# Chapter 33: Cyanobacteria blooms: effects on aquatic ecosystems

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## Introduction

Lakes, rivers and estuaries that experience frequent and/or prolonged blooms of cyanobacteria display an array of ecosystem properties that may have impacts on water quality, biological communities and ecosystem services. Some impacts of blooms may be direct, including possible effects of toxins on fish, invertebrates, and other aquatic fauna, or indirect, including: a reduction of submerged plants when plankton biomass becomes very high; and changes in fish community structure if summer cold water refuges are lost due to hypolimnetic anoxia. This paper is a concise overview of cyanobacteria blooms, focusing on their relationship to trophic state, their temporal dynamics, and their potential impacts on ecosystem structure and function.

## Cyanobacterial blooms and trophic state

When phytoplankton biomass increases during eutrophication, there are coincident changes in taxonomic structure. Most notably the relative biomass of cyanobacteria increases with eutrophication. This relationship has been documented in boreal, temperate, subtropical and tropical ecosystems, and a typical pattern of change in phytoplankton taxonomic structure along the trophic gradient can be found in Auer and Arndt (2004). In general, the potential for cyanobacteria dominance rises rapidly as total phosphorus (TP) increases from 30 to 100 μg $L^{-1}$ (Downing et al. 2001); how-

ever, the response pattern in any given system also depends on other fac-
tors, such as mean depth, mixing regime, flushing rate and water tempera-
ture. Occurrence of blooms correlates positively with TN and TP in lakes,
rivers and coastal waters (Paerl 1988), and these correlative relationships
have been used in TMDL (Total Maximum Daily Load) development. For
example, Havens and Walker (2002) identified a positive relationship be-
tween TP concentration and the risk of chlorophyll *a* exceeding 40 µg $L^{-1}$
(a concentration associated with blooms in a Florida lake) and used this to
identify the lake water TP goal to establish TMDL guidelines. Although
the positive relationship between relative cyanobacteria biomass, blooms
and nutrient concentrations holds true for most cases of eutrophication, a
point can be reached along the trophic continuum where eukaryotic algae
(flagellated chlorophytes) replace the cyanobacteria. This phenomenon is
common in Denmark, where some hyper–eutrophic lakes have extremely
high levels of TP and TN (TP > 1 mg $L^{-1}$ and TN > 5 mg $L^{-1}$) and nutrients
do not limit algal growth. At such high levels of nutrient availability, small
r–selected green algae can out compete certain cyanobacteria (Jensen et al.
1994). This situation is not common in the USA.

## Temporal dynamics of cyanobacteria blooms

Cyanobacteria blooms display a range of temporal dynamics. Some lakes,
rivers and estuaries have seasonal blooms that start in summer and last into
autumn, some have persistent blooms that encompass all seasons, and
some have blooms that occur as extreme peaks and crashes lasting just
days or weeks. The temporal aspect of a cyanobacterial bloom in a particu-
lar ecosystem depends on the extent to which different environmental fac-
tors influence bloom dynamics. In deep temperate eutrophic lakes with
stable summer stratification, phytoplankton typically progresses through
stages of diatom dominance in spring, followed by a relatively clear water
phase and then cyanobacteria dominance in mid to late summer. Cyano-
bacteria dominance often occurs when water temperature rises above $20^{\circ}C$
when there is depletion of dissolved inorganic N and free $CO_2$ from the
water. This pattern also occurs in subtropical waters, including coastal sys-
tems. For example, a regular seasonal pattern is observed in Pensacola
Bay, Florida, where there are summer blooms of cyanobacterial pico–
plankton (Murrell and Lores 2004).

In extremely shallow lakes (mean depth < 2 m), dominance of cyano-
bacteria may persist for years if the ratio of photic depth to mixed depth
never falls to levels that prevent net growth of low–light adapted taxa such

as *Oscillatoria agardhii* (Berger 1989), but remains low enough to exclude other plankton. At the opposite end of the spectrum is one of the most extreme examples of temporal variation – eutrophic Hartbeespoort Dam (Zohary et al. 1995).  In this system, high irradiance in the surface mixed layer and low wind velocities result in short–lived hyper-scums of *Microcystis aeruginosa*. The bloom is often followed by a population crash during periods of high outflow volume, and washed out to downstream systems, at which times other algae can become dominant. As noted below, there is uncertainty as to which factors are coincident with, vs. the actual cause of cyanobacteria blooms and their seasonal and inter–system variation.

## Predicting cyanobacteria dominance and bloom occurrence

There has been a long–standing discussion about the relative importance of nutrient concentrations, nutrient ratios, and other factors such as light and water column stability in determining whether or not cyanobacteria dominate the plankton. This discussion relates back to a paper by Smith (1983) that suggested low TN:TP ratios are responsible for cyanobacteria dominance under eutrophic conditions. This hypothesis is consistent with resource ratio theory and was supported by observations from some temperate lakes with varying ratios of TN:TP. Since that time, certain observational and experimental studies have shown that cyanobacteria become increasingly dominant at low TN:TP (Smith and Bennett 1999), yet some scientists discount this as coincidental rather than causal (Reynolds 1999). Others question the value of nutrient ratios as a predictive tool for resource management. Downing et al. (2001), for example, note that concentration of TP is a better predictor of cyanobacteria dominance than TN:TP ratios. Studies have suggested other potential causal factors (summarized by Dokulil and Teubner 2000), including high pH and scarcity of free $CO_2$, which theoretically should favor cyanobacteria that have a low $K_s$ for $CO_2$ uptake and can use bicarbonate as a C source. Others have suggested that greater resistance to zooplankton grazing may favor cyanobacteria, and that certain cyanobacteria produce allelopathic chemicals that inhibit growth of other algae. Accessory pigments that allow net growth to occur at low irradiance (Scheffer et al. 1997) and buoyancy that allows certain taxa to bloom at the water surface (Reynolds et al. 1987) also are considered important to cyanobacteria dominance. In eutrophic dimictic lakes, summer bloom development also has been linked with emergence of

cyanobacteria from sediment akinete populations (Tsujimura and Okubo 2003).

All of these explanations may be correct under specific environmental conditions because cyanobacteria are a diverse group, as are the aquatic ecosystems in which they occur. There is greater certainty about controlling factors when one considers certain ecotypes of cyanobacteria in particular types of lakes, rivers or estuaries. In regard to ecotypes, a key difference is between taxa that form water blooms and have relatively low light requirements vs. taxa that form surface blooms and have high light requirements. In regard to ecosystems, key differences are shallow vs. deep and mixed vs. thermally stratified. In shallow mixed lakes with high TP, there is extreme and highly predictable dominance by *Oscillatoria* when a low ratio of euphotic to mixed depth ($z_{eu}/z_{mix}$) allows these cyanobacteria to out compete other algae (Scheffer et al. 1997). In contrast, predominance of high light requiring $N_2$ fixers such as *Anabaena circinalis* and *Aphanizomenon flos aquae* predictably is linked with stable water columns, depletion of dissolved inorganic N and high temperature. Both species are more common in relatively deep lakes, but can bloom in shallow lakes during calm summer periods. For example, Havens et al. (1998) observed a shift from *Oscillatoria* dominance under mixed / low irradiance conditions, to *Anabaena*, *Aphanizomenon* and *Microcystis* dominance during periods of water column stability and increased underwater irradiance. Phlips et al. (1997) documented that changes in biomass of $N_2$ fixing cyanobacteria and density of heterocysts were strongly coupled with depletion of dissolved inorganic N, N–limitation in bioassays, relatively high irradiance, and high N fixation rates. Thus, we can generally predict that if an ecosystem is enriched with P, it is likely to have cyanobacteria dominance. If it is a shallow mixed system, the $z_{eu}/z_{mix}$ ratio is critical to determining whether *Oscillatoria* (low ratio) or other cyanobacteria will be dominant. An interesting exception to this pattern is *Cylindrospermopsis raciborskii*, which can develop blooms in shallow lakes under relatively high or low irradiance conditions, losing its terminal heterocysts in that later situation and functioning much like *Oscillatoria* (Phlips, personal communication).

Despite this knowledge, predicting the onset of a bloom at the daily or weekly timescale is very challenging because of the importance of stochastic variables such as wind and rain, which affect water column stability and underwater irradiance. For example, in Lake Mendota, Wisconsin, Soranno (1997) documented short–lived surface blooms throughout the summer and fall, and linked them with periods when there was a combination of low wind velocity, absence of rainfall and higher than average solar radiation. Surface blooms collapsed when wind velocities increased or

cloudy weather or rainfall occurred. Yet even with this retrospective information it was not possible to accurately forecast the onset of blooms. Research must continue to focus on defining the underlying conditions that allow blooms to occur, to determine if controllable variables including P and N loading rates, N:P loading ratios, flushing rate, etc. can be manipulated to reduce the overall risk of blooms, even when atmospheric conditions are favorable for their occurrence. An over–arching premise must also be to determine whether occurrence of a particular bloom is natural or related to human activities.

Predicting toxin levels produced by cyanobacteria is even less certain than predicting cyanobacterial bloom occurrence. Toxin production is linked with dominance by particular taxa of cyanobacteria, including species of *Microcystis*, *Anabaena*, *Aphanizomenon*, *Oscillatoria*, *Nostoc*, and *Aphanocapsa*. However, factors controlling the amount of toxin produced during a bloom are not well understood. Studies have suggested links between toxin concentrations and ratios of particulate to dissolved nutrients (Oh et al. 2001), concentrations of soluble P (Jacoby et al. 2000), TP (Rapala et al. 1997), TN and irradiance (Rolland et al. 2005). It is not possible to say whether these relationships are causal or coincidental. This is an area where additional research is required.

It is important to recognize that conditions associated with blooms and toxins may lead to reduced competition or predation on the taxa forming the blooms. This positive feedback stimulates further development of the bloom until environmental conditions become unfavorable (e.g., multiple cloudy days, intense rainfall, dramatically increased flushing rate, or input of turbid or stained water) and the bloom collapses. Feedback loops add further complexity to prediction of bloom dynamics and ecological effects.

## Biological effects of frequent or persistent cyanobacteria blooms

A simple conceptual model (Fig. 1) summarizes ecological effects of cyanobacteria blooms and their potential adverse impacts. When cyanobacterial blooms occur, irradiance is reduced in the water column, reducing the growth of producers that cannot maintain a position near the surface of the water, including epiphyton, benthic algae and rooted vascular plants. Thus, lakes with very dense blooms, especially if they are frequent or long–lasting, may not support large populations of other producers. In shallow eutrophic lakes, research has shown that the transition from plant to phytoplankton dominance can occur rapidly (Scheffer et al. 1993). In-

creased nutrient loading results in rather small increases in phytoplankton biomass when plants and periphyton are present, but when a critical turbidity is reached where net plant growth is negative, plants are replaced by phytoplankton. When this occurs, there is a rapid increase in the level of turbidity (phytoplankton biomass) with little or no further increase in nutrient loading. Furthermore, when that turbid state develops, the nutrient load required to bring plants back into dominance is lower than that at which they formerly occurred. This is a critical concept for management of cyanobacterial blooms and water quality in shallow eutrophic lakes. As illustrated by Scheffer et al. (1997), these alternative states also occur in shallow lakes that switch between *Oscillatoria* dominance and dominance by other algae – i.e., the phenomenon is not restricted to plant-algae switches. There remains some uncertainty about whether increased nutrient concentrations alone can bring about these changes, or whether they must be proximally driven by some additional forcing function, such as an intense wind storm uprooting plants or increasing water turbidity.

During intense blooms photosynthetic activity depletes free $CO_2$ from lake water and pH is driven up. Some have argued that this favors dominance of cyanobacteria, which for the most part are superior competitors when $CO_2$ is scarce. Low $CO_2$ also may stimulate formation of surface scums and extreme dominance by cyanobacteria taxa that can move to the air–water interface where $CO_2$ is most available, shading other algae in the process (Paerl and Ustach 1982). There is evidence that high pH during intense cyanobacteria blooms may be toxic to certain species of fish (Kann and Smith 1999), although this presumably might occur with blooms of any kind of phytoplankton (bacterial or algal) or in dense beds of plants. Oxygen depletion that occurs in the water during bloom senescence also can have biological impacts, the most visible being fish kills. There also are observations of adverse impacts of high levels of ammonia during bloom senescence. For example, during collapse of a dense *Anabaena circinalis* bloom in Lake Okeechobee, Florida, low oxygen levels and ammonia were considered the cause of mortality for snails and other macro–invertebrates (Jones 1987).
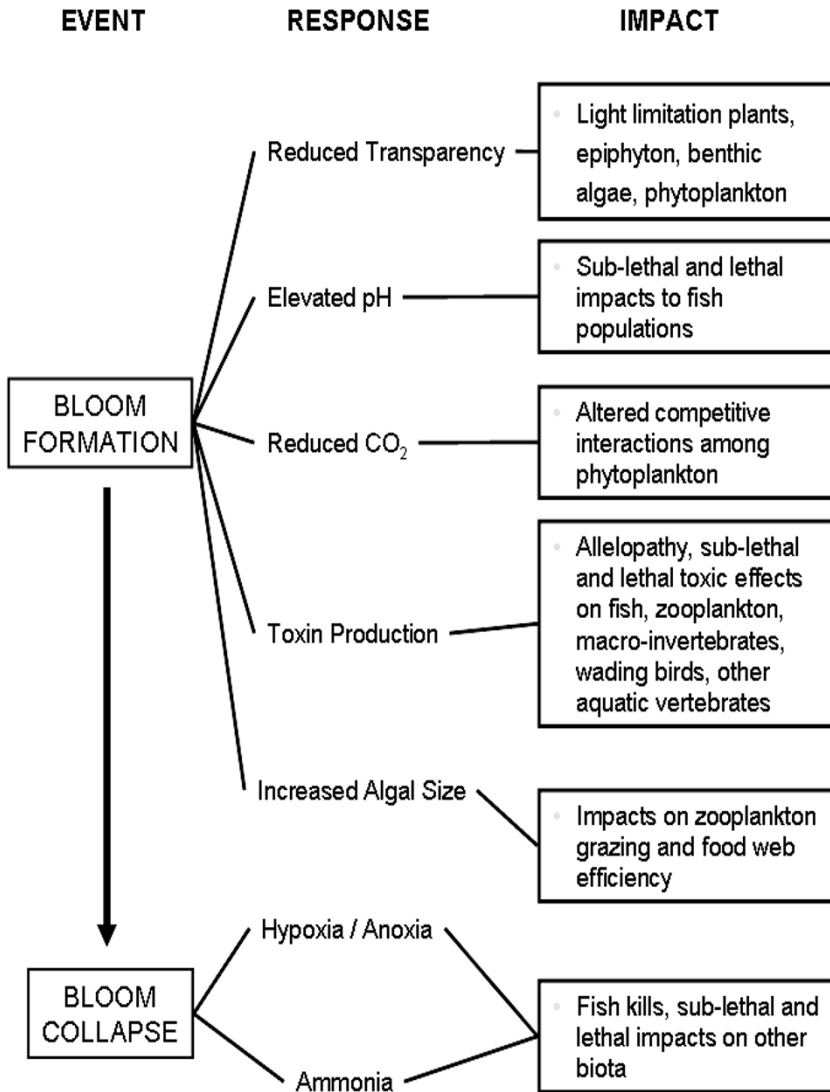
**Fig. 1.** A summary of ecological responses and impacts associated with blooms of cyanobacteria in lakes, rivers, and estuaries.

Toxin production by certain cyanobacteria (e.g., *Anabaena circinalis*, *Aphanizomenon flos–aquae*, *Cylindrospermopsis raciborskii*, *Microcystis aeruginosa*) may lead to a wide array of biological impacts, including: allelopathic effects on other phytoplankton (Suikkanen et al. 2004); suppression of zooplankton grazing, leading to reduced growth and reproductive rates and changes in dominance (Gilbert 1990, Ferrao–Filho et al. 2000, Ghadouani et al. 2003); hepatotoxic effects on fish (Andersen et al. 1993); and accumulation of toxins in tissues of invertebrates (Liras et al. 1998, Lehtiniemi et al. 2002) and fish (Magalhaes 2001). Toxins affected survival, growth and fecundity of snails in a laboratory exposure at typically observed concentrations (Gerard and Poullain 2005). Accumulation of toxins in tissues of freshwater clams has been suggested as a route of toxicity for muskrat (*Ondatra zibethicus*) and their predators (Prepas et al. 1997). There also are reports of impacts to waterfowl, such as the mass mortality of ducks that coincided with a *Microcystis* bloom in a Japanese lake (Matsunaga et al. 1999). These papers represent just a small percentage of the literature on potential effects of cyanobacterial toxins. Most studies are focused on single species and particular modes of exposure (e.g., feeding). At this time it is not possible to take this information and deduce with a high level of certainty what the actual impacts of toxins are on aquatic communities. Community–level responses depend on toxin concentration, frequency and duration of exposure, the combined outcome of direct and indirect effects, and possible synergistic effects with other natural and anthropogenic stressors. This represents a critical area for future research.

In addition to potential toxic effects, cyanobacteria blooms may affect grazing zooplankton by mechanical interference with the filtration apparatus (Gliwicz and Lampert 1990). It has been suggested that the high C:P ratios that occur during blooms may lead to growth limitation of zooplankton taxa like *Daphnia*, which have a high P requirement (Hessen et al. 2005). It is of interest that large *Daphnia*, which are generally considered the most effective grazers of algae and the taxa responsible for such things as the spring clear water phases in eutrophic lakes, are most sensitive to chemical stressors, including cyanobacterial toxins (Fulton 1988) and most sensitive to mechanical interference. As a result of this differential sensitivity, smaller zooplankton (e.g., *Bosmina* and rotifers) become increasingly dominant as lakes progress from mesotrophic to eutrophic. At the same time, the average size of phytoplankton increases. This convergence of zooplankton and phytoplankton size leads to an energetic bottleneck in the grazing food chain that restricts C and energy flow to higher trophic levels (Havens and East 1997). Microbial pathways become relatively more important and overall food web efficiency is reduced in eutrophic lakes with cyanobacterial blooms (Gliwicz 1969, Hillbricht–Ilkowska

1977). To a certain extent, the loss of *Daphnia* may be due to increased predation, because the biomass of planktivorous and omnivorous fish increases with eutrophication (Jeppesen et al. 2000).

Given these biological changes, it is important to consider what effects, if any, frequent or persistent cyanobacterial blooms have on biomass and taxonomic structure of fish, in particular the commercially and recreationally important species. The answer may depend on Latitude. In temperate and boreal regions, where piscivores (salmonids) require a cold water refuge during summer, eutrophication may eliminate those fish if the hypolimnion becomes anoxic (Colby et al. 1972). Temperate eutrophic lakes with dense cyanobacteria blooms in summer also may experience winterkill of fish under the ice cover in winter (Lee et al. 1991). In contrast, high densities of piscivores, such as largemouth bass (*Micropterus salmoides*), persist in highly eutrophic Florida, USA lakes, because fish in the subtropics have no cold water requirements and the winterkill situation cannot occur (Bachmann et al. 1996). A key factor determining success of bass and certain other sport fish is habitat structure – i.e., presence of a diverse assemblage of aquatic plants (Havens et al. 2005). As noted above, this habitat may be lost under highly eutrophic conditions if the lake is shallow and switches to a turbid state. Thus, eutrophication and dense algal blooms could lead to losses of economically important fish taxa in both temperate regions and the subtropics, although the underlying mechanisms differ. Additional research is needed to determine what additional effects, if any, the above mentioned declines in food web efficiency have on productivity of certain fish taxa. There is considerable evidence that fertilization can improve productivity of sport fish in ultra–oligotrophic lakes by increasing efficiency of plankton food webs, but the link between food web structure and fish productivity at the opposite end of the trophic spectrum is not as well documented, especially relative to other effects like hypolimnetic anoxia and loss of plant habitat.

## Effects on sediments, nutrient cycling and internal loading

Physical, chemical and biological processes occurring in the water column of lakes, rivers and estuaries have large influences on the sediments and their associated biota and nutrient cycles (Palmer et al. 2000). Systems with frequent and/or prolonged blooms of cyanobacteria display benthic responses. Because the particle size, nutrient stoichiometry and other properties (e.g., presence of toxins) of settling seston is altered when cyanobac-

teria become dominant, compared with diatoms or other algae, this affects the benthic chemistry and the biota that use that settling organic material as substratum or food. The enhanced organic export to sediments that occurs in eutrophic lakes leads to sediment anoxia, and this alters the taxonomic structure of benthic invertebrates and reduces the extent to which Fe binds to $PO_4$ at the sediment water interface. This may lead to increased diffusive internal P loading. Cyanobacterial blooms themselves may directly enhance internal P loading to surface waters if vertically migrating algae pick up P near the sediment surface and then move up into the epilimnion. Estimates of P loading by this process range from 2.0 to 3.6 mg P $m^{-2}$ $d^{-1}$ (Barbiero and Kann 1994, Head et al. 1999). Where such loading occurs at a high rate, there may be long–term consequences for lake rehabilitation. Head et al. (1999) note that "following reduction of external P loading, utilization of such internal P sources may delay expected reductions of bloom–forming cyanobacterial communities, and consequently delay improvements in other aspects of water quality." Research is needed to determine the extent of that delay in recovery time in lakes with a long history of high external loads. Modeling of response time in most TMDL related studies does not take into consideration this potentially important stabilizing feedback loop.

## Research needs and data gaps

Although the understanding of toxic cyanobacteria blooms has greatly increased in the last decade, there remain some major areas of uncertainty where additional research is required if scientists are to provide sound guidance to water resource managers. The following are some key questions that should be addressed with future research.

1. What physical, chemical and biological factors determine the level of toxins associated with a cyanobacteria bloom?

2. What are the realized ecological impacts of toxic cyanobacterial blooms, when one takes into consideration typically occurring levels of toxins, potential for both direct and indirect effects, and the possibility of synergistic effects of natural stressors?

3. What impacts, if any, do changes in food web function have on fish in nutrient–enriched lakes, rivers and estuaries that become dominated by cyanobacteria?

4. To what extent does dominance by vertically migrating cyanobacteria lengthen the response time of lakes, rivers or estuaries to external nutrient load reduction? Can this biological effect be incorporated into predictive models used to set a TMDL?

## Conclusion and Summary

Cyanobacteria become increasingly dominant as concentrations of TP and TN increase during eutrophication of lakes, rivers and estuaries. Temporal dynamics of cyanobacteria blooms are variable – in some systems persistent blooms occur in summer to fall, whereas in other systems blooms are more sporadic. Cyanobacteria blooms have a wide range of possible biological impacts including potential toxic effects on other algae, invertebrates and fish, impacts to plants and benthic algae due to shading, and impacts to food web function as large inedible algae produce a bottleneck to C and energy flow in the plankton food web. In lakes with dense blooms of cyanobacteria, accumulation of organic material in lake sediments and increased bacterial activity also may lead to anoxic conditions that alter the structure of benthic macro–invertebrates. Diffusive internal P loading may increase, and hypolimnetic anoxia may lead to a loss of piscivorous fish that require a summer cold water refuge in temperate lakes. Ecosystem changes associated with frequent blooms may result in delayed response of lakes, rivers and estuaries to external nutrient load reduction. Despite numerous case studies and a vast literature on species–specific responses, community level effects of cyanobacterial blooms are not well understood – in particular the realized impacts of toxins and changes in food web structure/function. These areas require additional research given the prevalence of toxic blooms in the nation's lakes, rivers and coastal waters – systems that provide a wide range of valued ecosystem services.

## Acknowledgements

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