonomic separation of species, especially the coccoid and nonheterocystous (see definition later) taxa, is believed to be artificial and not reflective of evolutionary relationships, and will likely be substantially revised as more genetic data become available.

All cyanobacteria contain chlorophyll *a* and most contain the blue phycobiliproteins phycocyanin and allophycocyanin, giving the cells their characteristic blue-green color. Many taxa also contain the phycobiliprotein phycoerythrin, making the cells red, or sometimes black. The phycobiliproteins are located in structures called phycobilisomes on the thylakoid (photosynthetic) membranes, and these are highly efficient 'light guides' for the transfer of captured solar energy (excitation energy) to the reaction centers of photosynthesis, specifically photosystem II. A group of photosynthetic microbes formally classified as a separate prokaryotic phylum, the Prochlorophyta, contains chlorophyll *b* in addition to *a*, but lacks phycobiliproteins and thus phycobilisomes. On the basis of genetic data (specifically, the gene sequence for 16S ribosomal RNA) this latter group is now placed within the Cyanobacteria. This group includes the species *Prochloroccus marinus*, one of the most abundant phototrophs in the sea, and a filamentous freshwater phytoplankton species, *Prochlorothrix*.

Although cyanobacteria lack membrane-bound organelles, they have a variety of cellular structures and inclusions that have specialized functions and that contribute to their ecological success. These include the photosynthetic thylakoid membranes containing the phycobilisomes, and the nucleoid region or centroplasm in the center of the cell,

Table 1 The five orders of cyanobacteria recognized in the classic botanical taxonomic scheme

Order	*Characteristics*	*Illustrative genera*
1. Chroococcales	Coccoid cells that reproduce by binary fission or budding	*Aphanocapsa, Aphanothece*, *Gloeocapsa, Merismopedia, Microcystis, Synechococcus, Synechocystis*
2. Pleurocapsales	Coccoid cells, aggregates or pseudo-filaments that reproduce by baeocytes	*Chroococcidiopsis*, *Pleurocapsa*
3. Oscillatoriales	Uniseriate filaments, without heterocysts or akinetes	*Lyngbya*, *Leptolyngbya*, *Microcoleus*, *Oscillatoria*, *Phormidium*, *Planktothrix*
4. Nostocales	Filamentous cyanobacteria that divide in only one plane, with heterocysts; false branching in genera such as *Scytonema*	*Anabaena*, *Aphanizomenon*, *Calothrix*, *Cylindrospermopsis*, *Nostoc*, *Scytonema*, *Tolypothrix*
5. Stigonematales	Division in more than one plane; true branching and multiseriate forms; heterocysts	*Mastigocladus* (*Fischerella*), *Stigonema*

In the bacterial classification scheme, the orders are referred to as subsections of Phylum BX: Cyanobacteria.

which contains the complex folded, circular DNA, often in multiple copies. The cells also contain various storage bodies, including glycogen (polyglucose) granules, which store carbon; cyanophycin granules, which are nitrogen stores composed of arginine and aspartic acid; carboxysomes composed of ribulose 1,5-bisphosphate carboxylase/oxygenase, which act as a store of this photosynthetic enzyme as well as of nitrogen; and polyphosphate granules. These inclusions allow cells to accumulate energy and nutrients far in excess of their present requirements when they are under favorable conditions, and to subsequently use these reserves for maintenance and growth when they encounter resource-poor conditions. The cells of several planktonic genera contain up to several thousand gas vacuoles (Figure 1), which are hollow, water-impermeable cylinders made up of protein subunits. These fill with gases that diffuse in from the surrounding medium. They provide buoyancy to the cells and colonies, allowing the cyanobacteria to float towards the surface where the light conditions are improved for photosynthesis. Some species may undergo diurnal migration up and down the water column by varying the amount of dense carbohydrate inclusions that act as ballast in their cells.

Many filamentous cyanobacteria produce different cell types that play specific physiological, reproductive, or ecological roles. The most well known of these is the heterocyte (often called a heterocyst, although it is not a cyst). This thick-walled cell (Figure 1) is formed by members of the Nostocales and Stigonematales and is the location of the enzyme nitrogenase for nitrogen fixation, the conversion of nitrogen gas into ammonium and then amino acids. This cell type is not a strict prerequisite for nitrogenase activity, however, because several nonheterocystous taxa in other orders are also known to fix nitrogen. Another specialized cell type is the akinete, a structurally reorganized cell that is formed under unfavorable conditions, and that allows cyanobacteria to overwinter in the sediments. Some genera such as *Nostoc* produce hormogonia, a motile series of cells formed for reproduction. In one order of coccoid forms, the Pleurocapsales, reproduction is via the production of up to several hundred minute cells called baeocytes.

Ecophysiology

Cyanobacteria photosynthesize using water as the electron donor and produce oxygen as in algae, although a small number of strains can also use hydrogen sulfide (H_2S) and convert it to elemental sulfur. In general, cyanobacteria can tolerate low oxygen conditions and concentrations of H_2S that are toxic to eukaryotic algae. This tolerance may contribute to their ability to survive in anoxic, eutrophic lake sediments as well as in certain mat environments.

Cyanobacteria are highly tolerant of UV radiation and have four major strategies to eliminate or mitigate the toxic effects of this most reactive waveband of underwater solar radiation. Some species avoid UV exposure by their choice of habitat, for example, by growing in dense macrophyte beds, in sand beneath the surface, or in the metalimnion (region of the thermocline) of lakes. Many species have effective UV-screens that include scytonemin (peak absorption in the UV-A waveband) and mycosporine-like amino acids (peak absorption in the UV-B). Some benthic (bottom-dwelling) species such as *Nostoc*, *Calothrix*, and *Gloeocapsa* have such high concentrations of scytomenin that they are black. All cyanobacteria produce carotenoids, for example, β-carotene, myxoxanthophyll, echinenone, oscilloxanthin, and canthaxanthin, which are effective scavengers of reactive oxygen species, the damaging photoproducts of UV exposure.

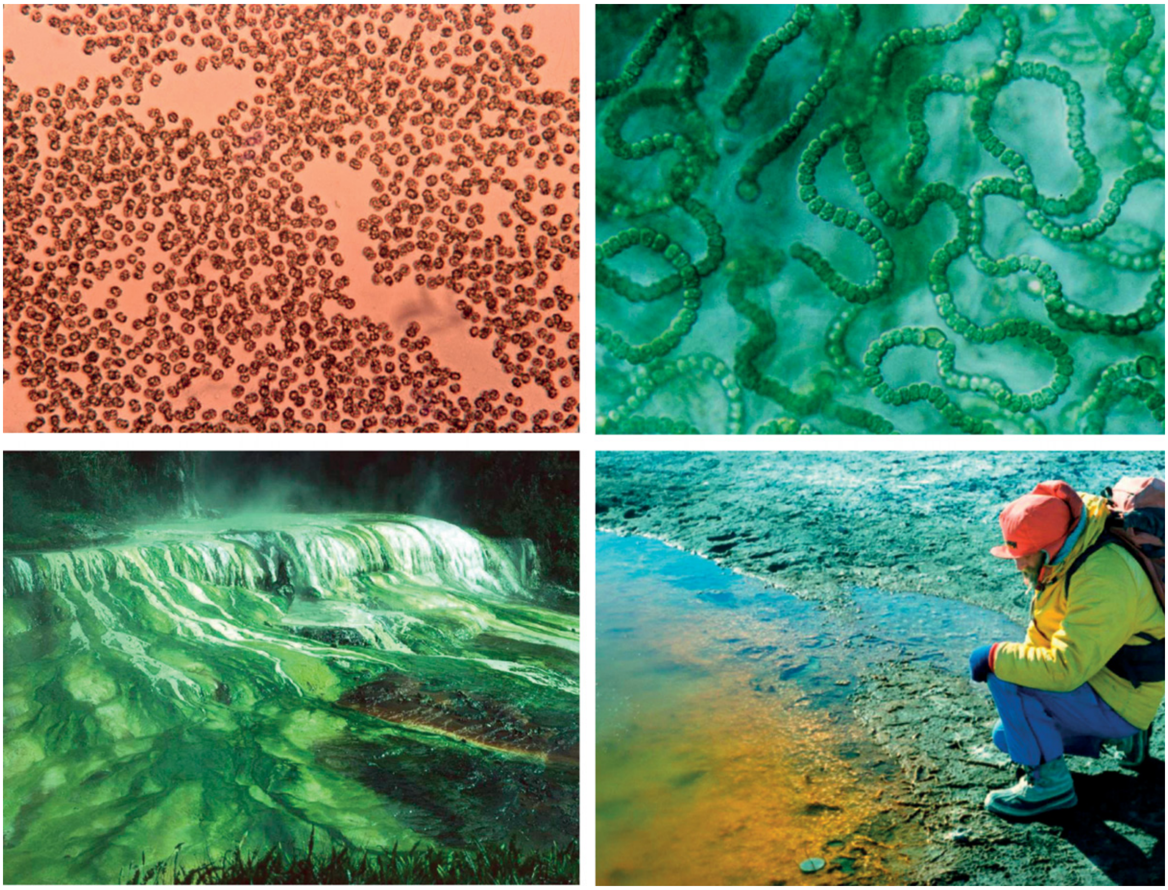

Figure 1 Cyanobacteria in inland water ecosystems. Top left: Photomicrograph of *Microcystis aeruginosa* from a eutrophic lake. The bright areas inside each cell are due to the scattering of light by the gas vacuoles. Top right: Photomicrograph of *Nostoc* from a high Arctic lake. The larger, more spherical cells are heterocysts, the sites of nitrogen fixation. Bottom right: A carotenoid-rich cyanobacterial mat in a pond on the McMurdo Ice Shelf, Antarctica. Bottom left: Cyanobacterial mats in a geothermal spring, New Zealand.

Cyanobacteria also have various enzymatic defences against reactive oxygen species, such as superoxide dismutase. Finally, cyanobacteria have a variety of damage repair mechanisms to identify and repair UV-damaged proteins, for example, in photosynthetic reaction centers, and DNA. This combination of mechanisms and high tolerance to UV radiation, perhaps also combined with the multiple ‘back-up’ copies (six or more identical ‘chromosomes’) of the cyanobacterial genome in each cell, likely contribute to the ecological success of cyanobacteria in many types of habitats exposed to bright sunlight, for example, as surface blooms, as benthic layers in shallow waters, and in the picoplankton of oligotrophic, transparent lakes.

Cyanobacteria occur over a wide temperature range; however, most tend to have warm temperature optima for growth. They occur in thermal springs, with the highest temperature limit of 74 °C recorded in Yellowstone National Park, USA. Bloom-forming cyanobacteria prefer temperatures over 15 °C, and even the mat-forming species that occur throughout the Polar regions in frigid waters or on ice are not psychrophilic (optimal growth at low temperatures). Instead they are psychrotolerant (also termed psychrotrophic); that is, they tolerate the cold and grow very slowly relative to their optimal growth rates at much higher temperatures.

In general, cyanobacteria prefer alkaline conditions, and during a bloom, the pH may rise to more than 9. Under these conditions, most of the inorganic carbon is in the form of carbonate and is unavailable to many eukaryotic algae. Cyanobacteria have excellent inorganic carbon concentrating mechanisms, with separate membrane transport systems for CO_2 and for bicarbonate (HCO_3^-). Once inside the cell, the carbon is largely present as bicarbonate, and the enzyme carbonic anhydrase catalyzes its dissociation into CO_2, the substrate for ribulose 1,5-bisphosphate carboxylase/oxygenase.

Some cyanobacteria are highly tolerant of salt and grow in media with high osmolarities. Saline and hypersaline lakes often contain picocyanobacteria, mat-forming species such as *Microcoleus chthonoplastes*, bloom-forming, nitrogen-fixing species such as *Nodularia spumigena*, and the salt-tolerant colonial species *Aphanothece halophytica*. Certain taxa are obligate halophiles, and can grow in environments with salt concentrations of up to 360 g of salt per liter, 10 times the salinity of seawater. Salt-tolerant cyanobacteria produce a range of osmolytes, that is, solutes that maintain their high internal osmolarity and turgor pressure without causing toxic effects on proteins and other cellular constituents. The most important of these are glucosylglycerol (which can account for up to 30% of dry weight in cells grown in hypersaline media) and glycine betaine.

The ability of some species of cyanobacteria to fix nitrogen gives them a competitive advantage in low nitrate, low ammonium waters, and may also contribute substantial quantities of new nitrogen to aquatic ecosystems. One particularly important habitat for cyanobacteria is the flooded rice fields, where the cyanobacteria increase the nitrogen content and fertility of the soil because of their nitrogen-fixing capability.

Taste, Odor, and Toxin Production

Cyanobacteria produce a variety of compounds that strongly affect water quality. These include molecules that affect the taste and odor of water, notably geosmin and 2-methylisoborneol, both of which impart an earthy or musty odor to the water. An additional cyanobacterial group of compounds is cyclocitrals, which are carotenoid breakdown products that impart a grassy odor to the water. Of greater concern to water resource managers is the production of three classes of toxins: hepatotoxins, which attack the liver; neurotoxins, which attack the nervous system; and dermatotoxins, which cause skin irritation. These toxins are especially produced by certain planktonic species. *Microcystis aeruginosa*, a bloom-forming species that is common in eutrophic lakes and reservoirs throughout the world, produces microcystin, a cyclic peptide that is a hepatotoxin. Two other bloom-forming genera *Anabaena* and *Aphanizomenon* often occur in association with *Microcystis* and produce the alkaloid neurotoxin anatoxin. *Cylindrospermopsis*, a tropical species that has been increasingly observed in temperate lakes, contains the potent hepatotoxin cylindrospermopsin, also an alkaloid. Several benthic species produce anatoxins as well as the dermatotoxins lyngbyatoxin and aplysiatoxins. Cyanobacterial toxins have been implicated in the death of animals, including birds, farm stock, dogs, and a small number of humans. The presence of toxic cyanobacteria in drinking reservoirs and recreational lakes is of particular concern, and often results in the temporary closure of such water supplies. The toxins are water-soluble and are not destroyed by boiling the water prior to drinking. The difficulty of managing such blooms is compounded by the large variability in toxin production among strains of the same species, and with environmental conditions.

Ecology

Mat-Forming Species

Cyanobacteria are a common component of the periphyton (the ensemble of microorganisms attached to submerged surfaces), forming crusts and films over rocks (epilithon), plants (epiphytes), sand (epipsammon), sediments (epipelon), and other substrates. In many environments, these biofilms accumulate from millimeters to centimeters in thickness as vertically structured, microbial mats that form a benthic layer at the bottom of the water column, or that detach and float at the surface.

Mat-forming cyanobacteria have a particularly long history. Some of these organisms form laminated, lithified structures called stromatolites that are well represented in the fossil record all the way back to the Precambrian. The fossils contain layered, filament-like inclusions and bear striking resemblance to living stromatolites that occur today in a small number of marine habitats, and also in certain lakes. The stromatolite communities are thought to have been the main primary producers on Earth for more than 1 billion years throughout the Proterozoic, and a major contributor to atmospheric oxygen that in turn set the stage for the rise of oxygen-requiring microbes and animals. They are less successful today, in part, because of the presence of grazing animals, including crustacean zoobenthos and zooplankton.

Cyanobacterial mats and films are common in wetland systems, especially in alkaline habitats where they are often encrusted in calcium carbonate. The common genera in swamps include *Chroococcus*, *Leptolyngbya*, *Lyngbya*, *Phormidium*, *Microcoleus*, *Schizothrix*, and *Scytonema*. Benthic cyanobacteria are especially important in rice-field wetlands because of nitrogen fixation capabilities, and include the heterocystous genera *Anabaena*, *Calothrix*, and *Tolypothrix*. Mats and films are common in many extreme environments, including cryoconites holes on glaciers, in pools on Arctic and Antarctic ice shelves, in saline and hypersaline lakes, and in geothermal springs.

The nitrogen-fixing cyanobacterium *Nostoc* is a frequent member of benthic lake, pond, stream, wetland, and semiaquatic communities throughout the world (Figure 1), and is well known for its ability to survive prolonged desiccation. It can form flattened mats, lobes, and sheets that coat the rocks and sediments, or discrete spherical colonies that range in size from less than a millimeter to 25 cm. These grape- or pearl-like colonies are harvested from lakes and wetlands in several parts of the world as a food source and for their medicinal properties. In China, *Nostoc commune* is known as *Tian-Xian-Mi* ('rice of heavenly immortals'), and has been used as a medicine for more than 1500 years.

Mat-forming cyanobacteria create their cohesive structure by the excretion of extracellular polymeric substances that bind together the individual cells or filaments. This polysaccharide-rich matrix likely confers desiccation and freeze tolerance to the mats in extreme environments such as semiaquatic habitats that periodically dry out. The extracellular polymeric substance traps sediment particles and forms the physical medium for a great variety of other organisms, including viruses, heterotrophic bacteria, protists such as diatoms, flagellates, and ciliates, and sometime microinvertebrates such as turbellarians (flatworms), rotifers, and nematodes. Detailed analyses of these mats and films have shown that they have very different chemical properties relative to the overlying water; for example, they may have much higher pH and concentrations of inorganic nitrogen and dissolved reactive phosphorus that are orders of magnitude greater than the bulk properties of the surrounding lake or river water. They are also highly differentiated vertically. There are typically strong gradients in oxygen concentration, ranging from supersaturated near the surface to (sometimes) anoxic, H_2S-rich conditions at the base of the mats, where photosynthetic sulphur bacteria may reside.

Microbial mats dominated by cyanobacteria are often brightly colored (Figure 1), with large changes in pigment composition down the mat profile. The surface layer is rich in photoprotective pigments, especially carotenoids (orange and red) but also sometimes scytonemin (black or brown), overlying a deeper blue-green layer rich in light-harvesting phycobiliproteins and chlorophyll *a*. Certain mat-forming species of cyanobacteria are motile and are able to change their position in the mats by a gliding motion through the extracellular polymeric substance matrix.

Some of the most spectacular examples of such mat-forming cyanobacteria occur in lakes, ponds, and streams in the Arctic and Antarctic (Figure 1). Cyanobacterial mats are typically 1–2 mm in thickness, but in some lakes and ponds they form mucilaginous mats up to several tens of centimeters in thickness. Similar mats and films also occur in abundance at the other thermal extreme, in hot pools and geothermal springs (Figure 1). Apart from their physiological adaptation to high temperatures, these communities have been of interest to microbial ecologists because of their biogeography. A long-standing theory of microbial distribution is that 'everything is everywhere' and that the local environment selects for a particular microbial flora that is globally distributed. Analyses of hot spring cyanobacteria indicate that certain taxa are indeed cosmopolitan and occur at many sites throughout the world. For example the species *Mastigocladus* (or *Fischerella*) *laminosus* occurs at temperatures of up to 58 °C, and is found in hot springs worldwide. However, the high-temperature form of *Synechococcus* that grows at temperatures of up to 74 °C appears to have a more restricted global distribution, suggesting some biogeographical separation of strains.

Bloom-Forming Species

Bloom-formers tend to be found in warm, stable, nutrient-rich lakes and are largely absent from the polar and alpine regions. Three genera are particularly common and often co-occur: *Anabaena*, *Aphanizomenon*, and *Microcystis*. Some lakes contain a metalimnetic bloom of *Planktothrix* (*Oscillatoria*). The factors causing the dominance of bloom-forming cyanobacteria are of great interest to water quality managers because of the production of toxins and other secondary metabolites by these organisms (see earlier), and the most important factors have been vigorously debated by researchers for several decades. No single factor has been identified, but rather a combination of several conditions appears to lead to cyanobacterial blooms. First, the overproduction of biomass requires large quantities of its elemental constituents, and in inland water environments the factor limiting biomass production is often phosphorus availability. The increased enrichment of lakes by phosphorus, leading to eutrophic conditions (high nutrients and dense phytoplankton concentrations), is generally accompanied by the development of cyanobacterial dominance and blooms. However, this does not occur in all seasons, nor even every year, implying that secondary factors also play a role. Nitrogen availability tends to be of lesser importance, and although many studies have pointed to low N:P ratios as a factor associated with cyanobacterial dominance, this is often a correlate rather than the cause of eutrophic water conditions. High pH and low CO_2 concentrations were also considered causative factors; however, these conditions are also the consequence of a large photosynthetic biomass. Iron availability has also been considered a secondary limiting factor for cyanobacterial growth development in some lakes.

Temperature clearly plays a role in tipping the balance towards cyanobacteria, with blooms becoming more likely as the water column warms above 15 °C. In part this is because cyanobacteria tend to have high temperature optima for maximum growth. However, it is also related to the increased frequency and strength of diurnal thermoclines (near-surface temperature and density gradients) that accompany warming and result in a more stable water column. The absence of mixing allows the cyanobacterial colonies to adjust their position in the water column via their gas vacuoles. This responsiveness to temperature suggests that cyanobacterial blooms will become increasingly common as the world heats up because of greenhouse gas emissions and global climate change. These effects may be exacerbated in regions that have reduced rainfall, and therefore longer lake residence times that favor eutrophication.

The positive buoyancy of bloom-forming cyanobacteria can lead to the sudden appearance of surface scums, which create aesthetic, health, and other water quality problems. These are blown by the wind and can accumulate from throughout the lake to spectacular concentrations along the shoreline and in bays. The shading of phytoplankton lower in the water column, and the rise in pH that accompanies the production of such surface blooms, are two of several mechanisms that continue to favor the ongoing growth and dominance of cyanobacteria once they become established. The production of resting spores (akinetes) and their resistance to grazing pressure by zooplankton are additional strategies that contribute to the ecological success of these bloom-forming organisms.

Picocyanobacteria

Picocyanobacteria are the smallest of cyanobacteria cells, often around one thousandth of a millimeter in diameter; however, they typically occur in high concentrations (the term pico refers to cells smaller than 2 μm). Two of the genera *Synechococcus* and *Prochlorococcus* are so widely distributed in the open ocean that they are probably the most abundant photosynthetic cell types in the biosphere. Freshwater picocyanobacteria are usually ascribed to the genus *Synechococcus*, although this is an artificial taxonomic category that encompasses diverse genotypes and phenotypes. They are readily observed by epifluorescence microscopy, and increasingly by flow cytometry, and comparative studies have shown that they contribute a large proportion of total photosynthetic biomass in oligotrophic lakes. Their high surface-to-volume ratio confers an advantage in low nutrient conditions, and their small size can also be an advantage for light capture because of a lack of internal shading (‘package effect’). These minute cells provide a nutrient and energy source to flagellates and ciliates in the microbial food web, and they are also subject to loss by viral attack (cyanophage).

Picocyanobacteria can reach very high concentrations in nutrient-rich saline lakes where the competition for light may be severe, and where their superior light-capturing ability confers an advantage. An interesting dichotomy is found in the Polar regions, where although picocyanobacteria are typically in low abundance or absent from the marine environment, they are often common in cold lakes and rivers. For example, picocyanobacteria are largely absent from the coastal Southern Ocean, but phycoerythrin-rich *Synechococcus* populations occur in the coastal, meromictic (incompletely mixed because of their salinity gradients) lakes of the Vestfold Hills, Antarctica, coloring the water red with cell concentrations of up to 10 billion per liter.

Other Ecological Groups

Some small-cell species of coccoid cyanobacteria form colonies, and although these rarely produce dense blooms, they are often abundant in the phytoplankton of mesotrophic and eutrophic waters. The most common genera are *Aphanocapsa*, *Aphanothece*, *Coelosphaerium*, *Gomphosphaeria*, and *Merismopedia*. The relationship between these genera and free-living picoplankton is still not clear, and it may be that some are simply an aggregate life-form of solitary cells. On the basis of genetic analyses, Bergey’s Manual of Systematic Bacteriology does not recognize many of these classic genera, and places them within genera containing solitary cells. For example, *Aphanocapsa* and *Merismopedia* are assigned to the form genus *Synechocystis*, and *Aphanothece* to *Cyanothece* or to *Synechococcus*. There is evidence from marine food web analyses that picocyanobacterial aggregates may provide a direct food source for higher trophic levels such as copepods, but little is known about their trophic role in inland waters, despite their frequent presence in the freshwater plankton.

Certain cyanobacterial taxa are often found in loose association with emergent plants in ponds and wetlands. This community is referred to as the metaphyton, and includes genera such as *Chroococcus*, *Leptolyngbya*, *Merismopedia*, and *Phormidium*. In peat bogs, genera such as *Aphanothece*, *Chroococcus*, *Hapalosiphon*, *Merismopedia*, and *Tolypothrix* are found in association with the *Sphagnum* moss, and occur at acidic pH's as low as 4.

Some cyanobacteria occupy both benthic as well as planktonic habitats. For example, the saline lake species *Aphanothece halophytica* commonly forms mucilaginous, benthic films, but it is also often found in the phytoplankton of such lakes, sometimes at high concentrations. One common freshwater species, *Gloeotrichia echinulata*, develops on sediments and plants in eutrophic lakes and ponds in spring and early summer, and then in late summer can become gas vacuolated, producing an abundant population of large (from submillimeter to several centimeters) spherical colonies in the plankton.

The symbiotic interactions of cyanobacteria include close associations with fungi to form lichens, sometimes found in semiaquatic habitats but usually in the surrounding terrestrial environment; on or inside mosses; as an endosymbiont within the semiaquatic angiosperm *Gunnera*; and within the floating fern *Azolla*, which is often cultivated in rice fields for its nitrogen content. Certain cyanobacterial species are also cultivated in artificial or naturally eutrophic ponds, lagoons, and lakes as a protein source for human consumption, animal feed, fertilizer, or health food. The most important of these is *Arthrospira* ('Spirulina'), which is commercially exploited because of its nutritional value, lack of toxins, high growth rates (doubling times less than 12 h), and tolerance to environmental stress.

See also: Aquaculture, Freshwater; Cyanoprokaryota and Other Prokaryotic Algae; Effects of Climate Change on Lakes; Harmful Algal Blooms; Microbial Food Webs; Nitrogen Fixation; Phytoplankton Productivity; Viruses.

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