

Toxic Cyanobacteria in Water: A guide to their public health consequences, monitoring and management

Edited by Ingrid Chorus and Jamie Bartram

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ISBN 0-419-23930-8

Chapter 2. CYANOBACTERIA IN THE ENVIRONMENT

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For management of cyanobacterial hazards to human health, a basic understanding of the properties, the behaviour in natural ecosystems, and the environmental conditions which support the growth of certain species is helpful. This chapter provides information on how cyanobacteria are structured and the abilities which they possess that support their proliferation in aquatic ecosystems.

2.1 Nature and diversity

2.1.1 Systematics

Plants and animals possess consistent features by which they can be identified reliably and sorted into recognisably distinct groups. Biologists observe and compare what the organisms look like, how they grow and what they do. The results make it possible to construct systematic groupings based on multiple correlations of common characters and that reflect the greatest overall similarity. The basis for such groupings is the fact that all organisms are related to one another by way of evolutionary descent. Their biology and phylogenetic relationships makes the establishment of systematic groupings possible (Minkoff, 1983).

However, microbial systematics has long remained an enigma. Conceptual advances in microbiology during the twentieth century included the realisation that a discontinuity exists between those cellular organisms that are prokaryotic (i.e. whose cells have no nucleus) and those that are eukaryotic (i.e. more complexly structured cells with a nucleus) within the organisation of their cells. The microalgae investigated by phycologists under the International Code of Botanical Nomenclature (ICBN) (Greuter *et al.*, 1994) included organisms of both eukaryotic and prokaryotic cell types. The blue-green algae (Geitler, 1932) constituted the largest group of the latter category. The prokaryotic nature of these organisms and their fairly close relationship with eubacteria made work under provisions of the International Code of Nomenclature of Bacteria (ICNB) (Sneath, 1992) more appropriate (Rippka *et al.*, 1979; Waterbury, 1992).

The prevailing systematic view is that comparative studies of the genetic constitution of the cyanobacteria will now contribute significantly to the revision of their taxonomy. Relevant classification should reflect as closely as possible the phylogenetic

relationships as, for example, encoded in 16S or 23S rRNA sequence data (Woese, 1987). The integration of phenotypic, genotypic and phylogenetic information render possible a consensus type of taxonomy known as polyphasic taxonomy (Vandamme *et al.*, 1996).

The names "cyanobacteria" and "blue-green algae" (Cyanophyceae) are valid and compatible systematic terms. This group of micro-organisms comprises unicellular to multicellular prokaryotes that possess chlorophyll *a* and perform oxygenic photosynthesis associated with photosystems I and II (Castenholz and Waterbury, 1989).

2.1.2 Occurrence in nature

The majority of cyanobacteria are aerobic photoautotrophs. Their life processes require only water, carbon dioxide, inorganic substances and light. Photosynthesis is their principal mode of energy metabolism. In the natural environment, however, it is known that some species are able to survive long periods in complete darkness. Furthermore, certain cyanobacteria show a distinct ability for heterotrophic nutrition (Fay, 1965).

Cyanobacteria are often the first plants to colonise bare areas of rock and soil. Adaptations, such as ultraviolet absorbing sheath pigments, increase their fitness in the relatively exposed land environment. Many species are capable of living in the soil and other terrestrial habitats, where they are important in the functional processes of ecosystems and the cycling of nutrient elements (Whitton, 1992).

The prominent habitats of cyanobacteria are limnic and marine environments. They flourish in water that is salty, brackish or fresh, in cold and hot springs, and in environments where no other microalgae can exist. Most marine forms (Humm and Wicks, 1980) grow along the shore as benthic vegetation in the zone between the high and low tide marks. The cyanobacteria comprise a large component of marine plankton with global distribution (Wille, 1904; Gallon *et al.*, 1996). A number of freshwater species are also able to withstand relatively high concentrations of sodium chloride. It appears that many cyanobacteria isolated from coastal environments tolerate saline environments (i.e. are halotolerant) rather than require salinity (i.e. are halophilic). As frequent colonisers of euryhaline (very saline) environments, cyanobacteria are found in salt works and salt marshes, and are capable of growth at combined salt concentrations as high as 3-4 molar mass (Reed *et al.*, 1984). Freshwater localities with diverse trophic states are the prominent habitats for cyanobacteria. Numerous species characteristically inhabit, and can occasionally dominate, both near-surface epilimnic and deep, euphotic, hypolimnic waters of lakes (Whitton, 1973). Others colonise surfaces by attaching to rocks or sediments, sometimes forming mats that may tear loose and float to the surface.

Cyanobacteria have an impressive ability to colonise infertile substrates such as volcanic ash, desert sand and rocks (Jaag, 1945; Dor and Danin, 1996). They are extraordinary excavators, boring hollows into limestone and special types of sandstone (Weber *et al.*, 1996). Another remarkable feature is their ability to survive extremely high and low temperatures. Cyanobacteria are inhabitants of hot springs (Castenholz, 1973), mountain streams (Kann, 1988), Arctic and Antarctic lakes (Skulberg, 1996a) and snow and ice (Kol, 1968; Laamanen, 1996). The cyanobacteria also include species that run through the entire range of water types, from polysaprobic zones to katharobic waters (Van Landingham, 1982).

Cyanobacteria also form symbiotic associations with animals and plants. Symbiotic relations exist with, for example, fungi, bryophytes, pteridophytes, gymnosperms and angiosperms (Rai, 1990). The hypothesis for the endosymbiotic origin of chloroplasts and mitochondria should be mentioned in this context. The evolutionary formation of a photosynthetic eukaryote can be explained by a cyanobacteria being engulfed and co-developed by a phagotrophic host (Douglas, 1994).

Fossils of what were almost certainly prokaryotes are present in the 3,450 million year old Warrawoona sedimentary rock of north-western Australia. Cyanobacteria were among the pioneer organisms of the early earth (Brock 1973; Schopf, 1996). These photosynthetic micro-organisms were, at that time, probably the chief primary producers of organic matter, and the first organisms to release elemental oxygen into the primitive atmosphere. Sequencing of deoxyribonucleic acid (DNA) has given evidence that the earliest organisms were thermophilic and thus able to survive in oceans that were heated by volcanoes, hot springs and bolide impacts (Holland, 1997).

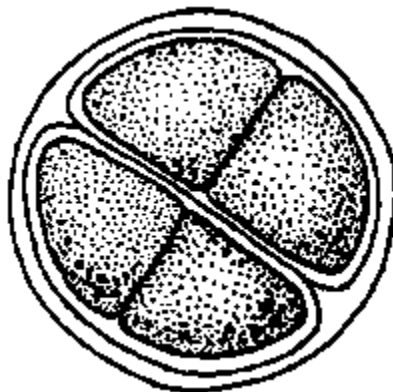
2.1.3 Organisation, function and behaviour

The structure and organisation of cyanobacteria are studied using light and electron microscopes. The basic morphology comprises unicellular, colonial and multicellular filamentous forms (Figure 2.1).

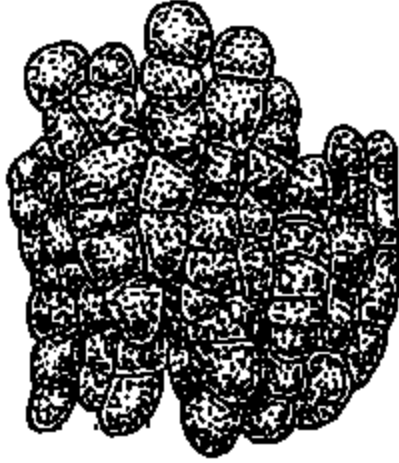
Unicellular forms, for example in the order Chroococcales, have spherical, ovoid or cylindrical cells. They occur singly when the daughter cells separate after reproduction by binary fission. The cells may aggregate in irregular colonies, being held together by the slimy matrix secreted during the growth of the colony. By means of a more or less regular series of cell division, combined with sheath secretions, more ordered colonies may be produced.

Figure 2.1 Basic morphology of cyanobacteria

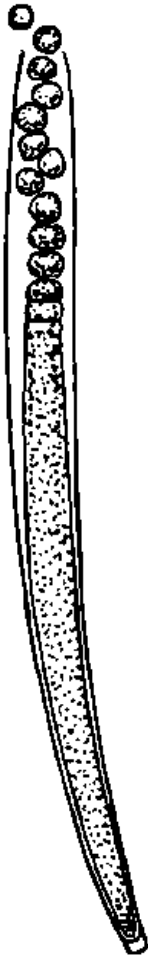
Unicellular, isopolar (Order: *Chroococcales*)



Pseudoparenchymatous (Order: *Pleurocapsales*)



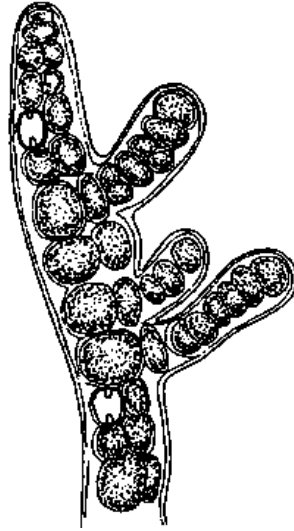
Unicellular, heteropolar (Order: *Chamaesiphonales*)



Multicellular, trichal, heterocysts not present (Order: *Oscillatoriales*)



Multicellular, trichal, with branches, heterocysts present (Order: *Stigonematales*)



Multicellular, trichal, heterocysts present (Order: *Nostocales*)



A particular mode of reproduction, which may supplement binary fission, distinguishes cyanobacteria in the order Chamaesiphonales and Pleurocapsales. In the Chamaesiphonales exospores are budded off from the upper ends of cells. In the second order, the principal mode of replication is by a series of successive binary fissions converting a single mother cell into many minute daughter cells (baecytes or endospores).

Filamentous morphology is the result of repeated cell divisions occurring in a single plane at right angles to the main axis of the filament. The multicellular structure consisting of a chain of cells is called a trichome. The trichome may be straight or coiled. Cell size and shape show great variability among the filamentous cyanobacteria. Species in the order Oscillatoriales, with uniseriated and unbranched trichomes, are composed of essentially identical cells. The other orders with a filamentous organisation

(orders Nostocales and Stigonematales) are characterised with trichomes having a heterogeneous cellular composition. Vegetative cells may be differentiated into heterocysts (having a thick wall and hyaline protoplast, capable of nitrogen fixation) and akinetes (large thick-walled cells, containing reserve materials, enabling survival under unfavourable conditions). In the order Stigonematales, the filaments are often multiseriated, with genuine branching. Both heterocysts and akinetes are present.

The only means of reproduction in cyanobacteria is asexual. Filamentous forms reproduce by trichome fragmentation, or by formation of special hormogonia. Hormogonia are distinct reproductive segments of the trichomes. They exhibit active gliding motion upon their liberation and gradually develop into new trichomes.

In contrast to eukaryotic microalgae, cyanobacteria do not possess membrane-bound sub-cellular organelles; they have no discrete membrane-bound nucleus; they possess a wall structure based upon a peptidoglycan layer; and they contain 70 S rather than 80 S ribosomes (Fay and Van Baalen, 1987; Bryant, 1994).

The photosynthetic pigments of cyanobacteria are located in thylakoids that lie free in the cytoplasm near the cell periphery. Cell colours vary from blue-green to violet-red. The green of chlorophyll *a* is usually masked by carotenoids (e.g. beta-carotene) and accessory pigments such as phycocyanin, allophycocyanin and phycoerythrin (phycobiliproteins). The pigments are embodied in phycobilisomes, which are found in rows on the outer surface of the thylakoids (Douglas, 1994). All cyanobacteria contain chlorophyll *a* and phycocyanine.

The basic features of photosynthesis in cyanobacteria have been well described (Ormerod, 1992). Cyanobacteria are oxygenic phototrophs possessing two kinds of reaction centres, PS I and PS II, in their photosynthetic apparatus. With the accessory pigments mentioned above, they are able to use effectively that region of the light spectrum between the absorption peaks of chlorophyll *a* and the carotenoids. The ability for continuous photo-synthetic growth in the presence of oxygen, together with having water as their electron donor for CO₂ reduction, enables cyanobacteria to colonise a wide range of ecological niches (Whitton, 1992). Phycobiliprotein synthesis is particularly susceptible to environmental influences, especially light quality. Chromatic adaptation is largely attributable to a change in the ratio between phycocyanin and phycoerythrin in the phycobilisomes. Thus, cyanobacteria are able to produce the accessory pigment needed to absorb light most efficiently in the habitat in which they are present.

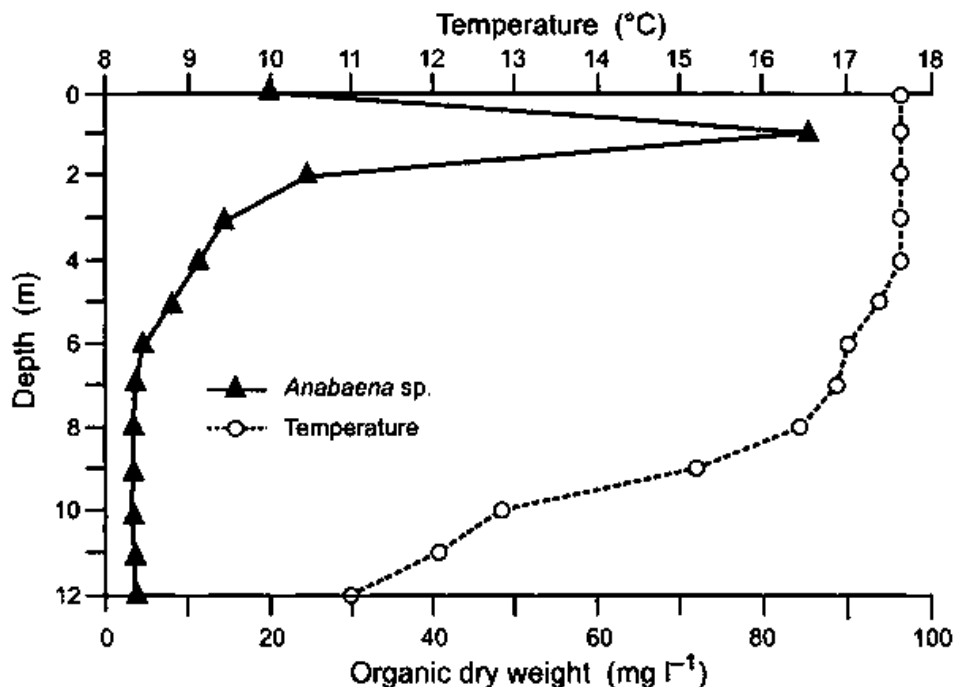
Cyanobacteria have a remarkable ability to store essential nutrients and metabolites within their cytoplasm. Prominent cytoplasmic inclusions for this purpose can be seen with the electron microscope (e.g. glycogen granules, lipid globules, cyanophycin granules, polyphosphate bodies, carboxysomes) (Fay and Van Baalen, 1987). Reserve products are accumulated under conditions of an excess supply of particular nutrients. For example, when the synthesis of nitrogenous cell constituents is halted because of an absence of a usable nitrogen source, the primary products of photosynthesis are channelled towards the synthesis and accumulation of glycogen and lipids.

Dinitrogen fixation is a fundamental metabolic process of cyanobacteria, giving them the simplest nutritional requirements of all living organisms. By using the enzyme nitrogenase, they convert N₂ directly into ammonium (NH₄) (a form through which

nitrogen enters the food chain) and by using solar energy to drive their metabolic and biosynthetic machinery, only N_2 , CO_2 , water and mineral elements are needed for growth in the light. Nitrogen-fixing cyanobacteria are widespread among the filamentous, heterocyst forming genera (e.g. *Anabaena*, *Nostoc*) (Stewart, 1973). However, there are also several well documented examples of dinitrogen fixation among cyanobacteria not forming heterocysts (e.g. *Trichodesmium*) (Carpenter *et al.*, 1992). Under predominantly nitrogen limited conditions, but when other nutrients are available, nitrogen fixing cyanobacteria may be favoured and gain growth and reproductive success. Mass developments (often referred to as "blooms") of such species in limnic (e.g. eutrophic lakes, see Figure 2.2 in the colour plate section) and marine environments (e.g. the Baltic Sea) are common phenomena world-wide.

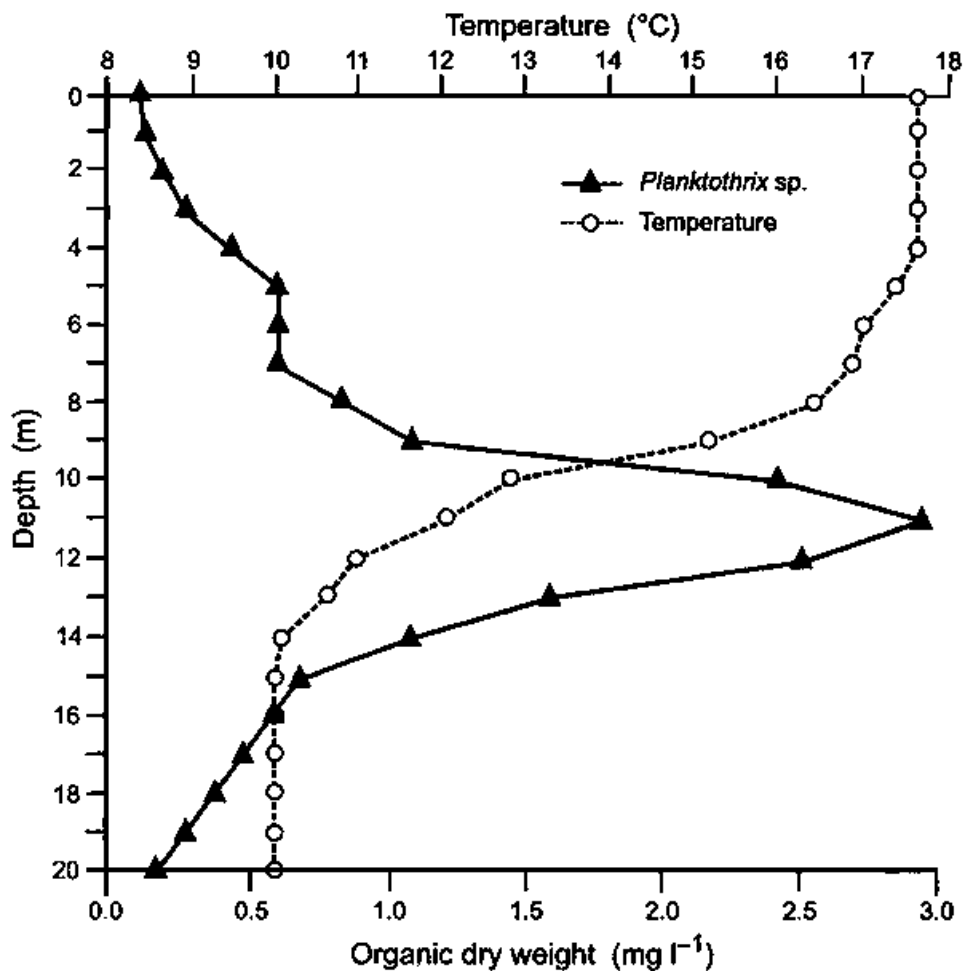
Many species of cyanobacteria possess gas vesicles. These are cytoplasmic inclusions that enable buoyancy regulation and are gas-filled, cylindrical structures. Their function is to give planktonic species an ecologically important mechanism enabling them to adjust their vertical position in the water column (Walsby, 1987). To optimise their position, and thus to find a suitable niche for survival and growth, cyanobacteria use different environmental stimuli (e.g. photic, gravitational, chemical, thermal) as clues. Gas vesicles become more abundant when light is reduced and the growth rate slows down. Increases in the turgor pressure of cells, as a result of the accumulation of photosynthate, cause a decrease in existing gas vesicles and therefore a reduction in buoyancy. Cyanobacteria can, by such buoyancy regulation, poise themselves within vertical gradients of physical and chemical factors (Figures 2.3A and 2.3B). Other ecologically significant mechanisms of movement shown by some cyanobacteria are photomovement by slime secretion or surface undulations of cells (Häder, 1987; Paerl, 1988).

Figure 2.3A Vertical distribution of *Anabaena* sp. in a thermally stratified eutrophic lake during bloom conditions



The presence of very small cells of cyanobacteria (in the size range 0.2-2 μm) has been recognised as a potentially significant source of primary production in various freshwater and marine environments. These cyanobacteria constitute a component of the picoplankton in pelagic ecosystems. Cells can be recognised and estimates of their abundance made by using epifluorescence microscopy (e.g. observing the orange fluorescence due to phycoerythrin). The unicellular genus *Synechococcus* is one of the most studied, and geographically most widely distributed, cyanobacteria in the picoplankton. Toxigenic strains of *Synechococcus* have been reported (Skulberg *et al.*, 1993).

Figure 2.3B Vertical distribution of *Planktothrix* sp. in a thermally stratified meso-oligotrophic lake during bloom conditions



2.1.4 Biological diversity

Although cyanobacteria probably evolved as a group of organisms about 2,000 million years before the advent of eukaryotes, they comprise fewer taxa than eukaryotic microalgae (Bisby, 1995). The concept of species in the cyanobacteria has, however, no distinct boundaries. The situation is similar for most organisms, except for those that are sexually reproductive. Depending on the classification system used, the number of species recognised varies greatly. Based on the International Code of Botanical

Nomenclature the class Cyanophyceae, for example, contains about 150 genera and 2,000 species (Hoek *et al.*, 1995).

Chemotaxonomic studies include the use of markers, such as lipid composition, polyamines, carotenoids and special biochemical features. The resulting data support the more traditional examinations of phenotypic and ecological characteristics. Physiological parameters are conveniently studied using laboratory cultures (Packer and Glazer, 1988).

The diversity of cyanobacteria can be seen in the multitude of structural and functional aspects of cell morphology and in variations in metabolic strategies, motility, cell division, developmental biology, etc. The production of extracellular substances and cyanotoxins by cyanobacteria illustrates the diverse nature of their interactions with other organisms (i.e. allelopathy) (Rizvi and Rizvi, 1992).

A molecular approach to the systematics of cyanobacteria may be most fruitful for inferring phylogenetic relationships. Macromolecules, such as nucleic acids and proteins, are copies or translations of genetic information. The methods applied involve direct studies of the relevant macromolecules by sequencing, or indirectly by electrophoresis, hybridisation, or immunological procedures (Wilmotte, 1994). Nucleic acid technologies, especially the polymerase chain reaction (PCR), have advanced to the point that it is feasible to amplify and sequence genes and other conserved regions from a single cell. To date, 16S rRNA has given the most detailed information on the relationships within the cyanobacteria (Rudi *et al.*, 1997). However, the molecular results obtained should be integrated with other characteristics as the base for a polyphasic taxonomy (Vandamme, *et al.*, 1996). A considerable morphological, as well as a genotypical, polymorphism exists in the cyanobacteria, although as data from rRNA sequencing indicates they are correlated to a high degree.

The phylogenetic relationship of cyanobacteria is the rationale behind the meaningful systematic groupings. However, it is difficult to set up a system of classification that serves both the everyday need for practical identification, and offers an expression of the natural relationship between the organisms in question (Mayr, 1981). Meanwhile, it will be necessary to use the available manuals and reference books to help in these investigations and with the proper identification of the cyanobacteria. Table 12.1 shows examples of how cyanobacteria with toxigenic strains are treated for determinative purposes according to the prevailing classification systems.

Because they are photoautotrophs, cyanobacteria can be grown in simple mineral media. Vitamin B₁₂ is the only growth factor that is known to be required by some species. Media must be supplemented with the essential nutrients needed to support cell growth, including sources of nitrogen, phosphorus, trace elements, etc. Toxigenic strains of cyanobacteria are deposited in international-type culture collections (Rippka, 1988; Sugawara *et al.*, 1993). Clonal cultures are distributed for research, taxonomic work and teaching purposes.

2.1.5 Practical scope

The cyanobacteria have both beneficial and detrimental properties when judged from a human perspective. Their extensive growth can create considerable nuisance for

management of inland waters (water supply, recreation, fishing, etc.) and they also release substances into the water which may be unpleasant (Jüttner, 1987) or toxic (Gorham and Carmichael, 1988). The water quality problems caused by dense populations of cyanobacteria are intricate, many and various (Skulberg, 1996b) and can have great health and economic impacts. As a consequence, the negative aspects of cyanobacteria have gained research attention and public concern.

The properties that make the cyanobacteria generally undesirable are also the qualifications for possible positive economic use. Blue-greens are the source of many valuable products (Richmond, 1990) and carry promising physiological processes, including light-induced hydrogen evolution by biophotolysis (Skulberg, 1994). Extensive research has taken place in the relevant fields of biotechnology. Cyanobacteria may be used for food or fodder because some strains have a very high content of proteins, vitamins and other essential growth factors and vital pigments of interest can also be produced (Borowitzka and Borowitzka, 1988). Cyanobacteria are also sources for substances of pharmaceutical interest (such as antibiotics) (Falch *et al.*, 1995). These examples are only a few of the possible applications of cyanobacteria for economic development and their exploitation is among the many challenges for biotechnology for the next millennium. Also in this context, their secondary metabolites and health relationships will become important.

2.2 Factors affecting bloom formation

Cyanobacteria have a number of special properties which determine their relative importance in phytoplankton communities. However, the behaviour of different cyanobacterial taxa in nature is not homogeneous because their ecophysiological properties differ. An understanding of their response to environmental factors is fundamental for setting water management targets. Because some cyanobacteria show similar ecological and ecophysiological characteristics, they can be grouped by their behaviour in planktonic ecosystems as "ecostrategists" typically inhabiting different niches of aquatic ecosystems. A number of properties and reactions to environmental conditions are discussed below in order to describe these ecostrategists and to aid the understanding of their specific behaviour.

2.2.1 Light intensity

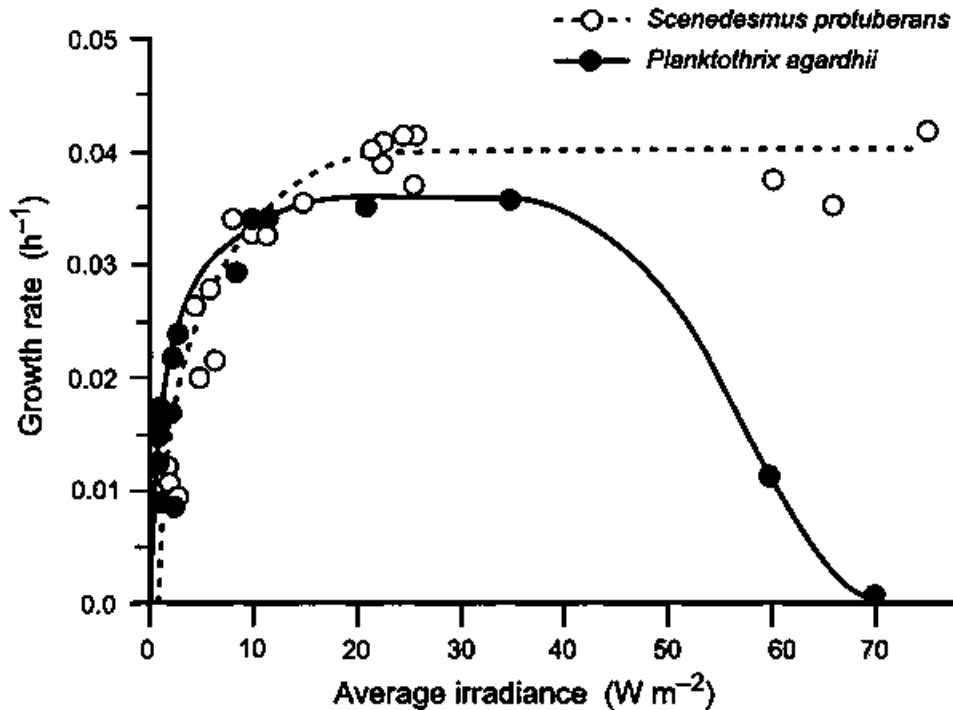
Like algae, cyanobacteria contain chlorophyll *a* as a major pigment for harvesting light and conducting photosynthesis. They also contain other pigments such as the phycobiliproteins which include allophycocyanin (blue), phycocyanin (blue) and sometimes phycoerythrin (red) (Cohen-Bazir and Bryant, 1982). These pigments harvest light in the green, yellow and orange part of the spectrum (500-650 nm) which is hardly used by other phytoplankton species. The phycobiliproteins, together with chlorophyll *a*, enable cyanobacteria to harvest light energy efficiently and to live in an environment with only green light.

Many cyanobacteria are sensitive to prolonged periods of high light intensities. The growth of *Planktothrix* (formerly *Oscillatoria*) *agardhii* is inhibited when exposed for extended periods to light intensities above $180 \mu\text{E m}^{-2} \text{s}^{-1}$. Long exposures at light intensities of $320 \mu\text{E m}^{-2} \text{s}^{-1}$ are lethal for many species (Van Liere and Mur, 1980). However, if exposed intermittently to this high light intensity, cyanobacteria grow at their

approximate maximal rate (Loogman, 1982). This light intensity amounts to less than half of the light intensity at the surface of a lake, which can reach 700-1,000 $\mu\text{E m}^{-2} \text{s}^{-1}$. Cyanobacteria which form surface blooms seem to have a higher tolerance for high light intensities. Paerl *et al.* (1983) related this to an increase in carotenoid production which protects the cells from photoinhibition.

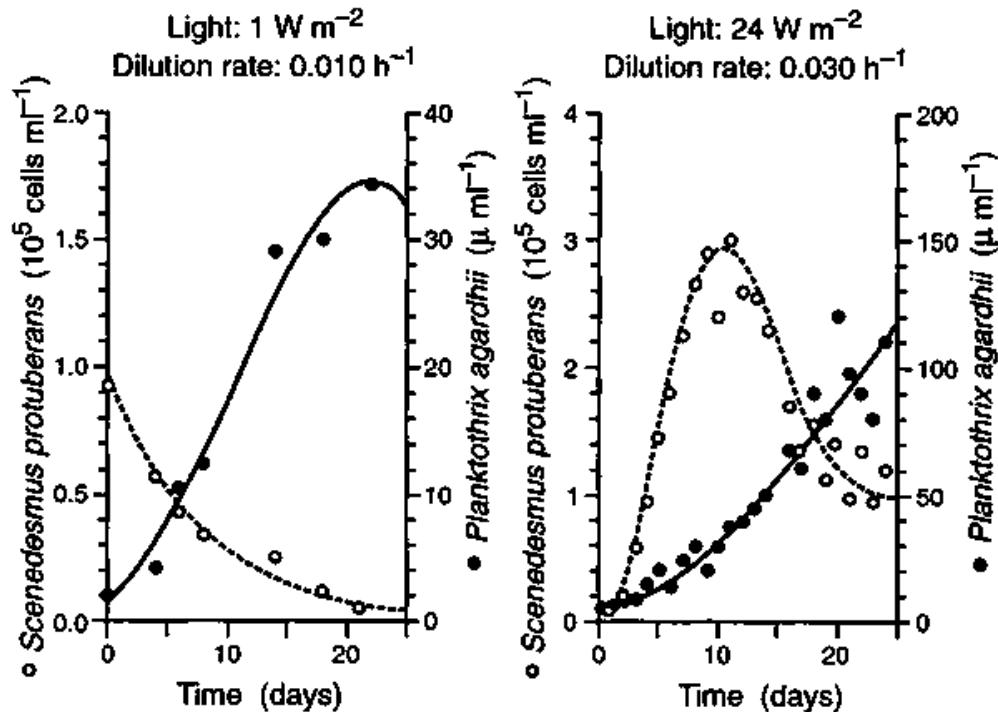
Cyanobacteria are further characterised by a favourable energy balance. Their maintenance constant is low which means that they require little energy to maintain cell function and structure (Gons, 1977; Van Liere *et al.*, 1979). As a result of this, the cyanobacteria can maintain a relatively higher growth rate than other phytoplankton organisms when light intensities are low. The cyanobacteria will therefore have a competitive advantage in lakes which are turbid due to dense growths of other phytoplankton. This was demonstrated in an investigation measuring growth of different species of phytoplankton at various depths in a eutrophic Norwegian lake (Källqvist, 1981). The results showed that the diatoms *Asterionella*, *Diatoma* and *Synedra* grew faster than the cyanobacterium *Planktothrix* at 1 m depth, while the growth rate was about the same for all these organisms at 2 m depth. At the very low light intensities below 3 m only *Planktothrix* grew. The ability of cyanobacteria to grow at low light intensities and to harvest certain specific light qualities, enables them to grow in the "shadow" of other phytoplankton. Van Liere and Mur (1979) demonstrated competition between cyanobacteria and other phytoplankton. Whereas the green alga (*Scenedesmus protuberans*) grew faster at high light intensities, growth of the cyanobacterium (*Planktothrix agardhii*) was faster at low light intensities (Figures 2.4A and 2.4B). If both organisms were grown in the same continuous culture at low light intensity, *Planktothrix* could out-compete *Scenedesmus* (Figure 2.4A). At high light intensities, the biomass of the green alga increased rapidly, causing an increase in turbidity and a decrease in light availability. This increased the growth rate of the cyanobacterium, which then became dominant after 20 days (Figure 2.4B). Although cyanobacteria cannot reach the maximum growth rates of green algae, at very low light intensities their growth rate is higher. Therefore, in waters with high turbidity they have better chances of out-competing other species. This can explain why cyanobacteria which can grow under very poor nutritional conditions (see section 2.2.4) often develop blooms in nutrient-rich eutrophic waters.

Figure 2.4A Competition for light between a cyanobacterium and a green alga. Growth rates of *Planktothrix agardhii* Gomont and *Scenedesmus protuberans* Fritsch as a function of average light intensities at pH 8.0, 20 °C with continuous illumination (Redrawn after Van Liere, 1979)



The light conditions in a given water body determine the extent to which the physiological properties of cyanobacteria will be of advantage in their competition against other phytoplankton organisms (Mur *et al.*, 1978). The zone in which photosynthesis can occur is termed the euphotic zone (Z_{eu}). By definition, the euphotic zone extends from the surface to the depth at which 1 per cent of the surface light intensity can be detected. It can be estimated by measuring transparency with a Secchi disk (see Chapter 11) and multiplying the Secchi depth reading by a factor of 2-3. The euphotic zone may be deeper or more shallow than the mixed, upper zone of a thermally stratified water body, the depth of which is termed the epilimnion (Z_m) (Figure 2.5). Many species of planktonic algae and cyanobacteria have little, or only weak, means of active movement and are passively entrained in the water circulation within the epilimnion. Thus, they can be photosynthetically active only when the circulation maintains them in the euphotic zone. In eutrophic waters, phytoplankton biomass is frequently very high and causes substantial turbidity. In such situations, the euphotic zone is often more shallow than the epilimnion, i.e. the ratio Z_{eu}/Z_m is < 1 , and phytoplankton spend part of the daylight period in the dark. Thus, the Z_{eu}/Z_m ratio is a reasonable (and easy to measure) approach to describing the light conditions encountered by the planktonic organisms.

Figure 2.4B Competition for light between a cyanobacterium and a green alga. Outcome of competition between *Planktothrix agardhii* Gomont and *Scenedesmus protuberans* Fritsch in continuous cultures at two different light intensities and dilution rates (Redrawn after Van Liere, 1979)



2.2.2 Gas vesicles

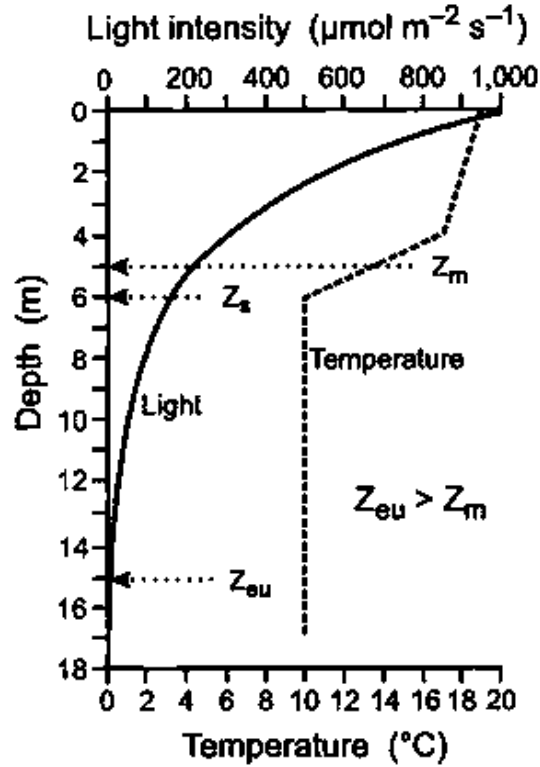
Many planktonic cyanobacteria contain gas vacuoles (Walsby, 1981). These structures are aggregates of gas-filled vesicles, which are hollow chambers with a hydrophilic outer surface and a hydrophobic inner surface (Walsby, 1978). A gas vesicle has a density of about one tenth that of water (Walsby, 1987) and thus gas vesicles can give cyanobacterial cells a lower density than water.

2.2.3 Growth rate

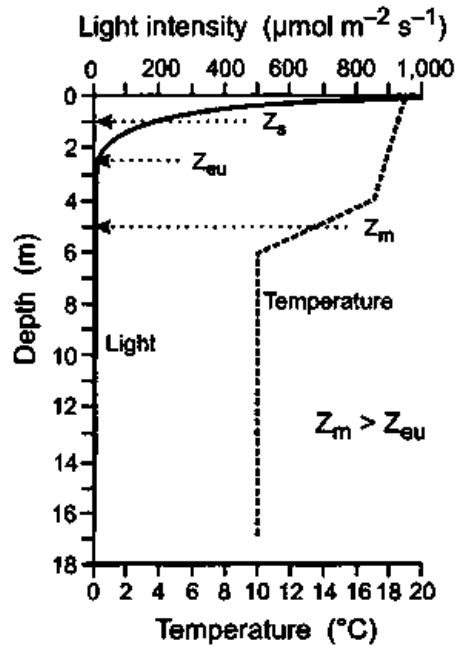
The growth rate of cyanobacteria is usually much lower than that of many algal species (Hoogenhout and Ames, 1965; Reynolds, 1984). At 20 °C and light saturation, most common planktonic cyanobacteria achieve growth rates of 0.3-1.4 doublings per day, while diatoms reach 0.8-1.9 doublings per day and growth rates of up to 1.3-2.3 doublings per day have been observed for single-celled green algae (Van Liere and Walsby, 1982). Slow growth rates require long water retention times to enable a bloom of cyanobacteria to form. Therefore cyanobacteria do not bloom in water with short retention times. A comprehensive overview of mechanisms determining the growth rates of planktonic algae and cyanobacteria under different field conditions is available in Reynolds (1997).

Figure 2.5 Vertical extension of the euphotic zone (Z_{eu}) in relation to depth of the epilimnion (Z_m) in situations with different turbidity.

A. Euphotic zone is deeper than epilimnion;



B. Euphotic zone is not as deep as epilimnion. Secchi depth (Z_s) is included as rough measure of euphotic depth (Z_{eu}) ($Z_s \times 2.5 \cong Z_{eu}$)



2.2.4 Phosphorus and nitrogen

Because cyanobacterial blooms often develop in eutrophic lakes, it was originally assumed that they required high phosphorus and nitrogen concentrations. This assumption was maintained even though cyanobacterial blooms often occurred when concentrations of dissolved phosphate were lowest. Experimental data have shown that the affinity of many cyanobacteria for nitrogen or phosphorus is higher than for many other photosynthetic organisms. This means that they can out-compete other phytoplankton organisms under conditions of phosphorus or nitrogen limitation.

In addition to their high nutrient affinity, cyanobacteria have a substantial storage capacity for phosphorus. They can store enough phosphorus to perform two to four cell divisions, which corresponds to a 4-32 fold increase in biomass. However, if total phosphate rather than only dissolved phosphate is considered, high concentrations indirectly support cyanobacteria because they provide a high carrying capacity for phytoplankton. High phytoplankton density leads to high turbidity and low light availability, and cyanobacteria are the group of phytoplankton organisms which can grow best under these conditions.

A low ratio between nitrogen and phosphorus concentrations may favour the development of cyanobacterial blooms. A comparison between the optimum N:P ratios for eukaryotic algae (16-23 molecules N:1 molecule of P) with the optimum rates for bloom-forming cyanobacteria (10-16 molecules N: 1 molecule P), shows that the ratio is lower for cyanobacteria (Schreurs, 1992).

2.2.5 Population stability

While many planktonic algae are grazed by copepods, daphnids and protozoa, cyanobacteria are not grazed to the same extent, and the impact of grazing by some specialised ciliates and rhizopod protozoans is usually not substantial. Cyanobacteria are attacked by viruses, bacteria and actino-mycetes, but the importance of these natural enemies for the breakdown of populations is not well understood. Because they have few natural enemies, and their capacity for buoyancy regulation prevents sedimentation, the loss rates of cyanobacterial populations are generally low. Thus, their slow growth rates are compensated by the high prevalence of populations once they have been established.

2.2.6 Temperature

Maximum growth rates are attained by most cyanobacteria at temperatures above 25 °C (Robarts and Zohary, 1987). These optimum temperatures are higher than for green algae and diatoms. This can explain why in temperate and boreal water bodies most cyanobacteria bloom during summer.

2.3 Cyanobacterial ecostrategists

The physiological properties of cyanobacteria discussed above vary between different species. As a consequence, different "ecostrategists" inhabit different types of water bodies. A preliminary approach to describing these ecostrategists, based on

ecophysiological laboratory work together with field observations (largely from north-western Europe), is described below. This information may be useful for management, because it helps to predict which cyanobacteria can be expected to occur under certain conditions. Further development of this approach will be possible as more data on occurrence of cyanobacteria under different growth conditions are collected from other continents.

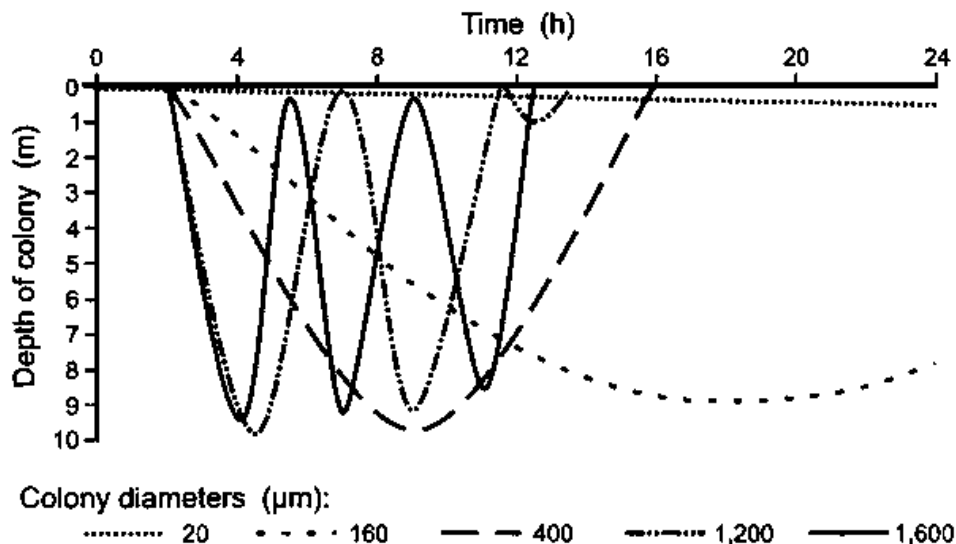
2.3.1 Scum-forming ecostrategists

During the vegetation period, a number of cyanobacteria develop large aggregates (colonies) of coccoid cells or filaments which are not homogeneously distributed over the water column. Important genera showing this development are *Microcystis*, *Anabaena* and *Aphanizomenon*. At the water surface the rate of photosynthesis of the colonies is high and the cells store large quantities of carbohydrates. Although the cells contain gas vesicles, the heavy carbohydrates acts as ballast and induce sinking within the colonies. According to Stoke's Law the sinking rate is dependent on the difference in density between the water and the cells, and on the square of the colony size (d^2). Large colonies sink faster than small ones, and single cells hardly show any vertical migration. By sinking, colonies move out of the euphotic zone into the deeper, dark water layers, where they use their carbohydrates during respiration and synthesise new gas-vesicles (Utkilen *et al.*, 1985). They then become buoyant again and return to the euphotic zone. Buoyancy regulation enables the colonies to position themselves in light conditions which are optimal for their growth. A prerequisite is that the water body is not too turbulent. During the night, all colonies may become buoyant and some of the population may be accumulated on the water surface where they can be blown together by wind, forming stable scums along downwind shores. Vertical movement by buoyancy regulation is illustrated in Figure 2.6. The frequency of vertical migration is dependent upon colony size.

In temperate regions, as temperatures decline in the autumn, photosynthesis becomes more rapid than respiration, and the carbohydrate "ballast" is not consumed. The colonies therefore sink to the bottom of the water body where they may survive the winter, gradually consuming their carbohydrate stores by respiration or fermentation. Cells which re-ascend from the bottom in the spring are unicellular or formed into very small colonies. During this period *Microcystis* spp. is difficult to recognise in plankton samples, and only becomes more conspicuous when the colonies increase in size during early summer.

Buoyancy regulation can be a substantial advantage in competition with other phytoplankton organisms. However, this type of regulation is only possible in water bodies with a shallow euphotic zone in relation to the depth of vertical mixing ($Z_{eu} < Z_m$). Therefore, in temperate climates, blooms of *Microcystis* spp. are found particularly in water bodies deeper than 3 m, because the euphotic zone is likely to be substantially more shallow than the mixed depth. However, even in shallow lakes, where they do not have the competitive advantage of vertical migration, *Microcystis* spp. may become dominant and form substantial blooms, as has been reported from Hungary, Australia, and particularly from subtropical and tropical regions. Reynolds (1997) characterises *Microcystis* spp. as notoriously and overwhelmingly dominant in some lakes of the lower latitudes that exhibit diel stratification.

Figure 2.6 Effect of colony size on vertical movement of *Microcystis aeruginosa* by buoyancy regulation (simulation). Colonies with diameters <20 μm scarcely migrate, colonies with diameters <160 μm accomplish less than one migration per day, and colonies up to 1,600 μm diameter can migrate down to 10 m depth and back up to the surface three times per day

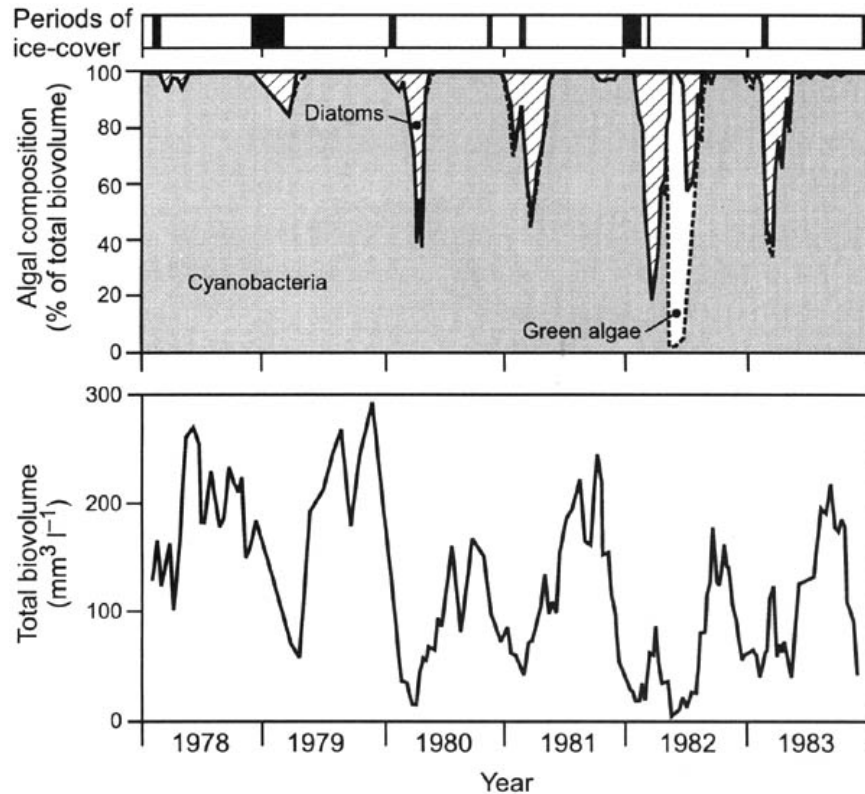


Many cyanobacteria cannot survive high light intensities over longer periods. This may limit their distribution to more turbid, eutrophic ecosystems. However, *Microcystis* species are less sensitive to high light intensities because buoyancy regulation enables them to find light conditions that are optimal for their growth. This means that the presence of *Microcystis* cannot be related strictly to the level of eutrophication. The genus is therefore found in mesotrophic, eutrophic and in hypertrophic waters. However, the amount of biomass that this species can attain depends on the level of eutrophication. Most *Microcystis* blooms are found in lakes with an average summer chlorophyll *a* concentration of 20-50 $\mu\text{g l}^{-1}$ and a Secchi transparency of 1-2 m.

2.3.2 Homogeneously dispersed ecostrategists

This ecotype comprises filamentous species, such as *Planktothrix (Oscillatoria) agardhii* and *Limnothrix (Oscillatoria) redekei*. These species are extremely sensitive to high light intensities and do not form colonies (Reynolds, 1987). Because the filaments are quite small, vertical migration by buoyancy regulation is less pronounced than their passive entrainment by water circulation. Therefore, these species are homogeneously dispersed throughout the epilimnion.

Figure 2.7 Distribution of phytoplankton in Lake Veluwe, The Netherlands, showing an almost permanent bloom of cyanobacteria during the years 1978-83. The dominant bloom of *Planktothrix agardhii* was only interrupted by periods of ice cover (Redrawn from RIZA, 1996)



This type of ecostrategist is found in eutrophic and hypertrophic shallow lakes. Many lakes with blooms of dispersed ecotypes have a depth of not more than 3 m and chlorophyll concentrations of 50 $\mu\text{g l}^{-1}$ and, in extreme cases, greater than 200 $\mu\text{g l}^{-1}$. The filaments are hardly grazed and do not sediment. Blooms of this type often lead to virtual monocultures which can prevail year-round for many years (Figure 2.7). Population dynamics in such lakes can be limited. In temperate regions, the autumn population can even survive under ice in winter. In such situations, the spring population starts growth with a relatively high density and thus has an advantage in competition with other species (Visser, 1990). By causing high turbidity, these cyanobacterial populations effectively suppress the growth of other phytoplankton species. Thus, the next summer population establishes itself almost without any seasonal succession between different species of phytoplankton. This high stability of the population precludes any redistribution of phosphorus and nitrogen to other components of the ecosystem and this can cause a resilience effect in lake restoration projects (see Chapter 8).

Figure 2.2A Micrograph of *Planktothrix (Oscillatoria) agardhii*

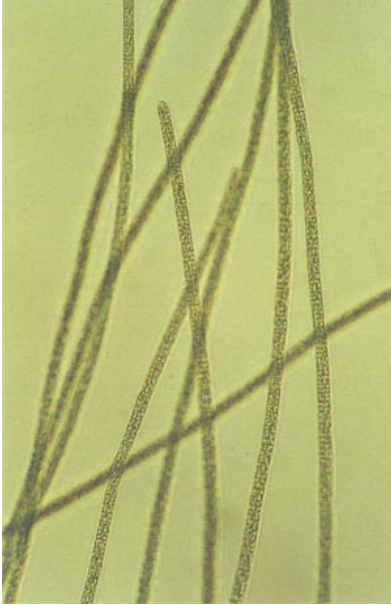


Figure 2.2B Micrograph of *Anabaena lemmermannii*

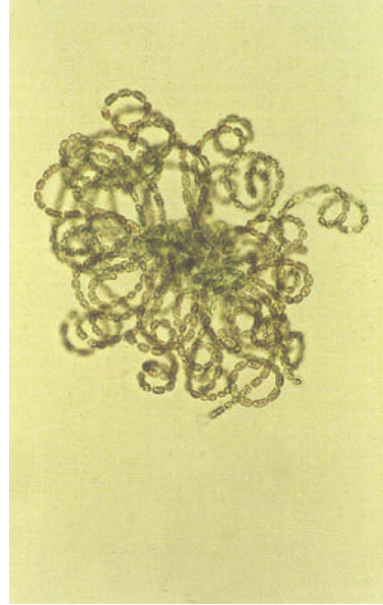


Figure 2.2C Micrograph of *Microcystis aeruginosa*

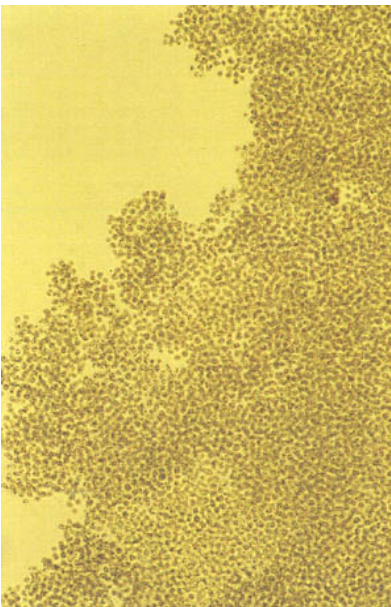


Figure 2.2D Surface bloom of *Planktothrix (Oscillatoria)*



Figure 2.2E Surface bloom of *Microcystis*



Figure 2.2F Aerial photograph with infrared colour film of a freshwater bloom of cyanobacteria



Figure 2.2G Use of a barrier or boom to keep surface scums of algae and cyanobacteria away from water offtake structures (Photograph courtesy of Peter Baker, Australian Water Quality Centre)



2.3.3 Stratifying ecostrategists

Representatives of this ecotype develop stable summer populations in the intermediate zone of thermally stratified lakes and reservoirs known as the metalimnion (see Figure 2.3). The organisms contain the red pigment phycoerythrin to absorb the green light, which is the prevailing wave length at this depth. The most common of these species is *Planktothrix (Oscillatoria) rubescens*, but red varieties of other *Planktothrix* species can also form metalimnic populations (Aune *et al.*, 1997).

The single filaments of these species hardly show any vertical migration. However, in late autumn at the end of the growing season, the cells can become buoyant and then form red surface scums (Walsby *et al.*, 1983). The niche of this type of *Planktothrix* is very limited. It needs sufficient light in the metalimnetic zone, but may be inhibited by too much light. Most metalimnetic blooms are found at light intensities of 1-5 per cent of the surface irradiance and in a range of Z_{eu}/Z_m between 0.7 and 1.2.

2.3.4 Nitrogen fixing ecostrategists

The mass development of species capable of fixation of atmospheric nitrogen (species of the genera *Anabaena*, *Aphanizomenon*, *Cylindrospermopsis*, *Nodularia*, and *Nostoc*) can often be related to periodic nitrogen limitation. Examples are found in deep, as well as in shallow, systems. However, while these ecostrategists often dominate in ecosystems with low levels of inorganic dissolved nitrogen, the reverse does not necessarily apply. Numerous lakes with clear nitrogen limitation are not dominated by nitrogen-fixing cyanobacteria. Low light availability may be the reason for this, because nitrogen fixation requires high amounts of energy. In turbid lakes, insufficient light energy may be available for effective nitrogen fixation (Zevenboom and Mur, 1980). A number of nitrogen fixing species can form colonies and possess gas vesicles. This means that they can regulate buoyancy, like *Microcystis*, and can form stable scums along downwind shores.

Restoration measures which simultaneously reduce phosphate and nitrogen loading (sewage diversion, isolation) may strengthen prevailing nitrogen-limiting conditions and hence the probability of large populations of nitrogen-fixing cyanobacteria.

2.3.5 Small, colony-forming taxa

Cases of large populations of the small, colony-forming genus *Aphanothece* have been reported. Little information is available on buoyancy regulation and scum formation by the species involved. In several water bodies, *Aphanothece* dominance has occurred after a decrease of *Planktothrix rubescens* populations. Reynolds (1997) reported them as the only cyanobacteria present in the summer plankton of small, intermittently flushed lakes in England. The dominance of this group is not strictly related with phosphate or nitrogen limitation, and there are no obvious relationships that can explain the sudden dominance of these cyanobacteria. They seem to dominate in an intermediate state during lake recovery after restoration measures have been taken; their ecology is unknown.

2.3.6 Benthic cyanobacteria

Besides the planktonic ecostrategists described above, cyanobacteria may grow on the bottom sediments of water bodies which are sufficiently clear to allow light penetration to these surfaces. These benthic species may form coherent mats. Especially high rates of photosynthesis by such mats sometimes leads to trapping of the photosynthetically produced oxygen as bubbles within the mats; parts of the mats may then become sufficiently buoyant to tear loose and rise to the surface. For monitoring and management of toxic cyanobacteria, awareness of these is important because cyanotoxin problems are usually not expected in clear, oligotrophic waters. However, toxic benthic cyanobacteria have caused animal deaths in Scotland, where beached mats along the shore of a clear loch were scavenged by dogs (Gunn *et al.*, 1992), and in Switzerland where toxic benthic populations of *Oscillatoria limosa* were ingested by cattle drinking from pristine mountain lakes (Metz *et al.*, 1997, 1998).

2.4 Additional information

It is beyond the scope of this book to give a detailed account of the taxonomy and ecology of cyanobacteria. However, in addition to the references cited in the previous sections of this chapter there are many useful texts that are widely available. Taxonomy and species identification are covered in some detail by Anagnostidis and Komárek (1985), Staley *et al.* (1989), Larsen and Moestrup (1990) and Waterbury (1992). Detailed accounts of plankton ecology, including cyanobacteria, are available in Sommer (1989) and Reynolds (1997) and cyanobacterial ecophysiology is described by Mur (1983).

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