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# Harmful Cyanobacterial Blooms: Causes, Consequences, and Controls

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**Abstract** Cyanobacteria are the Earth's oldest oxygenic photoautotrophs and have had major impacts on shaping its biosphere. Their long evolutionary history (~3.5 by) has enabled them to adapt to geochemical and climatic changes, and more recently anthropogenic modifications of aquatic environments, including nutrient over-enrichment (eutrophication), water diversions, withdrawals, and salinization. Many cyanobacterial genera exhibit optimal growth rates and bloom potentials at relatively high water temperatures; hence global warming plays a key role in their expansion and persistence. Bloom-forming cyanobacterial taxa can be harmful from environmental, organismal, and human health perspectives by outcompeting beneficial phytoplankton, depleting oxygen upon bloom senescence, and producing a variety of toxic secondary metabolites (e.g., cyanotoxins). How environmental factors impact cyanotoxin production is the subject of ongoing research, but nutrient (N, P and trace metals) supply rates, light, temperature, oxidative stressors, interactions with other biota (bacteria, viruses and animal grazers), and most likely, the combined effects of these factors are all involved. Accordingly, strategies aimed at controlling and mitigating harmful blooms have focused on manipulating these dynamic factors. The applicability and feasibility of various controls and management approaches is discussed for natural waters and drinking water supplies. Strategies based on physical, chemical, and biological manipulations of specific factors show promise; however, a key underlying approach that should be considered in almost all instances is nutrient (both N and P) input reductions; which have been shown to effectively reduce cyanobacterial biomass, and therefore limit health risks and frequencies of hypoxic events.

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## Introduction

Cyanobacteria (blue-green algae) are the Earth's oldest known oxygenic photoautotrophs. Their proliferation during the Precambrian era (~3.5 bya) dramatically altered the previously anoxic biosphere which led to the evolution of higher terrestrial plant and animal life [129]. Many genera have the ability to fix atmospheric nitrogen ($N_2$) (an anaerobic process)[45], while they can store phosphorus (P) and sequester iron (Fe) and a range of essential trace metals [15, 165, 166]. These traits have enabled them to exploit both nutrient-scarce and nutrient-enriched, diverse terrestrial and aquatic environments worldwide. In modern times, cyanobacteria have exhibited ecophysiological strategies allowing them to exploit anthropogenic modifications of these environments; specifically nutrient over-enrichment and hydrologic alterations to ecosystems with dramatic examples spanning the globe from alpine lakes to coastal oceans [39, 94, 108, 113, 119].

The most obvious and troublesome sign of their contemporary ecological "success" is increasingly frequent and highly visible harmful cyanobacterial blooms, or CyanoHABs (Fig. 1)[59]. The "harmful" aspect of these blooms from an environmental context begins with a loss of water clarity, which suppresses aquatic macrophytes, and negatively affecting invertebrate and fish habitats. Bacterial decomposition of dying blooms may lead to oxygen depletion (hypoxia and anoxia), and subsequent fish kills. In

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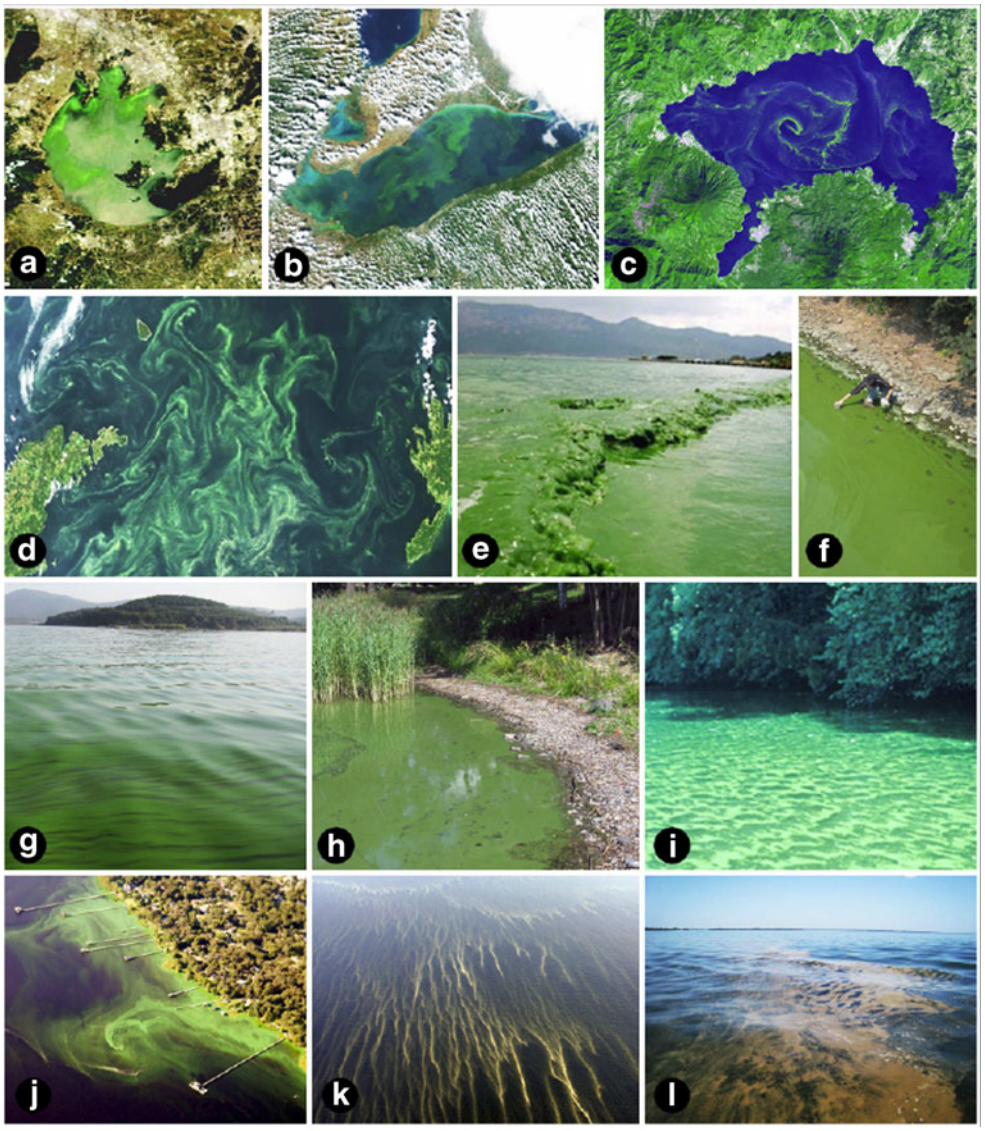


**Fig. 1** Harmful cyanobacterial blooms (CyanoHABs) in a variety of aquatic environments. Where known, specific genera are indicated. **a**–**d** Remote sensing views of surafe blooms in; **a** Lake Taihu, China (*Microcystis* spp.) (courtesy NASA MODIS), **b** Lake Erie, USA–Canada (*Microcystis*) (courtesy NASA MODIS, **c** Lake Atitlan, Guatamala (*Lyngbya*) (courtesy NASA MODIS), **d** Baltic Sea-Gulf of Finland (*Nodularia*, *Anabaena*, *Microcystis*) (courtesy NASA MODIS). **e** Lake Dianchi, China (*Aphanizomenon* sp.) (courtesy Chinese Academy of Sciences). **f** and **g** Lake Tahiu, China (*Microcystis* spp.) (Photos by H. Paerl). **h** Taivallahti Bay, Baltic Sea, Finland (Finnish Environment Institute-SYKE). **i** Neuse River Estuary, North Carolina, USA (*Microcystis* sp.) (photo H. Paerl). **j** St. John's River, FL (photo, J. Burns).**k** Baltic Sea, Gulf of Finland (*Nodularia*) (Finnish Border Guard). **l** Sanibel Inlet, coastal Gulf of Mexico, Florida USA (*Trichodesmium* sp.) (photo, H. Paerl)

addition, many CyanoHABs produce toxic secondary metabolites which can cause serious, acute intoxication in mammals (including humans) affecting the hepatopancreatic, digestive, endocrine, dermal, and nervous systems [14, 17, 19] (Table 1). Some of the most common toxin-producing cyanobacteria include the $N_2$-fixing genera: *Anabaena*, *Aphanizomenon*, *Cylindrospermopsis*, *Lyngbya*, *Nodularia*, *Oscillatoria*, and *Trichodesmium*; and the non-$N_2$ fixers: *Microcystis* and *Planktothrix* (Fig. 2). Several of these genera thrive in both fresh- and estuarine environments and some are also found in marine systems. CyanoHABs threaten the ecological integrity and sustainability of aquatic ecosystems depended upon for drinking water, irrigation, fishing, and recreation. Recurring blooms can be found in some of the world's largest inland freshwater ecosystems, including: Lake Victoria (Africa), Lake Erie and Lake Michigan (USA–Canada), Lake Okeechobee (Florida, USA), Lake Ponchartrain (Louisiana, USA), Lake Taihu (China), and estuarine and coastal waters, e.g., the Baltic Sea, Caspian Sea, tributaries of Chesapeake Bay, North Carolina's Albemarle-Pamlico Sound, Florida Bay, the Swan River Estuary in Australia, the Patos, and other coastal lagoonal estuaries in Brazil, to mention a few [105].

## Environmental Factors Controlling CyanoHAB Dynamics

### Nutrient Inputs

There is broad agreement that nutrient over-enrichment of freshwater and marine ecosystems from anthropogenic sources (urban, agricultural, and industrial) has promoted CyanoHAB expansion and persistence [59, 97, 105, 106]. Phosphorus has traditionally been considered the principle nutrient limiting primary productivity and algal biomass

**Table 1** Major harmful cyanobacterial bloom-forming genera and their known toxins

| Toxin | Detection method(s) | CyanoHAB genera |
|---|---|---|
| Aeruginosin | HPLC, MS | *Microcystis*, *Planktothrix* |
| Anatoxin-a/homoanatoxin-a | ELISA, HPLC, MS | *Anabaena*, *Aphanizomenon*, *Cylindrospermopsis*, *Lyngbya*, *Oscillatoria*, *Phormidium*, *Planktothrix*, *Raphidiopsis*, *Woronichinia* |
| Anatoxin-a(S) | AEIA, MS | *Anabaena* |
| Aplysiatoxins | MS | *Lyngbya*, *Oscillatoria*, *Schizothrix* |
| beta-Methylamino-L-alanine (BMAA) | ELISA,HPLC, MS | *Anabaena*, *Aphanizomenon*, *Calothrix*, *Cylindrospermopsis*, *Lyngbya*, *Microcystis*, *Nostoc*, *Nodularia*, *Planktothrix*, *Phormidium*, *Prochlorococcus*, *Scytonema*, *Synechococcus*, *Trichodesmium* |
| Cyanopeptolin | HPLC, MS | *Anabaena*, *Microcystis*, *Planktothrix* |
| Cylindrospermopsin | ELISA, HPLC, MS | *Anabaena*, *Aphanizomenon*, *Cylindrospermopsis*, *Oscillatoria*, *Raphidiopsis*, *Umezakia* |
| Jamaicamides | MS | *Lyngbya* |
| Lyngbyatoxin | HPLC, MS | *Lyngbya* |
| Microcystin | ELISA, HPLC, MS, PPIA | *Anabaena*, *Anabaenopsis*, *Aphanizomenon*, *Aphanocapsa*, *Cylindrospermopsis*, *Gloeotrichia*, *Hapalosiphon*, *Microcystis*, *Nostoc*, *Oscillatoria*, *Phormidium*, *Planktothrix*, *Pseudoanabaena*, *Synechococcus*, *Woronochinia* |
| Nodularin | ELISA, HPLC, MS, PPIA | *Nodularia* |
| Saxitoxin | ELISA, HPLC, MS | *Anabaena*, *Aphanizomenon*, *Cylindrospermopsis*, *Lyngbya*, *Oscillatoria*, *Planktothrix* |

*AEIA* acetylcholine esterase inhibition assay, *ELISA* enzyme-linked immunosorbent assay, *HPLC* high-performance liquid chromatography, *MS* mass spectrometry, *PPIA* protein phosphatase inhibition assay

accumulation in freshwater ecosystems [75, 127]; whereas N inputs are often cited as controlling "new" production in the marine environment [4, 88, 101]. Estuarine systems tend to fall between these nutrient limitation "paradigms," with P limited conditions often characterizing the low salinity oligohaline (<5), upstream regions, and N limitation typifying more saline (>5), downstream waters [23, 38, 101]. Phosphorus enrichment, especially relative to N enrichment, may favor the development of CyanoHABs, especially $N_2$ fixing cyanobacterial genera which can supply their own N needs by enzymatically converting atmospheric N ($N_2$) to biologically available ammonia ($NH_3$) [28, 39, 45]. Nutrient-enriched water bodies are especially prone to CyanoHABs if they also have long residence times (low flushing rates), water temperatures periodically exceeding 20 °C, calm surface waters and persistent vertical stratification [94, 119, 134]. While these conditions are most common in freshwaters, some brackish systems such as the estuaries of the Baltic Sea and oligohaline regions of rivers (Albemarle-Pamlico Sound, Chesapeake Bay, San Francisco Bay Delta), as well as geographically-diverse lagoons, can support CyanoHABs, especially if they experience periods of low flushing (long residence times) and vertical stratification [67, 94, 98].

High P (relative to N) loading is not a universal "trigger" for CyanoHAB formation. Agricultural, urban, and industrial nutrient sources have accelerated rapidly in the past several decades, with N loads frequently eclipsing P inputs [33, 47, 115, 157]. This change is attributable to increased application of N-fertilizers, human and agricultural wastes, stormwater runoff, groundwater discharge and atmospheric deposition; all of which can be rich in N relative to P, leading to elevated N loading in already nutrient-impacted water bodies [6, 96, 115]. Nitrogen-rich aquatic ecosystems (high N:P) can also be plagued by CyanoHABs, especially non-$N_2$-fixing genera [98]. These primarily include *Microcystis* and *Planktothrix* species, although other non-$N_2$-fixing genera such as *Aphanocapsa*, *Raphidiopsis*, and *Woronochinia*, are all capable of aggressive expansion in N-enriched waters. While in many instances, total maximum daily loads (TMDL) for P have been established and implemented, N inputs remain less strictly controlled, and as a result have increased in many systems. N augmentation, in both developed and developing regions [46, 157], has raised concerns that excessive N loading is accelerating eutrophication and promoting CyanoHABs in downstream freshwater and marine ecosystems [33, 102].

Therefore, the "P only" paradigm for control of CyanoHAB blooms [128] needs to be revised [21, 73, 130]. This approach was based on the assumption that $N_2$ fixation supplies all the physiological needs for CyanoHABs, and therefore control of N inputs was considered unneccesary [127]. Recent studies, however, have shown that cyanobacterial $N_2$ fixation does not meet phytoplankton or ecosystem N demands [36, 73, 104, 130] for several reasons, including: (1) $N_2$ fixation has high energy requirements, (2) oxygen production by photosynthesis in blooms can inhibit this anaerobic process, (3) turbulence and

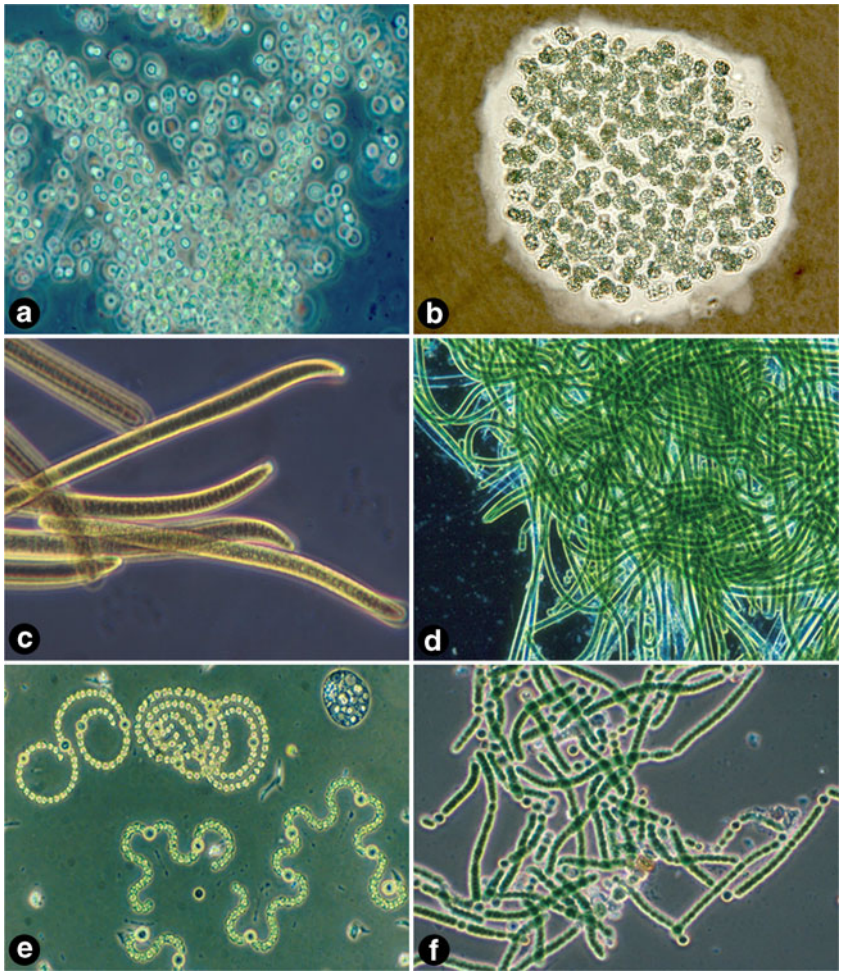


**Fig. 2** Photomicrographs of major harmful cyanobacterial bloom groups, based on cellular morphologies. **a**–**b** Aggregated single-cell coccoid genera, including **a** *Merismopedium* and **b** *Microcystis*. **c**–**d**, filamentous, non-heterocystous genera, including **c** *Oscillatoria* sp., **d** *Lyngbya* sp. **e**–**f** Filamentous, heterocystous genera, including **e** *Anabaena* spp., and **f** *Nodularia* sp.

wind mixing can disrupt $N_2$ fixation, and (4) other cofactors may be limiting such as Fe, Mo, and/or other trace metals [57, 84, 95].

In water bodies where $N_2$ fixation fails to meet ecosystem-level N requirements, external N inputs play a crucial role in enhancing fertility, with excessive N inputs often leading to undesirable excessive algal production. Hence, eutrophic systems already subject to CyanoHAB events are prone to further expansion of these blooms due to additional N inputs, especially if they already contain sufficient autochthonous P. Indeed, eutrophic systems worldwide exhibit the capacity to absorb increasing amounts of N as they increase their trophic states [4, 33, 101]. Recent surveys of algal productivity in response to nutrient enrichment across geographically diverse eutrophic lakes, reservoirs, estuarine and coastal waters and a range of experimental enclosures (<1 L to over 10,000 L) reveal that strongest stimulation is routinely observed in response to both N and P additions; indicating nutrient co-limitation is widespread [35, 74, 100, 107, 139, 140]. These results strongly suggest that reductions in both N and P inputs are needed to stem eutrophication and CyanoHAB expansion [74, 106, 172].

## Climate Change and CyanoHAB Expansion

While nutrient over-enrichment promotes CyanoHABs [59, 98], climate change provides an additional catalyst for their expansion. Rising global temperatures and changing precipitation patterns both stimulate CyanoHABs [64, 99, 103, 106, 110]. Warmer temperatures favor surface bloom-forming cyanobacterial genera because they are adapted to hot conditions and their maximal growth rates occur at relatively high temperatures; often in excess of 25 °C [12, 40, 120, 122]. At these elevated temperatures, cyanobacteria routinely outcompete eukaryotic algae [32, 64, 105, 164]. Specifically, as the growth rates of the eukaryotic taxa decline in response to warming, cyanobacterial growth rates reach their optima (Fig. 3). Warm surface waters are also prone to intense vertical stratification. The strength of vertical stratification depends on the density difference between the warm surface layer and the cold water beneath. In marine systems, salinity gradients also induce stratification. As temperatures rise due to climate change, waters will begin to stratify earlier in the spring and the stratification will persist longer into the fall [111, 142, 143, 159, 167].

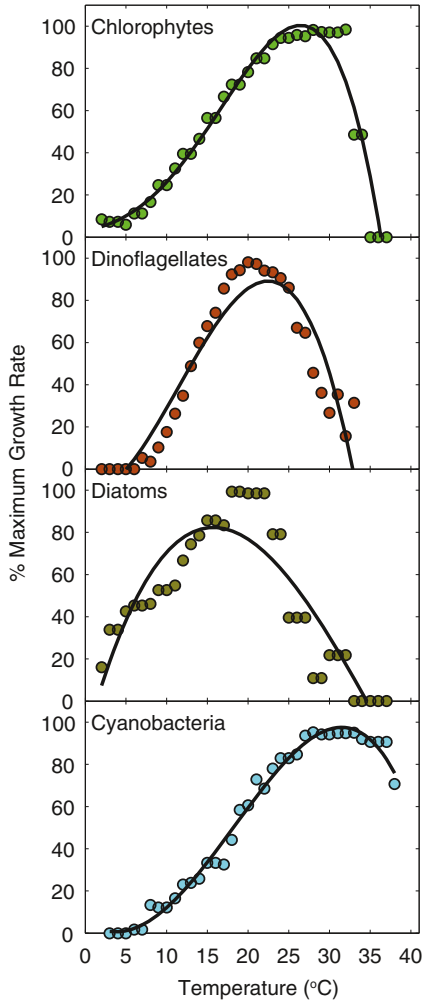


**Fig. 3** Temperature dependence of the specific growth rates of three eukaryotic phytoplankton classes and of CyanoHAB species common in temperate freshwater and brackish environments. Data points are 5 °C running bin averages of percent maximum growth rates from three to four species within each class. *Fitted lines* are third-order polynomials and are included to emphasize the shape of the growth versus temperature relationship. Percent maximum growth rates of individual species are provided in Paerl et al. [105]. Original data sources are [8, 12, 52, 68, 69, 76, 120, 150, 173]

Many cyanobacterial genera readily exploit stratified conditions by forming gas vesicles which provide buoyancy, enabling them to maintain their position within the euphotic zone and near the surface [59, 120](Fig. 1). These surface blooms maintain high rates of photosynthesis, even under high ultraviolet radiation, while shading out underlying, non-buoyant phytoplankton and macrophytes, thereby suppressing their growth [58, 60, 160].

Cyanobacterial surface blooms may locally increase surface water temperatures, due to light energy absorption via an array of photosynthetic and photoprotective pigments (chlorophylls, carotenoids, and phycobilins) [92, 93]. Kahru et al. [66] used remote sensing to demonstrate that cyanobacterial surface blooms in the Baltic Sea could locally increase temperatures by at least 1.5 °C above ambient waters. Likewise, Ibelings et al. [61] showed that surface temperatures within cyanobacterial blooms in Lake Ijsselmeer, Netherlands, were consistently higher than surrounding surface waters. This represents a positive feedback mechanism by which cyanobacterial bloom species can optimize their growth rates and provide competitive dominance over eukaryotic phytoplankton.

Global warming also alters weather patterns and amounts of precipitation, which may further enhance cyanobacterial dominance. The frequency of extreme rainfall events is projected to increase [103]. This will lead to larger surface and groundwater nutrient discharge events into water bodies. Under conditions of excessive freshwater discharge, blooms may be prevented by enhanced flushing; at least in the short term. However, when the high discharge period subsides and water residence time increases, the deposited terrestrial nutrient load associated with these events can then be sequestered. This scenario is particularly relevant during warm summer months in large water bodies that have long water residence times (i.e., large lake and reservoir systems, coastal lagoons and semi-enclosed bays and sounds). Therefore, the settings most likely to result in extreme cyanobacterial dominance are predicted to begin with elevated winter–spring rainfall and runoff, followed by protracted periods of summer drought where temperatures, vertical stratification, and water residence times all increase simultaneously. Examples of this sequence of events include the Swan River and Estuary (Australia), Hartbeespoortdam (South Africa), the Neuse River Estuary (North Carolina, USA), the Potomac River (Chesapeake Bay, USA), and Lake Taihu (China) [98, 105]. Attempts to regulate discharge of rivers and lakes by dams and sluices may increase residence time, and thus enhance CyanoHAB proliferation.

Salinization, due to summer droughts, rising sea levels, and increased use of freshwater for agricultural irrigation has increased worldwide. Several common bloom-forming cyanobacterial genera are salt-tolerant, despite the fact that they are most often found in freshwater systems. These include the $N_2$ fixers *Anabaena*, *Anabaenopsis*, *Nodularia*, and *Lyngbya*, as well as non-$N_2$ fixing genera,such as *Microcystis* [59, 165, 166] and *Oscillatoria*. Some strains of *Microcystis aeruginosa* remain unaffected by salinities up to 10, which is 30 % of that of seawater [7, 148], and in Patos Lagoon, Brazil, it thrives under "mixohaline" conditions [85]. Likewise, some *Anabaena* and *Anabaenopsis* species can withstand salinities up to 15, while toxic *Nodularia spumigena* can tolerate salinities exceeding 20 [81, 84]. These salt-tolerant species are present in brackish systems; presumably spurred on by a combination of nutrient over-enrichment, climatic changes and salinization. Examples of brackish systems prone to CyanoHAB events include: the Baltic Sea (N. Europe), Caspian Sea (W. Asia), Swan River Estuary (Australia), San Francisco Bay (California, USA), and Lake Ponchartrain (Louisiana, USA) [98, 106].

The filamentous toxin-producing diazotroph *Cylindrospermopsis raciborskii*, shows remarkable recent expansion of its geographical range. *Cylindrospermopsis* first gained widescale attention following an outbreak of severe hepatitis-like disease on Palm Island (Australia), the so-called "Palm Island mystery disease" [14]. The outbreak occurred after the local water supply was treated with copper sulfate to control an algal bloom. A subsequent epidemiological study confirmed the linkage between the "mystery disease" and the presence of *Cylindrospermopsis* [14]. Lysis of the *Cylindrospermopsis* bloom released the highly stable toxin, *cylindrospermopsin*, into the water supply.

*Cylindrospermopsis* was originally described as a tropical/subtropical genus [91]. However, *C. raciborskii* was documented in Europe during the 1930s, and showed a progressive colonization from Greece and Hungary towards higher latitudes near the end of the twentieth century [91]. It was described in France in 1994, in the Netherlands in 1999, and it is now widespread in lakes in northern Germany [142, 167]. *C. raciborskii* was noted in Florida almost 35 years ago, after which it aggressively proliferated throughout lakes and rivers [16]. It is now commonly found throughout the USA in reservoirs, lakes, rivers, and even oligohaline estuarine waters experiencing various degrees of eutrophication and loss of water clarity [13, 98]. *C. raciborskii* is adapted to low light conditions typifying eutrophic waters, it prefers water temperatures above 20 °C, and survives adverse conditions using specialized vegetative resting cells (akinetes) [91, 142, 167]. These bloom characteristics suggest a link to eutrophication and global warming.

Recent studies have shown that the activation of akinetes in the broadly distributed heterocystous species *Aphanizomenon ovalisporum* is strongly temperature regulated [20]. Increases in ambient temperatures may thereby play an important role in the geographic dispersal strategy, and potential expansion of this and other akinete-forming taxa.

Blooms of filamentous, non-heterocystous, toxin-producing *Lyngbya* have become increasingly common and problematic in nutrient-enriched freshwater and marine ecosystems, including those that have experienced human disturbances such as: dredging, municipal waste inputs, and the discharge of nutrient laden freshwater through coastal canals [2, 89, 98, 100, 163]. *Lyngbya* is a ubiquitous genus, with various species being found in both planktonic and benthic habitats. *L. majuscula* (marine-benthic) and *L. wollei* (freshwater-benthic and planktonic) are opportunistic invaders. Following large climatic and hydrologic perturbations such as hurricanes, *L. wollei* is an aggressive initial colonizer of flushed systems [98, 106]. *Lyngbya* blooms can proliferate as dense, attached or floating mats that shade other primary producers, which enables *Lyngbya* to dominate the system by effectively outcompeting them for light (Fig. 4). As is the case with *Cylindrospermopsis* and *Microcystis*, this CyanoHAB benefits from *both* human and climate-induced environmental change.

## Controls on Bloom Persistence and Collapse

Once a cyanobacterial bloom is established, it may persist for months; even after nutrients (N and P) are reduced. Sediment–water column exchange of previously loaded, stored, and recycled nutrients, as well as regeneration from cell turnover and nutrient recycling by closely associated heterotrophic bacteria and microzooplankton grazers (e.g., protozoans and rotifers), can help sustain bloom biomass [94]. Key biotic factors involved in bloom control include zooplankton (and possibly benthic fauna and fish) grazing, bacterial interactions, and viral lysis.

## Cyanobacteria and Grazers

There is considerable debate as to how much influence zooplankton grazers have on CyanoHABs [51, 132, 155]. There is evidence that grazers in oligotrophic lakes exert a greater impact on algae than those in eutrophic lakes [18]. This is possibly due to increased phytoplankton productivity resulting from nutrient-rich conditions, which allows the cells to simply overwhelm any negative-grazing effects. Many CyanoHAB genera also benefit by their tendencies to congregate as large filamentous and colonial colonies, which reduces zooplankton predation and interferes with the filtering capacity of bivalves. Therefore, an overabundance of cyanobacteria relative to more beneficial phytoplankton groups (e.g., diatoms) can negatively affect natural populations of zooplankton fitness by their morphology (size exclusion) [42], toxicity [25, 43, 44], or lack of nutritional value [37, 158].

Furthermore, ingestion of cyanobacteria by grazers does not necessarily indicate that they are digested or assimilated. Porter [112] showed that gelatinous algae were not digested by *Daphnia* and that the cells could take up nutrients as they passed through the animal's gut. Van Donk et al. [153] found that nutrient deficiency in phytoplankton led to their accumulation of carbon and extra cellular compounds that could block digestive enzymes in grazers. When cyanobacteria and other phytoplankton are physiologically stressed by low nutrients, they may increase their colony size to reduce grazing pressure. Not only can they take up nutrients and remain viable through zooplankton gut passage; they can also cause a decline in zooplankter fitness due to malnutrition.

There is evidence that large cladocerans can control cyanobacterial blooms. Elser [34] reviewed the steps necessary for cyanobacterial bloom formation. High nutrients favor all phytoplankton, while nutrient stoichiometry and physical conditions determine the potential for CyanoHAB formation. It is

**Fig. 4** Benthic and mat-forming CyanoHABs. *Left*: *Lyngbya confervoides* covering a nearshore reef off Fort Lauderdale, FL (photo credit K. Lane). *Center*: *Lyngbya* spp. mats covering the surface waters of Ichetucknee Springs, FL. *Right*: blooms of *Lyngbya* sp. smothering seagrass beds near Sanibel Island, coastal Gulf of Mexico, Florida (photo credit H. Paerl)

possible that large *Daphnia* species can control bloom initiation if they are present in sufficient number before the bloom. Even though the cladocerans may not be grazing significantly on the cyanobacteria, the large numbers of grazers may still be enough to suppress the bloom.

Occasionally, grazing can remove a substantial portion of non-CyanoHAB blooms [131], but most often there is little to no grazing influence on algal blooms [152]. Sellner et al. [132] found that copepods reduced grazing on a river assemblage in the presence of *Microcystis*, although *Bosmina* seemed to ingest a significant amount of the bloom. Similarly, Leonard and Paerl [72] found that *Cylindrospermopsis* blooms discouraged copepod grazing, while rotifer grazing remained undeterred. Both studies concluded that a large portion of the bloom remained ungrazed.

Benthic mollusks have the potential to exert top down control on phytoplankton abundance [87]. With regard to cyanobacterial control, there are conflicting findings with some reporting that mollusks, such as the zebra mussel (*Dreissena polymorpha*), exhibit preferential (selective) grazing of non-cyanobacterial phytoplankton [154] which leads to increases in CyanoHAB abundance, whereas others report that cyanobacteria are consumed indiscriminately [27].

## Factors Initiating Bloom Collapse

Although grazers may restrict CyanoHAB expansion to some degree, they generally are unable to keep pace with an exponentially growing bloom [50]. However, blooms do not last indefinitely and the cells comprising a bloom will inevitably senesce and die, or enter a state of metabolic dormancy; a phenomenon which occurs even in tropical latitudes not prone to fall mixing events and cold temperatures. While there is always population turnover within a bloom, there appears to be a tipping point at which once a bloom begins to collapse, it does so rapidly (often within days) [56]. This rapid collapse, and the subsequent deposit of large amounts of organic matter to the benthos, can lead to hypoxia; a condition which can cause finfish and shellfish kills and alter biogeochemical cycling [94, 97]. Physiological cues such as internal P-depletion may prompt some cells to senesce and die while others choose to enter a vegetative resting state [136, 161]. Surface blooms may also disperse due to physical factors: cooler temperatures, water column destratification, high turbidity, and increased wind velocities which lead to mixing and phytoplankton entrapment below the photic zone [5]; although certain low-light adapted genera may be favored by these conditions (e.g., *Oscillatoria*) [126]. The factors initiating apoptosis in cyanobacteria are poorly understood; although similar to many types of cells a broad family of proteases, known as caspases, are largely believed to drive this process [3]. While there is some evidence for cyanobacterial control via predatory bacteria capable of secreting lysing agents [118], the other major driver of cyanobacterial cell death is likely viral lysis [145].

In general, viruses are ubiquitous in aquatic environments—and at concentrations upward of 10 million $ml^{-1}$, they are the most abundant biological entity in the oceans [10, 146]. The majority of these viruses are bacteriophages, and with respect to cyanobacteria, most of our knowledge of cyanophages has come from marine environments [9]. Numerous studies have demonstrated that cyanophages play an important, albeit poorly understood, role in shaping phytoplankton abundance, community structure, population succession, and on a larger scale,

marine food webs. Studies have shown that the virus infection frequency in cyanobacteria, based on visual detection, is 0.8–4.3 % of cells across diverse marine habitats [41], and that similar percentages have been reported in freshwater bacteria [80]. Since these numbers are based on visual observations of cells with late-stage lytic infection, the true number of cells infected is believed to be much higher.

In freshwater and estuarine systems, much less is known about the extent to which viruses impact cyanobacteria, although some in-roads have been made which suggest that these cyanophages are likely equally as important as their marine counterparts [168]. As of 2008, only ~40 cyanophages had been isolated from freshwaters [26], whereas isolated marine cyanophages likely exceed this by at least 1 to 2 orders of magnitude.

Many of the cyanophages isolated to date have exhibited strain- or species-specific infectivity, although some isolates have been found to infect hosts from multiple CyanoHAB genera [26]. Numerous studies have corroborated that viral-induced bacterial mortality is an important factor constraining and maintaining cyanobacterial abundances below their environmental resource limited carrying capacities; and this mortality may exceed the effect of zooplankton grazers, especially in nutrient-rich waters [71, 141]. Indeed, investigations of eutrophic freshwater lakes have often documented precipitous declines in CyanoHAB concentrations concomitant with 10–100-fold increases in cyanophage abundance due to an average burst size of 20 to 50 virions per host cell [169]. It has been estimated that viral lysis may be responsible for up to ~50 % of daily cyanobacterial cell mortality [151]. High cell turnover may play a significant role in bloom persistence due to the recycling of nutrients from lysed cells [135]. Considering that the majority of cyanotoxins remain intracellular, a sudden bloom collapse has the potential to release large quantities of dissolved toxins into the water column. Many of these toxins, such as the cyclic heptapeptide microcystins and polycyclic cylindrospermopsin, are highly stable with half-lives on the order of hours to weeks in natural settings depending on temperature, UV and the presence or absence of bacteria capable of degrading these compounds [54] (Table 1). These compounds may originate in inland lakes but can be transported along the freshwater–marine continuum where they can exert their effects on marine flora and fauna. This scenario occurred in Monterey Bay, CA (USA) when a microcystin-producing CyanoHAB event in a nearby lake (Lake Pinto) was flushed downriver and into the bay where the cells were filtered by marine bivalves and subsequently consumed by local sea otters. The result was that nearly two dozen sea otters died of acute intoxication and subsequent analyses identified that the microcystins bioaccumulated within the shellfish meat at levels much higher than the ambient concentration [82].

## Transduction and Acquired Virulence

Cyanobacteria produce a wealth of seemingly nonessential secondary metabolites—many of which possess antibiotic, toxic or siderophoric properties—although most have not been ascribed a function. One such group of secondary metabolites is the cyanotoxins (Table 1). While research to date has failed to conclusively identify the true physiological or ecological role of these compounds, they are known to exert potent health effects on eukaryotic organisms, including humans. Genetic analyses have determined that these gene clusters are not highly constrained within certain groups, but instead exhibit a patchy distribution across a variety of cyanobacterial genera [149]. Likewise, many cyanobacterial strains contain multiple toxin operons—for instance, *Oscillatoria* sp. (PCC 6506) produces anatoxin-*a*, cylindrospermopsin and saxitoxin [116] (Table 1).

Phage-mediated gene transfer events are widely believed to have played a significant role in microbial evolution and in shaping the ecological niches these organisms exploit today [41, 109]. Advances in genomic sequencing have allowed researchers to identify within cyanobacterial genomes the genes of cyanophages; and conversely, cyanophage genomes have been found to contain genes of cyanobacterial origin as well [78]. Cyanophages are important agents of lateral gene transfer [79, 144]; although there is no conclusive evidence that cyanotoxin genes are actively exchanged with other species or genera. However, there is compelling evidence to believe that parts of the microcystin synthetase operon (*mcy*) have undergone horizontal gene transfer events in the past [147, 175]. As such, it is hazardous to assume a given genus or species will always be nontoxic without verification by biochemical or molecular analysis.

## Managing Cyanotoxins

Eutrophic waters are often reported to contain high concentrations of cyanotoxins, a phenomenon likely attributable to the high concentration of cyanobacteria supported by abundant nutrients [90]. The cues for toxin synthesis are likely subject to multiple environmental and cellular factors acting in unresolved synergistic or antagonistic combinations [55, 86, 176]. The effect that cell density has on cellular toxin quota has not been adequately resolved due to contradictory reports [65, 170], although cells in exponential growth phase are reported to produce more microcystin than when in lag or stationary phase [162]. Cyanobacterial concentrations are often positively correlated with microcystins at a range of low and high cell densities because the intracellular toxin contents remain relatively balanced due to losses to daughter cells during periods of division [77]. An investigation of 22 Canadian lakes spanning from low to high trophic states identified toxic cyanobacteria in

all systems and observed increasing microcystin concentrations as trophy increased [48]. In that study, the authors identified total nitrogen (TN) as the best predictor of total microcystin, with increasing TN correlating with increased microcystins. The observation that increased concentrations of dissolved macronutrients, N and/or P, favors growth of toxigenic cyanobacteria and toxin production is routinely reported [29]; however, this is likely a function of increased cell concentrations as opposed to surplus N or P actually promoting toxin gene expression. In fact, from a molecular basis, increased N should result in decreased microcystin biosynthesis owing to multiple transcription factor binding sites for the global nitrogen regulator (NtcA) within the *mcy* promoter which lead to upregulation of toxin biosynthesis under nitrogen-limiting conditions [49, 174]. Likewise, there is a growing body of evidence that suggests microcystin transcription may be dual controlled by iron availability via the *Fur* family of transcriptional regulators [1, 133]. However, both of these groups of regulators may ultimately be controlled by the redox status of the cell [176]. Finally, for reasons unclear, warmer temperatures appear to favor the growth of toxigenic strains of *Microcystis* over nontoxic ecotypes [24, 30]; a troubling trend considering projections of future climate scenarios.

Cyanotoxins in drinking water reservoirs represent a potent human health threat on a global scale which to date has not been adequately managed from a public health perspective. The potential for physical transport and trophic transfer (biomagnification) from freshwater environments to marine ecosystems further increases exposure risks in environments not routinely screened for cyanotoxins. One of the reasons for the lack of broadscale regulation has been the lag between identifying these harmful metabolites and the subsequent years of toxicological and epidemiological studies required to fully characterize these risks. The other major hurdle facing CyanoHAB monitoring is the lack of standardized analytical tests to detect and quantify cyanotoxins. However, as more of these harmful compounds are discovered in cyanobacteria (e.g., BMAA, jamaicamides, aeruginosins, etc.), the more cumbersome their management will become [22, 31, 62]. For this reason, it makes more sense to address cyanotoxin management from a broader perspective. There is little reason not to manage CyanoHABs in a similar manner that *Escherichia coli* is currently managed; which is to say, on a presence/absence context in finished drinking waters and on a concentration basis (CFU per milliliter) in raw waters. Under this framework, management decisions are not based on serotyping an *E. coli* strain to determine its pathogenicity, instead its presence and/or abundance dictate what subsequent actions are required. Raw waters containing cyanobacteria could likewise be managed based on their cell concentrations. For brackish and/or freshwater cyanobacteria, there are at least 20 common bloom-forming genera that are known to produce cyanotoxins (Table 1). While species differences may exist with regard to their toxigenicity, the potential for toxin gene acquisition via transduction or other lateral gene transfer event in routinely nontoxic species cannot be overlooked; which is why management decisions should be based at the genus level. This approach would remove much of the subjectivity inherent to microscopic identification of morphologically plastic cyanobacteria—a considerable problem when attempting to characterize cyanobacteria down to the species level.

Research over the past two decades on microcystin-producing genera has demonstrated that in most cases the majority of cyanobacterial cells in a bloom are nontoxigenic [70]. While this level of insight is generally lacking at present for the other cyanotoxins, the patchy distribution of cyanobacterial toxin genes makes informed bloom management difficult without specialized equipment to directly measure for these genetic markers and/or their analytes. In an attempt to simplify CyanoHAB management, the World Health Organization (WHO) has issued provisional guidance for both drinking and recreational waters for the most ubiquitous cyanotoxin, microcystin (MC-LR), based on general metrics of cyanobacterial abundance such as chlorophyll-*a* and cell counts [171]. Figure 5 displays the recommended WHO guidelines for recreational exposure to microcystins and assumes a conservative, low risk of adverse health effect at 4 $\mu g l^{-1}$, although the WHO acknowledges exposures up to 10 $\mu g l^{-1}$ are likely to be relatively low risk; exposures between 10 and 20 $\mu g l^{-1}$ are considered moderate risks and anything above 20 $\mu g l^{-1}$ carries a high risk of adverse health effects. The data from Fig. 5 were adapted from three previous studies comparing microcystin-producing cyanobacterial (predominantly *Microcystis* spp., but also some *Anabaena* spp.) cell densities with microcystin concentrations from three distinct lake types and trophic states (Western Lake Erie, OH: mesotrophic; Missisquoi Bay–Lake Champlain,VT: eutrophic; and Zhushan and Meiliang Bays–Lake Taihu, China: hypertrophic). All samples were collected over two or three summer periods, non-detects and samples below the limits of detection were omitted and detailed information about these studies is described elsewhere [90, 121, 125]. Note that in the Lake Erie study microcystin-LR was measured by protein phosphatase 2A assay (PP2A) instead of enzyme-linked immunosorbent assay (ELISA) as was used in the other studies; although these methods have been shown to yield comparable results [117]. In this example, some samples that contained low cell concentrations exceeded the amount of toxin expected, although this only occurred in the higher trophic lakes (Lake Champlain and Lake Taihu). Most importantly, however, was that the WHO provisional guidelines adequately predicted maximal microcystin concentrations; with no samples containing less than $10^6$ cells $ml^{-1}$ exceeding the moderate risk level for microcystin (20 $\mu g l^{-1}$). This figure represents a simplified meta-analysis of the type of large-scale analyses encompassing all aquatic trophic states that will be

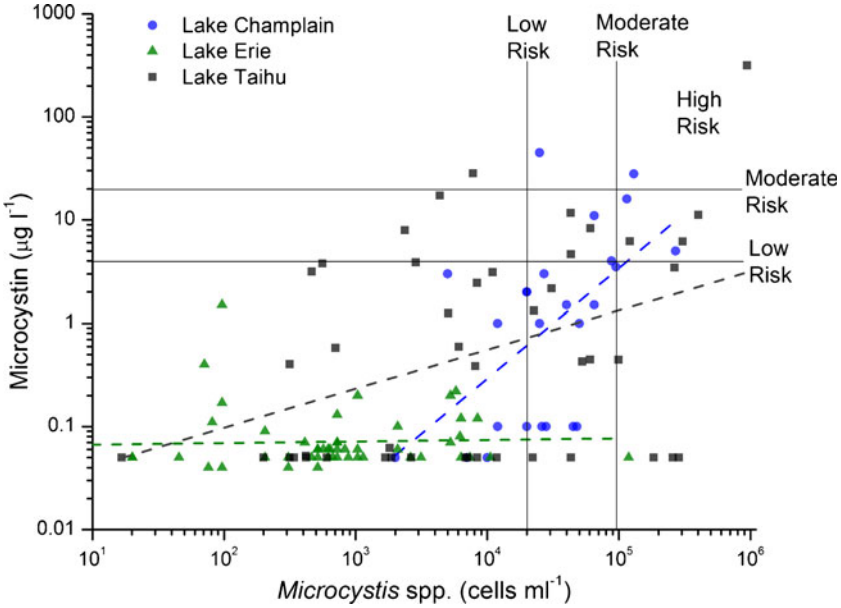


**Fig. 5** Comparison of CyanoHAB cell concentrations and microcystin-LR from mesotrophic (Western Lake Erie, OH, USA [121]), eutrophic (Missiquoi Bay, Lake Champlain, VT, USA [125]) and hypertrophic (Meiliang and Zhushan Bays, Lake Taihu, Jiangsu, China [90]) waters. The World Health Organization's (WHO) provisional guidelines for microcystin exposure in recreational waters [171] is included to illustrate how health alert levels could be based on simple water quality metrics such as CyanoHAB cell density

needed to characterize the exposure risks for all microcystins and the numerous other cyanotoxins endemic in many waterbodies worldwide. An extensive compilation of CyanoHAB events from around the world in which standardized measurements and units were utilized (e.g., micrograms of toxin per liter and cells per milliliter) would frame realistic toxin concentrations produced by these genera under natural settings in which management decisions could be based on broad, simple metrics such as cell concentration. For most cyanotoxins, these data likely already exist due to myriad studies over the years on cyanobacteria around the globe; although currently there is no central repository in which to store and view this information. The creation of a widely advertised, internet accessible database has the potential to make this a reality.

## Controlling CyanoHABs in Aquatic Ecosystems

The combination of anthropogenic nutrient loading, rising temperatures, enhanced vertical stratification, increased residence time and salination will favor cyanobacterial dominance and CyanoHAB proliferation in a wide range of aquatic ecosystems (Fig. 6). The recent geographic expansion, and in some cases intensification, of CyanoHABs has serious consequences for human water supplies, fisheries, and recreational resources.

Nutrient input reductions are the most obvious targets which can be altered and as such should be a central part of any CyanoHAB mitigation strategies in both freshwater and marine environments (Fig. 6). We have long been aware that P input reduction is an effective means of reducing cyanobacterial dominance in aquatic, and especially freshwater, ecosystems. However, there are numerous and increasing instances where N input reductions are also needed. This is especially the case in eutrophic, CyanoHAB susceptible lakes, rivers, estuaries, and coastal waters which are capable of assimilating more N and increasing their trophic state [104]. A key management priority is to establish N and P input thresholds (e.g., TMDLs), below which CyanoHABs can be controlled in terms of magnitude, temporal and spatial coverage. The ratios of N to P inputs should be considered when developing these thresholds. Ideal input ratios are those that do not favor specific CyanoHAB taxa over others, but there does not appear to be a universal ratio—above or below—which CyanoHABs can be consistently and reliably controlled. For this reason, total nutrient loads and concentrations need to be considered in CyanoHAB management [73, 74]. For example, it is generally thought that total molar N:P ratios above ~15 discourage CyanoHAB dominance [137]. However, if the nutrient load and internal concentrations of N and/or P are extremely high, a ratio approach for reducing CyanoHABs is not likely to be effective [105, 106, 172].

There are many ways to reduce nutrient inputs on a lake or larger ecosystem scale. Nutrient inputs have been classified as point source and non-point source. Point sources are often associated with well-defined and identifiable discharge sites; therefore, these nutrient inputs are relatively easy to control. It is therefore no surprise to see that most of the short-term successes in nutrient input control are those associated with point sources, including wastewater treatment plant, industrial effluent, and other distinct input sources. The major challenge that remains in many watersheds is targeting and controlling nonpoint sources, which in many instances are the largest sources of nutrients; hence, their controls are likely to play a critical role in mitigating CyanoHABs.

Nutrient management strategies may also include the removal of nutrients from receiving waters after they have been discharged. Examples of post-discharge removal

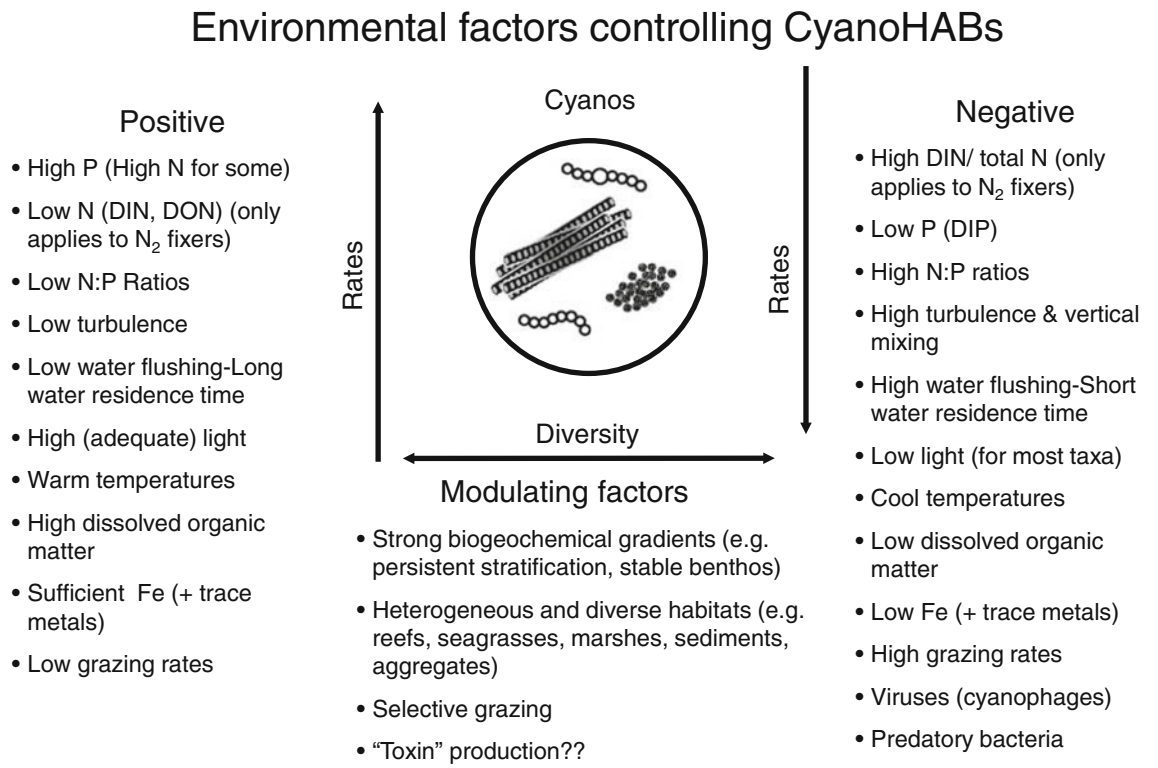


**Fig. 6** Suite of positive and negative effectors as well as modifying environmental and ecological factors that influence CyanoHAB potentials in aquatic ecosystems

which have been attempted include: dredging sediments, harvesting macrophytes that have assimilated nutrients, and in some cases stocking and then removing higher trophic level consumers (finfish and shellfish) to eliminate nutrient-containing biomass. Other approaches have involved precipitating, binding, and immobilizing nutrients in the sediments [53, 123]. All the above techniques have been variably effective [105], and in some cases, the results were even counterproductive. For example, sediment dredging can disrupt important biogeochemical processes in the surface sediments and benthos (e.g., denitrification), and it can lead to enhanced mobilization of previously retained nutrients. Also, disturbance of the sediment meso- and micro-fauna, as well as microbial communities, can disrupt nutrient, oxygen, and carbon cycling to the detriment of the ecosystems undergoing mitigation and restoration [138].

Manipulating physical factors that are known to play key roles in CyanoHAB competition versus other eukaryotic phytoplankton can, at times and under specific conditions, have some beneficial effects on water bodies plagued with CyanoHABs. Vertical mixing devices, bubblers, and other means of breaking down destratification have proven effective in controlling outbreaks and persistence of CyanoHABs in relatively small impoundments [59, 156]. Generally, these devices have limited applicability in large lake, estuarine, and coastal waters because they simply cannot exert their forces over such large areas and volumes. Increasing the flushing rates, and thereby decreasing water residence time, can be effective in reducing or controlling CyanoHABs [11, 83, 105]. However, care must be taken to make sure that the flushing water is relatively low in nutrient content, so as not to compound the enrichment problem. Furthermore, few catchments have the luxury of being able to use precious water resources normally reserved for drinking or irrigation for flushing purposes. This is especially true of regions where freshwater runoff is limited and/or is periodically impacted by droughts [124].

Lastly, flushing can alter the circulation regimes of receiving water bodies [114]. Care must be taken not to alter the physical environment in such a way (e.g., increasing thermal or chemical density stratification, entrainment bays and arms of water bodies) so that CyanoHABs are trapped in, rather than flushed out, of the system [114].

In a great majority of cases, nutrient input reductions are the most direct, simple, and ecologically/economically feasible CyanoHAB management strategy. Nutrient input reductions that are aimed at specifically reducing CyanoHAB competitive abilities, possibly combined with physical controls (in systems that are amenable to those controls) are often the most effective strategies. Nutrient (specifically N) treatment costs can be prohibitive, in which case, alternative nutrient removal strategies may be called for. These would

include construction of wetlands, cultivation and stimulation of macrophytes, stocking of herbivorous (and specifically cyanobacteria consuming) fish and shellfish species [63].

Overall, in addition to nutrient input reductions, water managers will have to accommodate the hydrological and physical–chemical effects of climatic change in their strategies. Without curbing greenhouse gas emissions, future warming trends and their impacts on aquatic ecosystems will likely only lead to further expansion and dominance of aquatic ecosystems by these nuisance species.

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