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Understanding Cyanobacterial Harmful Algal Blooms: From Ecological Drivers and Impacts to Management

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Figure 1. Field images of planktonic, scum-forming, periphytic, and benthic mat forming cyanobacterial blooms. Photos by West Bishop.

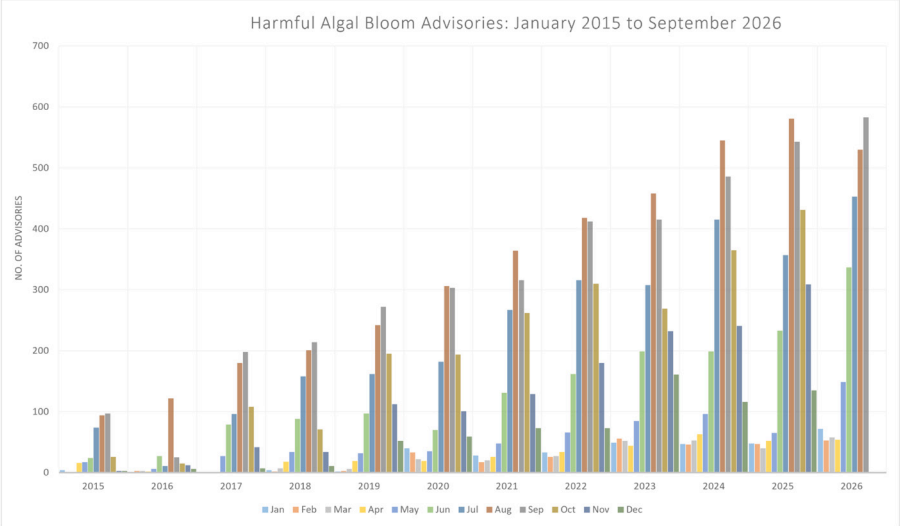
Introduction

Cyanobacteria, commonly known as blue-green algae, represent one of Earth's most ancient and successful microbial groups, having evolved approximately 3.5 billion years ago (Knoll 2008) with oxygenic photosynthesis first originating between 3.4 and 2.9 billion years ago (Fournier et al. 2021). These versatile primary producers are ubiquitous across terrestrial and aquatic environments, playing fundamental roles in biogeochemical cycles and ecosystem functioning (Whitton 2012) while producing thousands of bioactive secondary metabolites that contribute to their ecological success. However, when environmental conditions favor rapid proliferation, certain cyanobacterial species can form harmful algal blooms (cyanoHABs) that pose significant threats to agricultural operations (e.g., irrigation, livestock, aquaculture), as well as public health.

CyanoHABs manifest as dense accumulations of one or multiple species that can visibly discolor water, form surface scums, grow attached to surfaces, or cover benthic areas (Figure 1). These events are increasing in frequency, intensity, and duration across many regions globally, driven by the nutrient enrichment from agricultural and urban runoff, altered hydrological patterns, and changes in weather patterns (Paerl and Huisman 2009; Chapra et al. 2017). While enhanced monitoring capabilities and reporting systems contribute to the documented increase in bloom incidents, broad scientific consensus supports a genuine ecological trend toward more severe cyanoHAB events (Paerl et al. 2011). The US Environmental Protection Agency's state reporting system demonstrates this pattern, with escalating numbers of recreational and drinking water advisories issued annually since systematic tracking began in 2015 (Figure 2).

The economic and ecological impacts of cyanoHABs extend far beyond their immediate visual effects. These blooms interfere with multiple water uses, including drinking water supply, agricultural irrigation, livestock watering, aquaculture operations, and recreational activities. Many cyanobacterial species produce potent toxins, including microcystins, cylindrospermopsins, saxitoxins, anatoxins, and guanitoxins (previously known as anatoxin-a(s)) that can cause acute and chronic health effects in animals, including humans (Graham et al. 2010; Paerl and Fulton 2001). Additionally, cyanoHABs release taste and odor compounds (e.g., geosmin and 2-methylisoborneol) that compromise water and fish tissue palatability (Smith et al. 2008; Graham et al. 2010) and cyanoHAB biomass can clog water treatment infrastructure, increase disinfection byproduct formation, and create anoxic conditions leading to fish kills and ecosystem degradation.

The complexity of cyanoHAB formation and persistence stems from the diverse array of causative species and their varied responses to environmental drivers. Both planktonic and benthic cyanobacteria can form problematic blooms in freshwater, estuarine, and marine systems, with periphytic and benthic forms also causing issues when attached to vegetation and substrates. Bloom dynamics are influenced by multiple interacting factors, including water temperature,



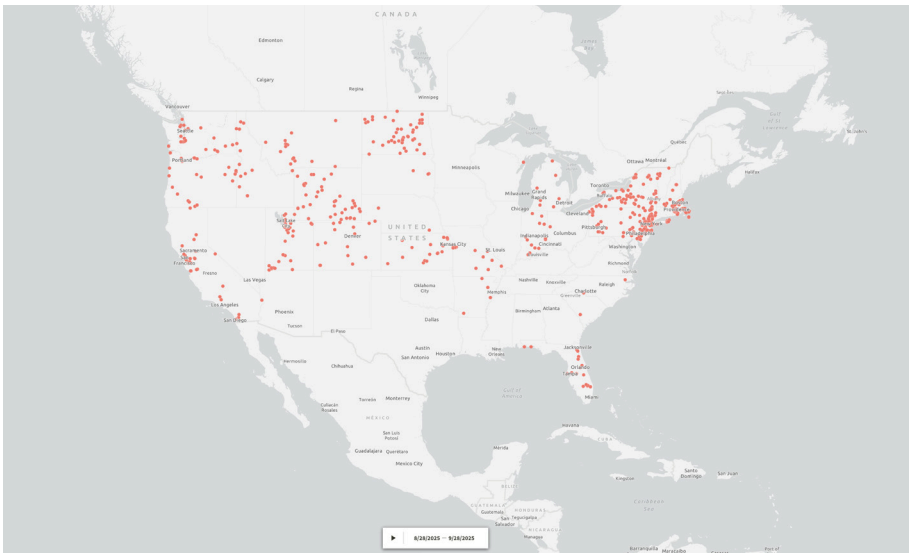


Figure 2. Numbers of state-issued advisories by month/year (from the 35 states that monitor and share information with USEPA) for recreational water and drinking water due to cyanoHABs since 2015 (A) and an associated incident map over the month of August 2025 (B). Data obtained from USEPA: https://storymaps.arcgis.com/stories/d4a87e6cdfd44d6ea7b97477969cb1dd.

light availability, hydrodynamics, and the concentration and bioavailability of macronutrients (i.e., nitrogen and phosphorus) and micronutrients (e.g., iron, manganese, silica) (Davis et al. 2009; Gobler et al. 2016). Recent research has expanded the understanding of how microbial community interactions and trace element availability affect bloom development and toxin production, adding layers of complexity to prediction and management efforts.

Detection, monitoring, and forecasting of cyanoHABs use a range of approaches, from traditional microscopy and pigment analysis to molecular techniques and satellite remote sensing, enabling both detection of blooms and early warning for management response; these methods are addressed in detail in Section 4.

Given the multifaceted nature of cyanoHAB challenges, effective management requires a comprehensive, adaptive approach tailored to specific water body characteristics, uses, and regional conditions (Steffen et al. 2014). No single intervention strategy proves universally effective across different systems, necessitating site-specific assessment of ecological factors, physical characteristics (depth, thermal stratification, residence time), surrounding land use practices, and the particular cyanobacterial species involved. This document provides agricultural, livestock, and aquaculture stakeholders with foundational knowledge of cyanobacteria biology, environmental drivers, health and economic impacts, and evidence-based management strategies. By establishing this scientific foundation, water resource managers and agricultural professionals can make informed decisions to protect both water resources and the communities that depend on them, ultimately supporting sustainable agricultural practices and safeguarding public health in an era of increasing cyanoHAB frequency and severity (Paerl and Huisman 2008; Paul 2008).

2. Cyanobacteria Biology

2.1 Common Bloom-Forming Cyanobacteria Species

CyanoHABs can be formed by a variety of different cyanobacterial genera. One of the most common and dominant bloom-forming species in national headlines is *Microcystis aeruginosa*, a colony-forming, buoyant, potentially toxic cyanobacterium. This species can dominate inland lakes and ponds, threaten aquatic life, and impede drinking water resources (Rinta-Kanto et al. 2009; Miller et al. 2010; Gibble et al. 2016; Peacock et al. 2018; Lefler et al. 2023). Other common planktonic bloom formers include several toxic species of *Anabaena, Aphanizomenon, Dolichospermum, Planktothrix*, and *Raphidiopsis* (formerly *Cylindrospermopsis*). Common benthic proliferating cyanobacteria differ from the planktonic ones and commonly include *Phormidium, Microseira, Microcoleus*, and *Heteroscytonema*. Each genus is known to produce its own suite of cyanotoxins (Table 1) that have an array of health impacts to humans and wildlife. Many cyanotoxins can irritate the skin (dermatoxins), eyes, nose, and throat, and they can cause abdominal discomfort or more seriously impact the liver (hepatotoxins) and nervous (neurotoxins) systems (Stewart et al. 2006; Funari and Testai 2008). Additionally, some studies have found that toxins from cyanobacteria can damage cell DNA, potentially causing cancer, or lead to reproductive defects (e.g., Carmichael 1997; Laughinghouse et al. 2012; Loftin et al. 2016; Fastner and Humpage 2021).

2.2 Emerging CyanoHABs of Concern

Benthic cyanobacteria are those that grow in, on, or near the bottom of a body of water, including sediment and other substrates (Pokrzywinski et al. 2021; Wood et al. 2020). Toxic benthic freshwater cyanobacterial proliferations were initially reported in the 1990s (Edwards et al. 1992; Gunn et al. 1992). Over the past 10 years there has been an increase in the number of publications on both freshwater and marine benthic cyanobacteria "blooms" (i.e., proliferations), although there are still more than four times the number of publications on planktonic HAB events compared to benthic blooms (e.g., Berthold et al. 2021, 2022; Wood et al. 2020). However, distinguishing between benthic and planktonic species remains a challenge given that benthic species can be found in the water column during resuspension events from substrate disturbances or differing life stages. Benthic species are comparatively less studied than planktonic species owing to the challenges associated with monitoring at depth, despite their ability to form dense mats and biofilms that negatively impact public and ecosystem health. Toxic benthic blooms have been associated with dog deaths in the US and abroad, but health advisory postings are rare due in part to limited monitoring and posting standards or requirements (as opposed to beach postings due to pelagic HABs). Benthic blooms can also alter macroinvertebrate community structure by smothering sessile organisms like freshwater bivalves (Wood et al. 2020). When benthic blooms detach from the benthos, they can contribute to a reduction in water quality through the production of gas from metabolic activity within the mat, accumulation of fine sediments beneath the mats, or from fast-moving water that can scour dense accumulations of benthic taxa (Bouma-Gregson et al. 2018).

When mats become dislodged from the benthos, cyanotoxins and other metabolites can disperse freely from floating aggregates (Newcombe et al. 2010) and contribute to diminished water quality. Much of the effort on benthic cyanobacteria to date has focused on identifying and characterizing benthic cyanobacteria species and their toxins (Nienaber and Steinitz-Kannan 2018; Puddick et al. 2014, Quiblier et al. 2013), as well as detecting and tracking these species and their toxins in the environment (Cadel-Six et al. 2007; Fletcher et al. 2015; Wood et al. 2010; Zastepa et al. 2015). Also, other studies have examined the role of environmental factors (temperature, light, flow, nutrients) in toxin production (D'Agostino et al. 2016; Loftin et al. 2016; Zastepa et al. 2017) and downstream effects of cyanotoxins and bioaccumulation (Bouma-Gregson et al. 2018; Miller et al. 2010). Moving forward, the ecology of benthic cyanobacteria requires considerable research on the environmental conditions that promote bloom events and toxin production, benthic cyanotoxin fate and transport, and best practices for sampling, monitoring, and controlling/managing benthic cyanobacterial proliferations. A more detailed understanding of all life stages of benthic cyanobacteria will allow researchers and water resource managers the ability to more accurately predict and subsequently better manage benthic cyanobacteria blooms (Hense and Beckman 2006).

2.3 Environmental Drivers of CyanoHAB Formation

The proliferation of cyanoHABs in freshwater systems is driven by a complex set of physical, chemical, and biological factors, including elevated temperature, increased light availability, water column stratification, and high concentrations of nutrients, primarily nitrogen (N) and phosphorus (P), as well as unique physiological traits of cyanobacteria (Huisman et al. 2018).

Nutrient Sources and Loading Patterns

Nutrient inputs to aquatic ecosystems are strongly influenced by land use patterns. Native landscapes like forests contribute very little N and P, while human activities such as agriculture and urban development have greatly increased the loading of these nutrients into water bodies (Elliot 2012; O'Neil et al. 2012; Paerl 2014; Almanza et al. 2019). Agricultural runoff, particularly from urea-based fertilizers, remains a major source of N and P (Wang and Huang 2021), and nutrient contributions from suburban and urban runoff are also rising (Toor et al. 2017). However, advances in wastewater treatment have helped reduce nutrient discharges into many water resources by removing P and converting N into nitrogen gas (N_2).

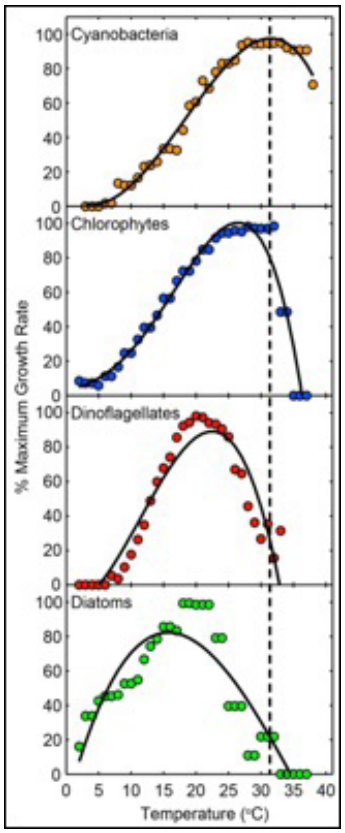


Figure 3. Algal and cyanobacterial growth responses to water temperatures (Paerl 2014).

Both eukaryotic algae and cyanobacteria depend on external loading of N and P to support growth. When nutrient enrichment becomes excessive and is coupled with favorable physical conditions, such as warm temperatures and calm waters, it can lead to a shift in the community structure. Under these conditions, cyanobacteria often outcompete other algae, resulting in harmful algal blooms or proliferations that can disrupt ecosystem balance and water quality.

Physical Environmental Conditions

CyanoHABs are most prevalent in nutrient-rich waters during warm, calm, summer periods, when surface heating

and limited water mixing create conditions that strongly favor cyanobacterial growth. Key physical drivers include thermal stratification, where layers of water with different temperatures form, and reduced mixing, which causes non-motile competitors to settle out of the epilimnion. This stratification not only minimizes competition for light and nutrients but also leads to low-oxygen (hypoxic or anoxic) conditions in deeper waters, promoting the release of N and P from sediments. Cyanobacteria can exploit these released nutrients either through their ability to migrate vertically or when mixing events bring nutrients back into the upper water column.

Many cyanobacteria regulate their buoyancy using specialized gas vesicles, enabling them to move vertically within the water column, rising to the surface during the day to capture sunlight for photosynthesis and descending at night to access deeper, nutrient-rich layers. This daily, or diel, vertical migration is driven by changes in cell density from carbohydrate accumulation and respiration. In calm, stratified waters, this ability gives cyanobacteria a distinct competitive advantage by allowing them to remain in optimal light and nutrient zones, while non-motile competitors settle out of the photic zone, reducing competition and promoting the formation of visible surface blooms. Additionally, many cyanobacteria can maintain high growth rates at elevated temperatures that inhibit many other types of phytoplankton, a thermal advantage that is expected to become even more pronounced with ongoing changes in weather patterns, further increasing the frequency and intensity of cyanoHABs (Paerl 2014; Chapra et al. 2017).

Nutrient Acquisition and Storage

Certain cyanobacteria enhance their survival in nutrient-poor conditions by fixing atmospheric nitrogen into usable forms through specialized cells called heterocytes or within low-oxygen microenvironments within colonies or mats. They can also rapidly uptake and store excess P, enabling growth when dissolved nutrients are limited. Additionally, photosynthesis can raise water pH above 9, which can mobilize P from sediments under certain conditions; however, sediment-bound P release is also driven by low oxygen (anoxia) in stratified systems and can occur across a range of pH conditions, both elevated and depressed, further increasing nutrient availability to support bloom development (Søndergaard et al. 2003; Paerl 2014; Solovchenko et al. 2020).

Competitive Suppression Mechanisms

Cyanobacteria can often outcompete other plankton, macroalgae, and aquatic plants. When dense surface aggregations of cyanobacteria shade underlying waters, it reduces light availability for other organisms relying on photosynthesis and further promotes cyanobacterial dominance, as they can grow under lower light conditions. Additionally, some cyanobacteria produce bioactive compounds that inhibit the growth of competing phytoplankton by disrupting photosynthesis or inducing oxidative stress (Gantar et al. 2008; Leão et al. 2009).

Defense Against Predation

Cyanobacteria use morphological (e.g., large colonies, filament bundles, small cell size) and chemical defenses to deter predation by zooplankton, benthic feeders, and fish (Ibelings et al. 2021; Nandini and Sarma 2023). Some species are too large to be ingested, while others pass through grazers undigested, and certain compounds they produce further reduce grazing pressure (Michalak et al. 2013).

Survival and Persistence Strategies

Cyanobacteria can survive adverse conditions such as winter by sinking to the bottom or forming thick-walled resting cells (akinetes) that can remain viable for decades until germination when conditions are favorable (Kwon et al. 2023).

Special Cases and Exceptions

Some species, like *Planktothrix rubescens*, are adapted to low-light conditions via accessory pigments (phycoerythrin), allowing them to thrive in deeper water layers and occasionally form surface blooms with high toxin concentrations, even in cooler or less-illuminated environments, such as during winter (Scheffer et al. 1997; Bonilla et al. 2011). Other genera, like *Raphidiopsis*, can thrive in well-mixed systems and scavenge P at low levels (Sinha et al. 2012). Increased occurrence of cyanoHABs in systems designated as oligotrophic or in cooler climates has been documented in many regions (Reinl et al. 2021, 2023).

Management Implications

CyanoHABs are favored by the convergence of high nutrient availability (from both external and internal sources), warm and stratified waters, and unique physiological and ecological adaptations of cyanobacteria. While reducing N and P inputs and availability of internal nutrient stores remains the most effective long-term strategy for cyanoHAB prevention, insufficient implementation of best management practices (BMPs) or continued inputs from diffuse sources often necessitates short-term interventions, such as artificial mixing or algaecide application, to disrupt bloom formation and persistence.

3. Cyanobacteria Toxins and Taste and Odor Compounds

3.1 Cyanotoxins: Types and Characteristics

There are now more than 300 known cyanobacterial toxins (Meriluoto et al. 2017) with the most common being microcystins (MCs), anatoxins (ATXs), guanitoxin (GNT) (formerly anatoxin-a[S]), cylindrospermopsins (CYNs),

nodularins (NODs), and saxitoxins (STXs) (aka paralytic shellfish poisoning toxins [PSPTs]). The observation that a bloom is "toxic" is a function of three elements: (a) there needs to be a toxigenic strain in the bloom that has the ability for toxin production, (b) biosynthetic pathways must be turned on to produce toxins, and (c) the bloom must obtain sufficient biomass for toxins to be measurable.

In many cases the hepatotoxins, such as microcystins and nodularins, share a common chemical structure, while cylindrospermopsins, though also hepatotoxic, have a distinct structure. For example, there are > 250 microcystin congeners with varying degrees of potency (Massey et al. 2020). The structural similarity with moiety variations makes diagnosing the causative toxin challenging for analytical chemists. Overall, these toxins can cause illness and mortality in animals, including humans. Upon ingestion of contaminated water, the toxins can enter the bloodstream and accumulate in the liver, causing liver failure or bleeding, and in serious cases, death (WHO 2020). Each type of hepatotoxin was first described in a single

Table 1. Common toxins associated with cyanobacteria, their toxic mechanism, and potential health effects.

Toxins	Variants/ analogues	Toxin producing genera	Toxic mechanism	Health effects
Microcystins	256+	*Anabaena, Anabaenopsis, Annamia, Aphanizomenon, Aphanocapsa, Aphanothece, Arthrospira, Calothrix, Cylindrospermum, Dolichospermum, Fischerella, Geitlerinema, Gloeotrichia, Hapalosiphon, Iningainema, Leptolyngbya, Limnothrix, Lyngbya, Merismopedia, Microcystis, Neolyngbya, Nostoc, Oscillatoria, Phormidium, Planktothrix, Plectonema, Pseudanabaena, Pseudocapsa, Radiocystis, Rivularia, Roseofilum, Schizothrix, Scytonema, Spirulina, Synechococcus, Tolypothrix, Westiellopsis*	Hepatotoxic, inhibits eukaryotic protein phosphatases	Gastrointestinal; liver inflammation, hemorrhage, and liver failure leading to death; pneumonia; dermatitis
Nodularins	10	*Aphanizomenon, Calothrix, Cyanothece, Iningainema, Leptolyngbya, Microcoleus, Nodularia, Nostoc, Wilmottia*	Hepatotoxic, inhibits eukaryotic protein phosphatases	Gastrointestinal; liver inflammation, hemorrhage, and liver failure leading to death; pneumonia; dermatitis
Cylindrospermopsins	5	*Anabaena, Aphanizomenon, Chrysosporum, Dolichospermum, Hormoscilla, Microseira, Oscillatoria, Phormidium, Raphidiopsis (Cylindrospermopsis), Sphaerospermopsis, Umezakia*	Hepatotoxic, cytotoxic, neurotoxic; inhibition of glutathione synthesis, protein synthesis and cytochrome P450	Gastrointestinal, liver inflammation and hemorrhage, pneumonia, dermatitis
Anatoxins	10	*Anabaena, Aphanizomenon, Arthrospira, Blennothrix, Chrysosporum, Cuspidothrix, Cylindrospermum, Dolichospermum, Geitlerinema, Kamptonema, Microcoleus, Microcystis, Microseira, Oscillatoria, Phormidium, Planktothrix, Raphidiopsis, Spirulina, Synechococcus, Tychonema*	Neurotoxic, mimics the neurotransmitter acetylcholine	Tingling, burning, numbness, drowsiness, incoherent speech, respiratory paralysis leading to death
Guanitoxin	1	*Aphanizomenon*, Cuspidothrix*, Dolichospermum, Sphaerospermopsis*	Neurotoxic, inhibits acetylcholinesterase leading to overstimulation of muscarinic and nicotinic cholinergic receptors	Excessive salivation, lacrimation, convulsions, respiratory paralysis leading to death
Saxitoxins	84+	*Anabaena, Aphanizomenon, Cuspidothrix, Cyanobium, Cylindrospermum, Dolichospermum, Geitlerinema, Heteroscytonema, Lyngbya, Microcystis, Microseira, Nostoc, Oscillatoria, Phormidium, Planktothrix, Pseudanabaena, Raphidiopsis, Scytonema*	Neurotoxic, blocks voltage-gated Na+ channels	Tingling, burning, numbness, drowsiness, incoherent speech, respiratory paralysis leading to death

Data summarized from: Borges et al. 2015; Carmichael 2001; Fastner and Humpage 2021; Huang and Zimba 2019; Humpage and Fastner 2021; Kuiper-Goodman et al. 1999; Pearson et al. 2010; Sant'Anna et al. 2011; Smith et al. 2025; Testai 2021; Van Apeldoorn et al. 2007; Wood et al. 2020; Berthold et al. 2021; Lefler et al. 2021. *Indicates genes for producing the toxin have been found in metagenome assembled genomes, but analytical confirmation is still needed (see Fiore et al. 2020; Lima et al. 2022).

cyanobacteria species; for example, the microcystin-LR congener was first described from *Microcystis aeruginosa* (Carmichael et al. 1988), nodularins were first described from *Nodularia spumigena* (Hunter 1995; Keevil 1991), and cylindrospermopsin was first isolated from *Raphidiopsis raciborskii* (formerly *Cylindrospermopsis raciborskii*) (Hawkins et al. 1985; Ohtani et al. 1992). Each of these toxins, and variants thereof, have since been found across many cyanobacteria (Table 1). The neurotoxins—including anatoxins, guanitoxins, and saxitoxins—target nerve synapses and, depending on the dose, can cause death by respiratory failure within minutes to hours (Carmichael 1994; Cestèle and Catterall 2000). Many cyanobacteria can produce these compounds and the genera and known toxins produced are summarized in Table 1.

The currently known number of toxic cyanobacteria is likely underestimated, in addition to the number of toxins/congeners associated with each taxon. It is also likely that more toxic taxa will be discovered as more isolates from different environments continue to be studied and screened. Many other cyanobacterial bioactive metabolites have been described but toxicity is still unknown (Huang and Zimba 2019; Jones et al. 2021). In addition to the toxins listed above, beta-methylamino-L-alanine (BMAA) is a non-protein amino acid produced by some cyanobacteria that has received increasing attention due to its potential links to neurodegenerative diseases, though these associations, putative risks, and analytical methods for testing are still being evaluated (Faassen et al. 2012; Chernoff et al. 2017). BMAA can accumulate in aquatic food webs and has been detected in dietary supplements, fish, and shellfish from bloom-affected waters, raising concerns for both human and animal health beyond the acute toxicity of the classical cyanotoxin classes. Thus, as a precaution, cyanobacteria should be considered potentially toxic.

3.2 Taste and Odor Compounds

In aquatic systems, cyanoHABs often occur after a rapid increase and accumulation of their population under favorable water and environmental conditions. Besides toxic metabolites (cyanotoxins), cyanobacteria that grow in water reservoirs and lakes can synthesize volatile secondary odorous metabolites which are usually referred to as "taste and odor" (T&O) compounds or "off-flavors" (Watson 2010). The production and occurrence of T&O compounds are known to be influenced by various environmental factors, such as community composition, light intensity, nutrient concentrations, water temperature, pH, and dissolved oxygen. Cyanobacterial T&O compounds belong to various chemical groups, including terpenoids, ionones, aldehydes, ketones, sulfurous compounds, amines, and others. Among those, the most frequently occurring compounds that are associated with many consumer complaints in drinking water supplies are geosmin (GEO) and 2-methylisoborneol (MIB), which confer undesirable flavors often described as petrichor odors or "earthy," "muddy," or "musty" (Kaloudis 2021). These compounds can also be detrimental to the aquaculture industry, imparting off-flavors in fish and making products unsuitable for human consumption (Smith et al. 2008; Moretto et al. 2022). Geosmin and MIB episodes in freshwater aquatic systems are largely caused by cyanobacteria, although these compounds may also be produced by other microorganisms, such as actinomycetes. In addition to GEO and MIB, several other T&O metabolites and cell degradation products may cause unpleasant "fishy," "septic," "grassy," or "swampy" smells in water (Zimba and Grimm 2003).

The metabolic potential of cyanobacteria makes them a source of many different molecules. More than 2,000 cyanobacteria metabolites have been reported, while this chemical space is further expanded by their "volatilome" (all volatile metabolites), which currently comprises more than 200 known compounds, including a large number causing T&O. A very small fraction of these molecules has been studied with respect to their bioactivities and effects in ecosystems and human health, while most studies relate to drinking water supplies. In sum, T&O have significant impacts on consumers' palatability of drinking water, on freshwater aquaculture and the food-chain, and on lake activities and local tourism. Recent advances in mass spectrometry and in vitro bioassays enable further study of cyanobacterial metabolites beyond the known cyanotoxins, and are expected to expand the known harmful and nuisance compounds and clarify their roles in aquatic ecosystems, aquaculture, agriculture, and the food chain.

3.3 Factors Affecting Toxin Production

Most of our understanding on the interplay among the factors affecting toxin production has focused on the production of the hepatotoxic microcystins by *Microcystis*. Here, recent molecular techniques have tremendously increased our understanding of factors that impact toxin production. Much less is known about environmental factors that impact other classes of cyanobacterial toxins, even though the biosynthetic pathways for the formation of all six classes of toxins are now known. The environmental factors associated with other toxin classes have been discussed elsewhere (Boopathi and Ki 2014; Neilan et al. 2013). Here we focus on the relationship of these three elements as they apply to microcystins.

(a) *The effects of environmental conditions on bloom biomass:* The presence of microcystin within a system requires the presence of cyanobacteria in the same system. Microcystins are primarily intracellular (inside cells), so the toxicity of a bloom is roughly related to the amount of toxin-producing *Microcystis* cells, or other microcystin- producing genera, in that same bloom (see below). However, at later growth stages and during cell lysis, much of this intracellular toxin may transfer to the dissolved state (Watanabe et al. 1992; White et al. 2005). This is not necessarily true for cyanobacteria neurotoxins, where a significant fraction of the toxin found in the water column may be extracellular (outside cells) (Shaw et al. 1999). Both ATX and STX have been detected in the water column in the absence of a

planktonic source, suggesting either a benthic producer for these dissolved toxins or a planktonic species that was not captured by normal monitoring protocols. As discussed in Section 3.1, bloom biomass is heavily dependent on the amount of nutrients entering the system and efforts to decrease bloom toxicity have often focused on a decrease in nutrient availability, with the overall goal of reducing bloom biomass.

(b) *Changes in the toxigenic strains within a bloom:* There are three main (geno)types of cyanobacteria: toxic, non-toxic, and potentially toxic. These individual genotypes respond to multiple different environmental cues including light, nutrient availability, temperature, population size, and grazing pressure. Genomic sequencing has shown that colonies within a *Microcystis* bloom are genetically diverse in how they respond to nutrient availability (Dick et al. 2021; Meyer et al. 2017), their interactions with surrounding bacterial populations or "phycosphere" (Smith et al. 2021), and in their potential to produce microcystins. As such, individual *Microcystis* colonies within a bloom respond to environmental changes differently, with each "type" occupying their own individual niche within the system (de la Escalera et al. 2022). On a broader scale, the abundance of microcystin-producing genotypes within a colony is positively correlated with colony size (Kurmayer et al. 2002).

Laboratory (Vézie et al. 2002) and field (Davis et al. 2009) studies suggest toxic (microcystin-producing) strains grow faster than non-toxic strains under elevated levels of N and P. However, there is a metabolic cost for microcystin production, and some conditions may encourage growth of non-microcystin producing strains (Briand et al. 2012, 2009, 2008). Elevated temperatures may also promote the growth of toxic cyanobacteria over non-toxic types (Davis et al. 2009), leading to an increase in the proportion of toxic genotypes in the population and thus a net increase in toxin production.

(c) The regulation of the biosynthetic pathways for microcystin production: The microcystin biosynthetic operon (i.e., cluster of genes regulating microcystin production) is large and contains two bidirectionally transcribed operons with six core biosynthetic gene modules (*mcyA-E* and *mcyG*) along with four small tailoring gene modules (*mcyF*, *mcyH-J*). All form part of a mixed non-ribosomal peptide synthetase/polyketide synthase (NRPS/PKS) complex (Tillett et al. 2000). There are two core regulators of gene transcription for the mcy operon. One is the global nitrogen control factor NtcA (Ginn et al. 2010) and second is the global regulator, the ferric (i.e., iron) uptake regulator (Fur) (Martin-Luna et al. 2006). These regulators can both up- and down-regulate gene expression in response to N and iron concentrations. Microcystins are nitrogen-rich compounds, and it is now generally accepted that increased N availability leads to increased microcystin production (Gobler et al. 2016). Inhibition of microcystin biosynthesis during times of N limitation by NtcA is therefore expected as would be the biosynthesis of most nitrogen-rich compounds. There is also increasing evidence that regulation of the microcystin biosynthetic operon is associated with the presence of reactive oxygen species (ROS). Studies have shown an increase in microcystin operon activity with higher light quality and exposure to high light intensities (Kaebernick et al. 2000; Salvador et al. 2016). However, the relation between light and cellular microcystin content is complex, probably reflecting our limited understanding of the cyanobacteria ROS responses in relationship to multiple environmental stressors and differences between different genera. Studies have shown that high light intensities either decreased (El Semary 2010; Wiedner et al. 2003) or increased (Tonk et al. 2005; Utkilen and Gjolme 1992) bloom toxicity. There appears to be an optimal light intensity where the *mcy* gene transcription increases with increasing light, only to decrease at light levels above that intensity. As reviewed in Salvador et al. (2016), this complex expression of the microcystin biosynthetic operon in relationship to light is dependent upon the genus in question, its stage in the cellular growth cycle, the intensities and quality of the light involved, and any prior existing cellular mechanisms for dealing with ROS.

In summary, the environmental factors that lead to increased bloom toxicity are complex. Recent models have addressed this complexity at the molecular level to predict how changes in nutrient ratios and other environmental parameters may change the overall toxicity of blooms in Lake Erie (Hellweger et al. 2022) and elsewhere. These models provide new insights into cyanotoxin production, but future experiments will determine if these findings are accurate.

4. CyanoHAB Detection, Monitoring, and Forecasting

Detection and monitoring capabilities inform both impact assessment and management response. A variety of techniques are applied to detect cyanoHABs, ranging from accessory pigments and cyanobacteria cell detection and quantification methods to field- and laboratory-based analytical methods focused on cyanotoxin production genes or toxin detection. Accessory pigments provide information on algal and cyanobacterial abundance and emerging methods are being developed to help distinguish these groups in samples based on pigments. Chlorophyll-a detection methods, whether in-situ, remote sensing sensors, or laboratory methods, are well established but cannot distinguish between cyanobacteria and other algae. Other pigments, including phycocyanin and phycoerythrin, are better indicators of cyanobacteria abundance, as these pigments are more specific to cyanobacteria. Newer pigment analytical methods, including in-situ (e.g., FluoroProbe [bbe Moldaenke]) and hyperspectral sensors or radiometers (e.g., for remote sensing), may be better able to fingerprint algal classes and distinguish between types of cyanobacteria. Benefits of in-situ and remote sensing pigment analyses include speed of analyses (instantaneous for sensors, can also provide near-continuous data) and ability to remotely detect bloom extent over very large areas (thousands of square kilometers). Cell counting techniques, either manual

or via semi-automated FlowCam systems (Yokogawa Fluid Imaging Technologies, Inc.), can more definitively calculate abundance and biomass and distinguish between genera known to produce cyanotoxins, but these methods are often time and labor intensive, require skilled analysts/phycologists, and can suffer from inter-analyst (or inter-laboratory) variability. Molecular methods provide another tool to identify algal communities and changes to communities over time (environmental metagenomics) and to determine potential for cyanotoxin production (typically through targeted qPCR assays for cyanotoxin production genes). Commercial multi-plex qPCR methods, including Phytoxigene's CyanoDtec (Standard Method 10120) and emerging molecular-based field tests, are providing faster alternate approaches for cyanoHAB detection. Multi-plex assays have the benefit of screening for the potential production of multiple cyanotoxins with one test. Due to enhanced sensitivity of these methods, it may be possible to detect the potential for toxin production days or weeks before toxin concentrations are high enough to be detected through traditional toxin-detecting techniques. This may provide early warning for lake managers and water system operators. Some studies have shown good correlation between cyanotoxin production genes and detection of cyanotoxins, and qPCR techniques are increasingly being relied upon as a screening tool, but presence of a gene does not guarantee toxin production or detection. Overall, none of the previously mentioned methods can determine bloom toxicity, just the potential for toxin production.

Multiple methods for cyanotoxin detection exist and each has associated limitations and benefits. These methods include the enzyme-linked immunosorbent assay (ELISA), receptor-binding assay (RBA), protein phosphatase inhibition assay (PPIA), 2-methoxy-3-methyl-4-phenylbutyric acid (MMPB) method, and liquid chromatography-mass spectrometry (LC-MS). ELISA and LC based methods are the most used and will be discussed further.

ELISA methods are available as both semi-quantitative field kits and quantitative laboratory methods for many of the commonly found toxins. While the field kits are often fast, the lack of precision in some of the field kits has led to reports of both false positives and negatives. Newer ELISA-based cartridge kits and readers are beginning to overcome some of the initial limitations of field kits, although achieving adequate cell lyses (breaking cell walls and membranes) is still a potential issue for any field-based, total cyanotoxin testing method. A standard ELISA lab method is available for total microcystins (MC) (US EPA Method 546) and was included as part of nationwide UCMR 4 drinking water monitoring. A benefit of the total microcystins ELISA method is the ability to detect the vast majority of the >250 microcystin variants due to the highly conserved ADDA ([all-S,all-E]-3-amino-9-methoxy-2,6,8-trimethyl-10-phenyldeca-4,6-dienoic acid—structural backbone for toxicity of MCs) target, although there is some variability in cross-reactivity between variants. ELISA kits not based on the ADDA moiety may have less cross reactivity or may be targeted to react with specific variants. Additional benefits of ELISA laboratory methods include relatively inexpensive analytical equipment (e.g., plate reader) and straight-forward analyses (can be conducted with minimal training). In addition, new semi-automated ELISA analytical instruments (e.g., CAAS cube) have reduced inter-analyst variability and streamlined processes. ELISA kits have also been developed for the detection of saxitoxins, cylindrospermopsin, anatoxin-a, and BMAA, but standard EPA methods are not yet available. If saxitoxins are detected via ELISA, follow-up analyses via LC-based techniques are recommended to confirm totals (Smith et al 2025). In some regions (e.g., Ohio) there was very good correlation between total saxitoxins via ELISA and LC-based methods, but in other regions (e.g., California) ELISA often underestimated total saxitoxins due to differences in cross-reactivity between analogues.

Liquid Chromatography-Tandem Mass Spectrometry (LC-MS/MS) analyses provide the most precise method for quantitation of individual microcystin variants. The EPA has established LC-MS-based methods for the detection of six microcystin variants and nodularin (US EPA Method 544) in drinking water. The recreational (raw water) US EPA method includes additional microcystin variants that have available standards. Limitations with targeted LC-based approaches include potentially underestimating total microcystin concentrations, as these methods are not quantifying all the >250 variants simultaneously. Non-targeted microcystins analyses overcome some of the limitations of targeted analyses, but these techniques require expensive analytical equipment, highly skilled analysts, and are typically time-intensive (with limited current commercial laboratory capacity). These techniques are helpful when investigating animal exposure cases or conducting toxicological studies.

A faster and less expensive LC-based option for total microcystins analysis is the 2-methoxy-3-methyl-4-phenylbutyric acid (MMPB) method (Sano et al. 1992). In this method the conserved ADDA moiety is first chemically cleaved and then analyzed, giving a measure of total microcystins, similar to the ELISA MC-ADDA method (Foss and Aubel 2015). This is a preferred approach for analyses of total microcystins in fish tissue and other complex matrices. The MMPB method poses challenges for use in treated drinking water matrices, however, due to potential for treatment chemicals to cleave the ADDA moiety and give false positives for total microcystins, although this can be partially overcome through subtraction methods. Additional chemical cleavage methods have been developed for detection of rarer microcystin variants that have modifications to the ADDA moiety (Foss et al. 2020).

USEPA developed a standard LC-MS/MS method for the combined detection of cylindrospermopsin and anatoxin-a (US EPA Method 545), but the method does not include variants of those toxins and there are no standard USEPA methods for the other cyanotoxins, most notably saxitoxin and saxitoxin variants. The analyses of freshwater saxitoxins poses some unique analytical challenges, which are covered in a recent review (Smith et al. 2025). Overall, the detection of cyanotoxins is complicated by the limited

availability of certified reference standards for the majority of cyanotoxin variants.

Over the last several decades, substantial research has focused on developing tools for early warning and monitoring of HABs on large spatial scales through advancements in forecasting science and satellite remote sensing technology. Specific advancements have been made in monitoring and forecasting for both HAB cells. In freshwater systems, there are four primary products for cyanobacteria satellite remote sensing monitoring and forecasting. The Cyanobacteria Assessment Network (CyAN) is a cross-agency effort that has revolutionized the surveillance and early detection of cyanoHABs through satellite remote sensing in inland waterbodies (>1 km wide), including key drinking water resources and recreational areas. CyAN's goal is to develop a unified and systematic approach to identifying cyanobacterial blooms across the contiguous US using satellite imagery. Additionally, NOAA's National Centers for Coastal Ocean Science (NCCOS) and partners provide an operational Lake Erie HAB Forecast to alert coastal managers, drinking water suppliers, and recreational end-users to cyanoHAB events and bloom movement before they cause serious public and ecosystem health threats and negative economic impacts. The NCCOS provides routine monitoring of freshwater blooms at various locations through their HAB Monitoring System and also provides daily monitoring of cyanobacteria in lakes and reservoirs nationally in support of other federal agencies and state governments. Lastly, the US Army Corps of Engineers (USACE) research laboratory is developing satellite image-based software tools ranging in complexity and functionality to account for various skill levels and mission-based needs that became publicly available in 2022 (Johansen et al. 2019, 2022). The US Geological Survey also maintains an active cyanoHAB monitoring program across the US, using field teams and sensors in substantial collaboration with the other federal programs.

These cyanoHAB monitoring and forecasting tools allow for refined, streamlined analysis and the development of image-based abundance maps of three common HAB indicators to support monitoring and management efforts across the nation. The integration of new remotely-sensed forecasting and monitoring products, like those described above, into comprehensive monitoring programs has and will continue to allow for the timely and proactive execution of potential cyanoHAB mitigation actions. In freshwater systems, this includes the optimization of drinking water treatment strategies and posting information/treating blooms in recreational waters, in many cases before a bloom becomes a significant health and environmental hazard. Although much progress has been made in forecasting freshwater bloom events, forecasting tools are not easily transferred among HAB species or between locations, and forecasts for smaller inland water bodies are just now being explored as higher spatial resolution satellite remote sensing becomes more widespread (e.g., Sentinel-2, Planet). For example, the USACE is collaborating with NCCOS and local stakeholders in Florida to develop a model for Lake Okeechobee that predicts cyanobacteria bloom location and intensity from 1-5 days (short-term forecast) and the likelihood a bloom will intensify or decline over the coming weeks to a month (seasonal forecast).

5. Impacts and Consequences of CyanoHABs

CyanoHABs occur in different environments and as noted above, can sometimes be toxic, threatening the functioning of the ecosystem and degrading the quality of water for drinking and recreation. Toxin production by these species can range from trace to lethal levels and cause severe impacts on humans, fish, livestock, and pets, as well as land plants and food crops, depending on the species present in the water body and the toxins (type and concentration) produced. Human, wildlife, and livestock health may be impacted by HAB toxins because of ingestion, inhalation, or contact, and fatalities due to consumption of cyanotoxins have been documented in several locations around the world (Stewart et al. 2008; Wood 2016). Symptoms of intoxication may include irritation of the skin, eyes, nose, or throat; abdominal discomfort, such as pain, vomiting, and diarrhea; neurological symptoms, including confusion, memory loss, seizures, headache, and paralysis; liver or kidney damage; and ultimately death. Symptoms differ according to type and density of cyanotoxin present and the method and duration of exposure (e.g., recreation, ingestion, inhalation). Domestic and wild animals are not immune to HABs and may experience excessive salivation, weakness, staggering gait, difficulty breathing, seizures, or even death, which can occur hours or days after exposure or ingestion of cyanotoxin-tainted water (CDC 2019). Thus, the negative effects of cyanobacterial blooms on aquatic ecosystems can cause serious ecological and public health problems.

Some recent research has also focused on the transfer of certain cyanotoxins across the freshwater to marine continuum (Peacock et al. 2018). Specifically, toxins originating from cyanobacteria in freshwater systems have been detected within connected coastal waters and marine environments (Miller et al. 2010). There are multiple exposure routes to cyanoHAB toxins, including contact recreation, food supply, potable source water, and aerosolization (Falconer et al. 1999; Jang et al. 2020). Aerosolization represents an understudied but important exposure route, particularly near water bodies with active blooms where wave action, boat wakes, or spray irrigation can disperse cyanotoxin-filled droplets. Studies have detected microcystin-LR in aerosols above bloom-affected water bodies (Jang et al. 2020), with potential inhalation risks for swimmers, recreational users, and agricultural workers irrigating with contaminated water.

5.1 Human Exposure Risk

Non-regulatory drinking water Health Advisory Levels (HAL) were established for microcystins and cylindrospermopsins by the US EPA in 2015 (Table 2). Several states have adopted US EPA's HALs into rule while others have established their own advisory levels for some or all the

cyanotoxins listed in Table 1. For example, Oregon has established drinking water thresholds for anatoxins and saxitoxins that are less than the World Health Organization (WHO) guideline values (Farrer et al. 2015). Given the lack of federal drinking water Maximum Contaminant Levels (MCLs), state thresholds for HALs can vary considerably.

The US EPA established recreational criteria and swimming advisory recommendations for microcystins and cylindrospermopsins in 2019 (Table 2). At that time, 35 states had already established cyanoHAB guideline values (US EPA 2019), but some states subsequently modified their guidelines to conform to US EPA recommendations and additional states may have adopted new advisory thresholds. As with drinking water thresholds, thresholds should be verified at the state-level as values vary. Given the large number of water bodies in the US and the variability in cyanoHAB response efforts between states, monitoring for cyanobacteria or toxins is often inconsistent and limited.

WHO establishes distinct operational timeframes for cyanotoxin exposure assessments that differ significantly from other regulatory agencies' approaches. WHO defines short-term exposure thresholds for human drinking water as "a period of about 2 weeks," which contrasts with the US EPA's 10-day exposure period for microcystins and cylindrospermopsin health advisory levels (ITRC 2022). For acute neurotoxins such as saxitoxin and anatoxin-a, WHO considers threshold values applicable to single-day or single-exposure events, while long-term exposure assessments are designed for entire lifetime exposures (ITRC 2022).

While the US Food and Drug Administration (FDA) established thresholds for saxitoxins in seafood causing paralytic shellfish poisoning (PSP) in 2015, no regulations have been established for the same compounds in freshwater systems (FDA 2005). In marine systems, PSPs are produced by dinoflagellates and can accumulate in seafood. Consuming as little as 1 mg of PSP of impacted mussels can cause illness or death in adults (Mulvenna et al. 2012; Ching et al. 2015; McIntyre et al. 2021). The same class of compounds is produced by freshwater cyanobacteria, but data on bioaccumulation within freshwater systems is limited (see Table 2).

Additionally, the FDA does not have established regulatory guidelines for microcystins, cylindrospermopsins, or anatoxins, but instead relies on provisional guidelines set by US EPA and WHO for drinking water exposure when determining exposure risk to cyanotoxins from blue-green algae supplements and food products. They have recalled both food supplements and drinks following detection of microcystins in those products at concentrations of concern (Miller et al. 2020; FDA 2024). States may have additional

Table 2. Cyanotoxin guidelines and regulations.

	Microcystins and Nodularin	Cylindrospermopsin	Anatoxin-a	Saxitoxins (Paralytic Shellfish Poisons)
Drinking Water (US HAL, Adult)[1,2]	1.6 µg/L	3.0 µg/L	-	-
Drinking Water (US HAL, Child)[1,2]	0.3 µg/L	0.7 µg/L	-	-
Drinking Water (WHO provisional guideline values, Adult)[3]	1 µg/L (long-term) 12 µg/L (short-term)	0.7 µg/L (long-term) 3 µg/L (short-term)	0.03 mg/L (short-term, no long-term level established)	3.0 µg/L (short-term, no long-term level established)
Drinking Water (individual states)	varies	varies	varies, acute ranges from 0.1 (MN) to 8 µg/L (CA)	varies, acute ranges from 0.2 (WA) to 1.6 µg/L (OH, adult level)
Recreational Waters – USEPA[4]	8 µg/L	15 µg/L	-	-
Recreational Waters -WHO[5]	24 µg/L	6 µg/L	60 µg/L	30 µg/L
Recreational Waters – USEPA[4]	Low risk: 20,000 cells/ml cyanobacteria or 10 mg/L chlorophyll-a/L if cyanobacteria dominance Moderate risk: 100,000 cells/ml cyanobacteria or 50 mg/L chlorophyll-a/L if cyanobacteria dominance High risk: Cyanobacterial scum formation			
Recreational Waters Individual States (individual states)	varies	varies	varies	varies
Seafood – FDA[7]	-	-	-	80 µg per 100 grams of meat
Blue-Green Algae Products – FDA[8]	Rely on "Current Good Manufacturing Practices (CGMPs) for Food and Dietary Supplements" rules and recall products with elevated cyanotoxins based on USEPA and WHO provisional guidelines listed above.			

[1]USEPA. 2015. Drinking Water Health Advisory for the Cyanobacterial Toxin Microcystins Toxins. EPA- 820R-15100
[2]USEPA. 2015. Drinking Water Health Advisory for the Cyanobacterial Toxin Cylindrospermopsin. EPA- 820R-15101
[3]World Health Organization (WHO). 2022. Guidelines for drinking-water quality: Fourth edition incorporating the first and second addenda. ISBN: 978-92-4-004506-4
[4]USEPA. 2019. Recommended Human Health Recreational Ambient Water Quality Criteria or Swimming Advisories for Microcystins and Cylindrospermopsin. EPA 822R-19-001
[5]World Health Organization (WHO). 2021. Toxic cyanobacteria in water - Second edition, A guide to their public health consequences, monitoring and management (USEPA references this document's cyanobacteria cell guidelines)
[6] World Health Organization (WHO). 2019. Guidelines for safe recreational water environments. Volume 1: Coastal and fresh waters. ISBN: 9241545801
[7]Food and Drug Administration (FDA). 2005. Clams, Mussels, Oysters, Fresh, Frozen or Canned - Paralytic Shellfish Poison. CPG Sec 540.250
[8]Food and Drug Administration (FDA). 2021. Blue-Green Algae Products and Microcystins. https://www.fda.gov/food/natural-toxins-food/blue-green-algae-products-and-microcystins

guidelines for food consumption. For example, the State of Ohio has conducted microcystins analyses in sports fish and may issue consumption advisories based on testing results. The US EPA is currently developing a fish tissue microcystins analysis methodology and assessing the need for federal microcystins fish consumption guidelines.

Although the majority of taste and odor (T&O) compounds produced in cyanoHABs are not known to cause health concerns, they negatively affect aesthetic water quality and consumers' acceptance and require costly advanced treatment to remove. Many T&O incidents worldwide concern water supply utilities, since conventional water treatment processes are largely ineffective for their removal, while some T&O can be sensed by the human nose at extremely low concentrations (low ng/L levels). As a result, water suppliers may receive complaints by consumers because the water has an undesirable flavor that renders it unacceptable for consumption. Geosmin and MIB are considered as a major source of drinking water T&O complaints, comparable to the chlorine disinfectant odors. Besides drinking water, unpleasant T&O caused by cyanobacteria and cyanoHABs may also negatively impact recreational activities and tourism in lakes. Large water systems can spend hundreds of thousands of dollars on activated carbon annually to try to remove taste and odor compounds from drinking water.

5.2 Ecosystem and Environmental Effects

CyanoHABs can have direct and indirect impacts to the biota associated with aquatic ecosystems. Cyanobacteria often exhibit gelatinous colonies, aggregated filaments, and other unique structural features that make them difficult to be consumed (DeMott et al. 2001; Mitra and Flynn 2006; Webster and Peters 1978). *Daphnia* are unable to capture or ingest many cyanobacteria and can instead selectively graze on green algae (Lampert 1987; Wang et al. 2010). As mentioned above, zebra mussels have also shown the ability to reject certain toxic strains of cyanobacteria (Vanderploeg et al. 2001). This selective grazing facilitates bloom formation and dominance of cyanobacteria in the planktonic photosynthetic assemblage. Direct toxin impacts to fish and zooplankton can occur, including embryo malformations, altering immune function, endocrine disruption, and decreased fecundity (Liu et al. 2002; Rogers et al. 2011). Toxins can also transfer up the food chain into predatory fish, birds, and mammals through aquatic and emergent invertebrates (Moy et al. 2016). A primary example would include mortalities of bald eagles from vacuolar myelinopathy due to accumulation of a cyanobacterial toxin through coots consuming epiphytic cyanobacterial growths on aquatic plants (Breinlinger et al. 2021). Direct physical impacts of cyanobacterial biomass are common, such as mats that clog intake pipes and smother native algae/vegetation. CyanoHABs can indirectly stress ecosystems through water quality alterations, such as large swings in dissolved oxygen and pH in bloom cycles, and typically lead to an overall decrease in biodiversity in ecosystems (Burkholder et al. 2018).

5.3 Aquaculture Impacts

Cyanotoxin accumulation in fish tissues has been documented in the US and abroad (Zimba et al. 2001). Microcystins are the most common compounds analyzed, and accumulation varies between fish species. Microcystin concentrations are typically highest in fish livers and viscera; in a study of Lake Erie sport fish, microcystins were shown to accumulate and persist in fish livers while muscle tissue concentrations were relatively low, though some detections in muscle tissue exceeded the WHO tolerable daily intake for microcystins, posing concerns for both fish health and the multimillion-dollar fishery (Shahmohamadloo et al. 2023).

In addition, proliferation of cyanobacteria may cause serious problems in the marketing of freshwater aquaculture products by changing the sensory quality of edible fish. The increased concentration of micronutrients and organic matter in aquaculture coupled with high temperatures may lead to the growth of cyanobacteria that produce taste and odor compounds (i.e., geosmin, MIB, pyrazines, ionones, etc.). Many T&O incidents have been reported in fisheries and aquaculture, such as ponds or recirculating aquaculture systems where off-flavors, most commonly GEO and MIB, accumulate in fish flesh and tissues. It has been found that gills and skin are the main sites of T&O uptake due to contact with water containing off-flavors. As a result, consumers are unwilling to purchase these products and the aquacultural economy is significantly affected by losses of production or lower selling prices (Moretto et al. 2022). Numerous studies have investigated methods to mitigate the off flavors in fish (e.g., by depuration) or to prevent these effects by reducing T&O in aquaculture systems (e.g., by ozonation, photocatalysis, oxidation, adsorption); however, their applicability strongly depends on economic and technical parameters (Antonopoulou et al. 2014; Rurangwa and Verdegem 2015).

5.4 Livestock Health Effects

Livestock deaths attributed to cyanotoxin poisoning, primarily from drinking contaminated water, have been documented routinely for decades and are the putative culprit for mortalities dating back thousands of years (Stewart et al. 2008 and references therein). Multiple cyanotoxins can cause livestock mortality. Acute mortalities can occur from massive exposure to hepatotoxins (e.g., microcystins) and/or neurotoxins (e.g., anatoxin) in surface scums. However, mortalities from chronic and longer-term exposures without notable scums also can occur. Cyanotoxins produced by benthic cyanobacteria, even in oligotrophic alpine streams, have caused multiple cattle mortalities (Mez et al. 1997).

Acute exposure to microcystins in high concentrations can cause intrahepatic hemorrhage, liver necrosis, and hypovolemic shock leading to death (Chia et al. 2022). Longer term impacts from chronic exposure can decrease kidney and liver function, which could lead to failure. Anatoxin-a mimics the neurotransmitter acetylcholine

and blocks neuromuscular transmission and generally causes, in part, paralysis of intoxicated organisms, muscle contractions, increased blood pressure, and respiratory arrest (Colas et al. 2021). Blooms may consist of a cyanobacterial species or assemblage capable of producing multiple toxins, and this interactive exposure to multiple different cyanotoxins can exacerbate animal intoxications (Al-Sammak et al. 2014). For example, consumption of neurotoxin and liver toxin from cyanobacterial blooms in Florida lakes was considered responsible for multiple cattle deaths (Carmichael 1992). Multiple organs can be impacted from cyanotoxins, including liver, intestines, brain, kidney, lung, gallbladder, heart, and reproductive system (Mez et al. 1997; Massey et al. 2018).

5.5 Agricultural and Food System Impacts

In addition, land plants and food crops can be exposed to cyanotoxins through contaminated irrigation water. Some plants can absorb and bioaccumulate cyanotoxins and therefore present potential hazards to animals, including human health. Land plants, cultivated plants, and vegetables are usually not killed by cyanotoxins (Milligan 2009), but the toxins can decrease seed germination, inhibit plant growth, induce phytotoxicity, and negatively affect crop yields (El Khalloufi et al. 2012; Lefebvre 2013; Manganelli et al. 2012; Milligan 2009; US EPA 2015). In rice cultivation, large mats of benthic algae can develop in flooded fields and interfere with rice seedling growth by entangling young plants and uprooting them when the mats dislodge from the sediment and float toward the surface. Also, planktonic chlorophytes and cyanobacteria can proliferate due to high levels of nutrients (N and P) and can shade or cling to rice seedlings during large blooms (Spencer et al. 2006). Therefore, cyanobacteria have the potential to directly reduce rice yield by damaging or outcompeting rice seedlings for available light (Spencer and Linquist 2014). Other studies have shown that the bioaccumulation of cyanotoxins in plants increases with rising concentration of toxins in irrigation water, regardless of irrigation type and conditions or experimental design (Miller and Russell 2017). Most of these studies focus on MC variants that can be taken up by roots and translocated to aerial parts of agricultural plants (Corbel et al. 2014; Peuthert et al. 2007). However, Levizou et al. (2020) found that root vegetables (i.e., carrot and radish) can also accumulate MCs from irrigation water, with a more pronounced effect when root vegetables are exposed to MCs at earlier stages of development. In addition to the internal accumulation of microcystins and other cyanotoxins, irrigation can lead to the accumulation of cyanobacteria and their toxins on the surfaces of edible plant materials after the contaminated water has dried on the surface of the plant. Indeed, studies reported the presence of *M. aeruginosa* and microcystins in lettuce (*Lactuca sativa*) leaves after cultivation, and accumulated toxins exceeded the tolerable daily intake recommended by the WHO (Codd et al. 1999; Crush et al. 2008). In 2016, the Utah Department of Agriculture issued an advisory to farmers and ranchers to avoid using water from Utah Lake for irrigation or livestock watering after a cyanoHAB was detected in the lake.

In addition, soils can be contaminated with cyanobacteria and cyanotoxins by using toxic blooms as organic fertilizers or through beneficial reuse of high toxin-containing water treatment residuals (Bouaïcha and Corbel 2016; Cao et al. 2018; Corbel et al. 2014; Pindihama and Gitari 2020; Wen et al. 2017; Ai et al. 2020). Many cyanotoxins are chemically stable due to their molecular structure and can leach into the soil after irrigation, resulting in soil and groundwater contamination (Bouaïcha and Corbel 2016; Machado et al. 2017). Although the absorption of cyanotoxins in soils is low, they can affect organisms in this environment, for example, reducing the reproduction of earthworms (Wen et al. 2017). Cyanotoxins can be removed from the soil by hydrolysis, photochemical degradation, and biodegradation, the main process of breaking down cyanotoxins in soils (Bouaïcha and Corbel 2016; Corbel et al. 2014; Pindihama and Gitari 2020). However, understanding the kinetics of cyanotoxin uptake via roots into the plant is still in its infancy and requires more research.

5.6 Food Supplements

Despite the harmful effects caused by cyanobacteria, the biomass of cyanobacteria has several biotechnological potentials, as they have a high content of proteins, carbohydrates, fibers, and enzymes. In addition, these organisms are also capable of producing vitamins (A, B1, B2, B3, B6, C) and have minerals that contain iodine, iron, potassium, calcium, and magnesium in their composition. They also store essential nutrients in their cells and can accumulate these products when excessive supply of specific nutrients occurs. Due to these characteristics, cyanobacteria are considered an unconventional food source (Rizwan et al. 2018; Spolaore et al. 2006). However, determination of cyanotoxin concentrations in the biomass is essential before consumption, given the health risks that cyanotoxins pose (Goss et al. 2013; Shmeis 2018). The FDA issued two voluntary recalls for dietary supplements in 2018 and a recall for a beverage in 2020 due to health concerns for elevated microcystins detected in those products. The health, ecological, and food system impacts described above translate directly into the economic consequences addressed in the following section, and ultimately into the management imperatives that make controlling cyanoHABs both a public health and agricultural priority.

6. Economic Impacts of CyanoHABs

Harmful algal blooms impose substantial economic burdens on the US economy, with conservative estimates placing the annual cost of cyanoHABs and associated eutrophication between $2.2-$4.6 billion (Dodds et al. 2009). These estimates are now over 15 years old and likely underestimate current losses given documented increases in bloom frequency and intensity; more recent analyses suggest substantially higher costs. However, quantifying the comprehensive social and economic impacts remains challenging due to their regionally-specific and event-dependent nature, compounded by insufficient data collection frameworks before, during, and after cyanoHAB

events (Wood et al. 2022; Stewart et al. 2006). The primary economic impacts stem from public health costs, recreational and tourism losses, impaired commercial and subsistence fishing, and expenses related to monitoring, mitigation, and management efforts (Anderson et al. 2000).

Water treatment represents a significant economic burden from cyanoHABs, as utilities struggle with cyanoHAB-contaminated source waters that require intensive chemical treatment, advanced treatment technologies, and operational disruptions, including temporary plant shutdowns and drinking water advisories (Price and Heberling 2018; Dodds et al. 2009). For example, Toledo's 2014 water crisis, where a cyanoHAB in Lake Erie contaminated the city's drinking water supply, affected 400,000 residents for three days and ultimately cost the city an estimated $65 million in economic impacts, with an additional $53 million required for water treatment infrastructure upgrades to prevent future contamination events (IJC 2015). While several economic assessments (US National Office for Harmful Algal Blooms 2024) have been conducted for Lake Erie, comprehensive socioeconomic studies remain limited, particularly for smaller inland water bodies that serve as critical drinking water sources and recreational resources for many communities (Hoagland et al. 2002; Moore et al. 2019).

Beyond direct costs, cyanoHABs create cascading economic effects through property value depreciation and lost recreational opportunities. Recent economic modeling suggests that a 10% improvement in water quality could increase US property values by $6 billion to $9 billion, highlighting the substantial financial stakes involved in HAB management (Mamun et al. 2023). Additionally, losses of over $70 million annually are projected just in the catfish aquaculture industry due to off flavor caused by cyanoHABs (Cheatham et al. 2024).

Several mitigation strategies show promise for reducing economic impacts, including fish relocation programs, targeted monitoring to identify safe harvesting zones rather than broad area closures, and real-time cyanoHAB status tools that enable tourists to make informed decisions about recreational activities (Rousso et al. 2020; Brown et al. 2020; Stumpf et al. 2016). While these approaches can help minimize negative economic effects, quantifying their benefits remains challenging. Moving forward, research priorities should include developing comprehensive cyanoHAB social and economic models that capture both direct and indirect costs at local and regional scales, establishing evaluation criteria for socioeconomic impact mitigation, and enhancing public awareness and risk communication strategies to build community resilience during cyanoHAB events (Wood et al. 2022).

7. Management and Mitigation Strategies

Management of cyanoHABs can fall into two broad categories, proactive and reactive, employing chemical, physical/mechanical, and biological methods (Table 3). Proactive management represents long-term (multi-year to decadal) strategies that focus primarily on nutrient mitigation or ecosystem alteration and aim to prevent formation of cyanoHABs through sustained ecosystem changes. These strategies include reducing external nutrient inputs, controlling watershed sources, implementing land-use practices that minimize nutrient runoff, and employing best management practices (BMPs) such as constructed wetlands, and in field and edge-of-field nutrient reduction management practices (Conley et al. 2009; Paerl et al. 2016). Reactive management encompasses short-term (days to seasonal) strategies that respond to active blooms and attempt to directly control or eliminate existing cyanoHABs through immediate intervention strategies. These include algaecides, mechanical treatments for biomass removal, emergency water diversions, and targeted biological controls designed as response to blooms (Gallardo-Rodriguez et al. 2019; Kibuye et al. 2021a,b). The distinction between these approaches is critical for understanding management timeframes and objectives. Proactive strategies, while requiring longer implementation periods to show effects, address root causes of eutrophication or ecosystem conditions and provide sustainable prevention of future bloom events. Reactive strategies, though offering immediate relief within days to weeks, primarily manage symptoms and typically require repeated applications to maintain effectiveness.

Within each cyanoHAB control category (proactive and reactive), methods can be further classified by their approach mechanism. Chemical control involves the application of chemical substances to either eliminate cyanobacteria directly (reactive) or manage nutrient availability (proactive). Physical and mechanical control encompasses interventions that use engineered systems and/or devices to alter the physical environment (proactive) or directly remove algal biomass (reactive). Biological control employs living organisms or biological processes to manage cyanoHABs (both proactive and reactive).

While strategies based on physical, chemical, and biological manipulations can be effective in reducing cyanoHABs, these approaches should be accompanied by nutrient input reductions to ensure long-term success and sustainability (Paerl 2017). For example, treatment benefits from mechanical and biological control are commonly offset by continued nutrient inputs, emphasizing that reactive measures should be coupled with proactive nutrient management for lasting effectiveness. CyanoHAB management has progressively shifted from prevention to control, with management considerations often implemented after bloom formation (Anderson et al. 2022). However, a universal "one-size-fits-all" management system fails to provide an effective path forward due to inherent complexities and site-specific characteristics of each water body (Anderson et al. 2022).

Each cyanoHAB control approach presents distinct advantages and limitations that influence management decisions. Chemical control offers rapid and effective bloom suppression, with algaecides providing immediate

Table 3. General proactive and reactive approaches to cyanobacteria management and water quality treatment. Examples provided represent common practices for each control category; by no means is this list exhaustive.

	Proactive (Long-term)	Reactive (Short-term)
Chemical	Reduced nutrient-loading, nutrient inactivation, water quality enhancement, P-binding compounds, colorants	Algaecides, colorants, enzymes, flocculants/coagulants, oxidizers, polymers, plant/bacteria extracts, toxin neutralization
Physical / Mechanical	Hypolimnetic aeration, artificial mixing, barriers/curtains, watershed restoration, stormwater management, constructed wetlands, buffer zones, dredging	Raking, skimming, filtration, shade cloth, flushing/ hypolimnetic withdrawal, ultrasonic devices, ultraviolet light, dissolved air flotation, ozonation, mechanical harvesting
Biological	Food web biomanipulation, bioremediation microbes, integrated aquaculture, native plant establishment, ecosystem restoration, turf scrubbers, floating islands, fish/invertebrate	Algaecidal bacteria/ viruses/parasites, biological flocculation

* Adapted from Laughinghouse et al. 2020a

**Note: Substances that are used or implied to control algae or cyanobacteria in the United States must be registered by the US EPA under FIFRA (Federal Insecticide, Fungicide and Rodenticide Act) and control devices must be manufactured in an approved facility.

improvements in water quality (Sukenik and Kaplan 2021). However, chemical methods have several drawbacks including the potential release of cyanotoxins, impacts on non-target aquatic plants and animals, environmentally persistent treatment residuals, and only short-term bloom control typically characterized by cyanobacterial rebound (Sukenik and Kaplan 2021; Kibuye et al. 2021a). Physical and mechanical control methods illustrate fundamental challenges including high capital and operational costs, limited scalability to large water bodies, and the need for site-specific optimization. While these methods can achieve significant biomass removal under controlled conditions, their practical implementation requires careful consideration of cost-effectiveness, treatment capacity, power requirements, and integration with broader management strategies (Kibuye et al. 2021b). Biological control methods can provide an environmentally sustainable approach with long-term treatment benefits and ecosystem restoration potential, but they require extended time frames to show effectiveness, have variable success rates depending on site-specific conditions, and often need integration with other management strategies to achieve optimal results (Kibuye et al. 2021b; Triest et al. 2016). All approaches require careful evaluation of site-specific factors, environmental impacts, and cost-benefit considerations for successful implementation.

Commonly used proactive and reactive treatment techniques are presented here at current operational scales. Specific details regarding current management approaches in each of the categories listed can be found in the Interstate Technology and Regulatory Council (ITRC 2021). Additional information on the status of strategies and recommendations for future research is included in the Harmful Algal Research and Response National Environmental Science Strategy report (HARRNESS 2024) and will not be discussed here. Integration of both proactive and reactive strategies represents the most effective approach to cyanoHAB management, as short-term interventions provide immediate public health protection while long-term strategies address underlying causes.

7.1 Long-term Proactive Management Practices

CyanoHABs in freshwater systems are commonly caused by excess nutrients (eutrophication), especially phosphorus (P) and nitrogen (N), warm weather, and increased water residence time. As a primary driver of cyanoHABs, nutrients can enter water bodies as point sources, such as direct wastewater; stormwater and industrial discharges, often from regulated communities and industries; and nonpoint sources, which represent diffuse runoff of nutrients from the landscape. Common nonpoint sources of nutrient runoff include agriculture (e.g., manure or chemical fertilizer), golf courses, residential and commercial turfgrass, faulty septic systems, and natural wildlife, such as waterfowl (Townsend and Howarth 2010; Nürnberg and LaZerte 2016). Additionally, changing coastlines and severe weather events can increase nutrient runoff and favor cyanoHABs (Paerl et al. 2016). Over time, some nutrients can accumulate in lake sediments and contribute to internal excess nutrient loading, fueling cyanoHABs even if external point and nonpoint nutrient sources are reduced (Søndergaard et al. 2003; Jarvie et al. 2013). Increased occurrence of cyanoHABs in low-nutrient systems has been documented, often due to diverse nutrient acquisition strategies by the species of cyanobacteria blooming (Isvanovics et al. 2000; Carey et al. 2008; Sinha et al. 2012; Reinl et al. 2021).

Chemical

Reduced nutrient loading: Long-term nutrient management strategies are needed and critically important for mitigating cyanoHABs. Given rising nitrogen and phosphorus fertilizer costs and increasing importance of soil health, finding strategies that promote nutrient-use efficiency and soil health while reducing nutrient losses is key to long-term cyanoHAB management. Where point sources of nutrients can be identified, reduction in nutrients into a receiving water resource can be realized (Mallin et al. 2005; Van Nieuwenhuyse 2007). However, for nonpoint input scenarios, implementation of best management practices for nutrient control needs local to national policy change and broad funding support, which is often beyond the authority

of individual lake and resource managers. Nutrient reduction could take years-to-decades to come to fruition and may not result in effectual change due to continued inputs from diverse sources that are difficult to address (Reddy et al. 2011; Nürnberg and LaZerte 2016).

Nutrient inactivation: Appropriately designed in-lake nutrient mitigation measures can be effective if accumulated legacy nutrients are the key contributor to blooms (Søndergaard et al. 2003). Many factors need to be considered to design effective treatments, such as lake residence time, watershed area, morphology, relative depth, rough fish presence, stratification, mixing, etc. (Huser 2012; Huser et al. 2016). Most common in-lake mitigation strategies that have been implemented target phosphorus removal from the water column and inactivation from sediments utilizing aluminum-based compounds and lanthanum-modified bentonite (Huser et al. 2016; Spears et al. 2016; Laughinghouse et al. 2020b), although other P-binding agents, such as calcium, iron, and magnesium, have some potential (Bacelo et al. 2019). Calculations for estimating dosages of aluminum-based compounds needed for effective treatment are presented in Osgood et al. (2017). These treatments can be highly effective when the primary source of nutrients to a lake are from lake sediments.

Physical/Mechanical

Constructed Wetlands: Constructed wetlands (CWs) are engineered systems that replicate natural wetland processes to remove nutrients, suspended solids, and other contaminants from water through physical, chemical, and biological mechanisms. These systems have been proven effective for nutrient removal, with vertical flow CWs typically more efficient at removing total phosphorus (64.6 ± 30%) while horizontal flow systems excel at total nitrogen removal (67.6 ± 20%) (Kamilya et al. 2022). Many factors are known to influence the success of nutrient removal from CWs including aeration, carbon sources, substrates, bioremediation microbes, and native plant species present (Kamilya et al. 2022). Aquatic plants/macrophytes are extremely important to healthy lake environments that drive the preservation of key functions and support biodiversity in freshwater ecosystems (Thomaz and da Cunha 2010). Specifically, macrophytes can reduce turbidity by retaining lake sediments and thereby drawing down bioavailable nutrients and stabilizing lake bottoms (reviewed in Hussner et al. 2017). The top three suitable substrates are gravel, zeolite, and slag, while emergent plants such as *Eleocharis dulcis*, *Typha orientalis*, and *Scirpus validus*, submerged plants including *Hydrilla verticillata*, *Ceratophyllum demersum*, and *Vallisneria natans*; the floating plants *Eichhornia crassipes* and *Lemna minor*; as well as the floating-leaved plants *Nymphaea tetragona* and T*rapa bispinosa* are the most effective plant species in CWs (Li et al. 2021).

Buffer Zones: Wetland buffer zones function as riparian areas between terrestrial and aquatic environments that intercept agricultural runoff and urban stormwater before reaching water bodies. The efficiency of wetland buffer zones for nutrient retention varies markedly depending on nutrient load and form, soil type/texture, vegetation, and flow pathways (Walton et al. 2020). These systems provide long-term, sustainable nutrient management while supporting biodiversity and requiring minimal energy inputs, making them particularly valuable for watershed-scale cyanoHAB prevention strategies.

Dredging represents an additional physical management option that can reduce internal nutrient loading by removing nutrient-rich sediments from the lake bottom. While effective in some settings, dredging is costly, logistically complex, and can temporarily resuspend nutrients and disturb benthic communities during implementation, so it is typically reserved for situations where sediment nutrient stores are the primary driver of blooms and other options have been exhausted.

Biological

Food Web Biomanipulation: Food web biomanipulation represents a long-term, ecosystem-based approach to cyanobacteria management that manipulates trophic interactions to restore natural ecological balance over multi-year timeframes. This approach encompasses both traditional biomanipulation (enhancing large zooplankton grazing through fish removal) and nontraditional biomanipulation (introducing filter-feeding fish to directly consume cyanobacteria), often combined with macrophyte re-establishment (Triest et al. 2016). There have been examples of success; integrated biomanipulation was implemented in Longhu Lake, China, controlling cyanobacterial blooms and improving water quality for 20 years, while Lake Donghu demonstrated long-term success using filter-feeding carp to eliminate persistent cyanobacterial blooms (Peng et al. 2021; Xie and Liu 2001). Food web biomanipulation shows promise as a restoration tool for cyanoHAB prevention but requires careful planning, monitoring, and management over decadal timescales to achieve sustained success. However, the best results have been achieved when integrated with other mitigation strategies that address external nutrient loading and internal ecosystem dynamics (Jeppesen et al. 2012).

Bioremediation Microbes: Bioremediation microbes encompass beneficial bacteria and other microorganisms that enhance nutrient cycling and water quality to prevent and control cyanobacterial blooms with an emphasis on ecosystem restoration. Bioaugmentation is an eco-friendly and economically viable approach for enhanced nutrient management involving the addition of bioremediation bacteria to existing microbial communities to significantly alter microbial community structure, nutrient cycling, and water quality (Wang et al. 2019; Tang et al. 2025). Microbial communities play important roles in nutrient immobilization, with long-term P inputs increasing microbial P immobilization while N inputs decrease the functional potential of microbial P solubilization and mineralization (Dai et al. 2020). These microorganisms can contribute to cyanoHAB prevention by enhancing N and P cycling, reducing excess nutrient availability that fuels bloom formation, improving overall water quality, and establishing

beneficial microbial networks that compete with cyanobacteria for resources to maintain balanced aquatic ecosystems.

The purity of the amended microbes and specific environmental tolerances need to be understood prior to amending to a water resource. The ability to mobilize some forms of nutrients to a bio-available state could also promote cyanoHAB growth in certain environments (Zhao et al. 2012).

7.2 Short-term Reactive Management Options

The use of reactive solutions for cyanoHAB management are also important in preserving the uses of water resources. Ideally, treating selectively for cyanoHABs at the early onset of a bloom can decrease concerns over oxygen loss and toxin/taste and odor release and require less algaecide to achieve control (Sukenik and Kaplan 2021 ; Laughinghouse et al. 2026).

Chemical

Algaecides: Algaecides are routinely and effectively used for cyanoHAB control, but due to potential ecosystem impacts, including to non-target organisms, they require appropriate federal approvals and state/local permits. Commonly used algaecides in surface waters include copper-based products, such as copper sulfate or chelated copper, or peroxide-based products, such as sodium carbonate peroxyhydrate or hydrogen peroxide with peroxyacetic acid (Kinley-Baird et al. 2021). Peroxide-based algaecides have several key benefits, including selectivity towards different types of cyanobacteria, benign break-down products (water and oxygen), rapid activity, potential for toxin oxidation and low ecotoxicity to many non-target species (Zhou et al. 2024; Weenink et al. 2015). Potential considerations when implementing this approach include the release of toxins, product cost, environmental factors (e.g., algal assemblage, DOC, light, temperature), and longevity of control (Yun et al. 2024; Chen et al. 2021). Copper products have been used for decades to control cyanoHABs, but different formulations significantly affect application rates required for effective cyanoHAB control (Bishop et al. 2018a). Copper can pose potential concerns to non-target species if present, but more advanced formulations that target or rapidly bind to the nuisance algae can offset risks to non-target species (Bishop et al. 2018b). Toxin release can occur following cyanoHAB control with copper algaecides (Jones and Orr 1994; Greenfield et al. 2014), although some copper algaecides and concentrations can control cyanobacteria without releasing toxin (Tsai 2015; Iwinski et al. 2016). Copper can accumulate in the environment through time (Crafton et al. 2021; ITRC 2020), but becomes less bioavailable as it binds within sediments (Liu et al. 2006; Iwinski et al. 2016; Willis and Bishop 2016). Several other active ingredients have been evaluated or used in combinations with copper or peroxide-based algaecides (e.g., diquat, endothall, colorants, flumioxazin) (Lefler et al. 2022). Many are not widely implemented in larger-scale cyanoHAB management and may contain water use restrictions for specific sites. Numerous factors need to be considered when using an algaecide, including characteristics of an exposure (e.g., concentration, duration, frequency), characteristics of the algae (e.g., density, biomass, mucilage, nutrient content), and water characteristics (e.g., temperature, light, pH, alkalinity) (Kibuye et al. 2021a). Ideally, algaecide treatments are conducted proactively or in early cyanobacteria growth stages, where toxins are predicted to be below risk levels, to minimize other potential water quality impacts that may result from decaying biomass (Koreivienė et al. 2014).

Coagulants/Flocculants: Coagulants/flocculants are a broad group of additives that include many different compounds, such as polyaluminum chloride, iron chloride, chitosan, polymers, and modified clays (Verspagen et al. 2006; Lürling et al. 2020). These are typically applied to remove cyanoHABs from the water column and have been used with success in many water treatment facilities and select field sites (Yu et al. 2017). Integrated approaches, such as flocculation followed by nutrient mitigation, can additive or synergistic benefits to managing cyanoHABs and increase the longevity of control (Lürling and van Oosterhout 2013; Noyma et al. 2016). Operational feasibility in surface waters, ecosystem risks, and permitting should be considered before wide-spread surface water use of these substances.

Nanobubble Ozone Technology: Nanobubble ozone technology (NBOT) represents an emerging treatment that disperses ozone-impregnated nanobubbles (<200 nm diameter) into water bodies to oxidatively destroy cyanobacterial cells and toxins. Incorporating ozone into nanobubbles improves ozone mass transfer efficiency, dispersal within the water body, and limits off-gassing to the atmosphere. Nanobubbles impregnated with ozone are more effective at controlling cyanobacteria and destroying cyanotoxins/chemicals than nanobubbles filled with oxygen or air (ITRC 2022). Recent controlled studies demonstrated significant NBOT efficacy, for both planktonic and benthic cyanoHAB control and destruction of microcystins, anatoxins, and anabaenopeptins (Chaffin et al. 2024), and also had less impact on nontarget zooplankton when compared to algaecides applied at label-approved rates (Stanislawczyk et al. 2026). Given the newness of the technology, there have been limited full-scale field applications. In initial trials, due to a lack of a control, it was difficult to determine if effectiveness was due to NBOT or natural decline in cyanoHABs. In short-duration follow-up trials, limited effectiveness of NBOT was likely due to high cyanobacteria biomass and dissolved organic carbon at the onset of treatment, low ozone to dissolved organic carbon ratio, and low percentage of lake water instantaneously treated , but algaecides and alum treatments were also ineffective at cyanoHAB control in that lake (Chaffin et al. 2024 ; Kuhn 2026). NBOT offers advantages, including scalability and controlled oxidant delivery, but may require infrastructure investment and faces challenges with treatment of higher biomass blooms in larger water bodies.

Physical/Mechanical

Several additional physical and mechanical approaches are used in practice, though controlled field evidence for their

efficacy remains limited and variable. Hypolimnetic aeration and artificial mixing disrupt thermal stratification and reduce the competitive advantage of buoyant cyanobacteria, but effectiveness depends heavily on lake morphology, residence time, and whether external nutrient loading has been adequately addressed. Ultrasonic devices aim to disrupt buoyancy regulation and cell integrity through targeted acoustic frequencies; results in the peer-reviewed literature are inconsistent, with some mesocosm studies showing reductions in surface scums while others report negligible effects, particularly at larger scales or higher biomass (Hao et al. 2004; Rajasekhar et al. 2012). Shade cloth and physical barriers can provide localized protection for small, high-priority areas such as intake structures or swimming beaches, but do not address the bloom itself. These approaches may be appropriate as supplementary tools within an integrated management program. Site-specific conditions and current literature should be carefully evaluated before implementation.

Surface Skimming/HABITATS: The Harmful Algal Bloom Interception, Treatment, and Transformation System (HABITATS) developed by the US Army Corps of Engineers represents an integrated approach combining surface skimming, dissolved air flotation, and biomass transformation technologies. HABITATS includes the following three steps: Interception—algae is collected from the surface of a natural waterbody with a floating weir skimmer aided by booms that focus the surface algae to the collection point; treatment—the water with algal biomass is clarified by dissolved air flotation and then by oxidation, which creates clean water while concentrating the algal biomass; and transformation—the concentrated algal biomass waste stream is transformed into biocrude fuel and fertilizer by means of hydrothermal liquefaction (Page et al. 2021). While showing promise for nutrient removal, there were two major limitations for the technology: huge capital and operations and management costs, as well as very high energy demand, with treatment costs estimated from $2 million to $18 million per year (ITRC 2022). Additionally, as both skimming and flotation cannot remove an entire bloom, the remaining populations could re-seed and cause additional blooms (ITRC 2022). The technology is most effective when surface cyanobacteria densities are elevated and it's currently best applied to smaller waterbodies or compartmentalized systems.

Biological

Algaecidal Bacteria/Viruses: In natural environments, heterotrophic bacteria and viruses are involved in influencing bloom dynamics. Heterotrophic bacteria can impact blooms through the production of algaecidal compounds or direct physical attacks, while viruses may cause direct bloom collapse through targeted infection mechanisms (Coyne et al. 2022). Cyanophages (viruses that specifically target cyanobacteria) represent a particularly promising biological control strategy with varying levels of host-specificity, ranging from single strain within a species to multiple genera (Grasso et al. 2022). However, challenges remain, including rapid emergence of resistant host mutants and complex environmental interactions. Diverse cyanobacterial strains, adaptability of the bloom, and multiple growth patterns may also limit the effectiveness and consistency of these approaches. Kibuye et al. (2021b) and Harris et al. (2024) discuss additional considerations and examples of biological control processes in managing cyanoHABs.

Biological Flocculation: Biological flocculation involves the use of microorganisms or biologically-derived compounds to aggregate suspended particles for easier removal from water systems. The agglomeration (coagulation/flocculation) phase is one of the most important steps in cyanobacteria removal. In this process, chemicals are added to destabilize suspended cells and colonies by neutralizing their surface charge (Sukenik and Kaplan 2021). Examples of the potential for flocculation have been shown in microalgae with different microalgae-associated bacteria (e.g., Wang et al. 2012). Fungal-assisted flocculation has shown particular promise, with studies demonstrating high harvesting efficiency for microalgae removal. The process utilizes natural biological polymers and extracellular substances produced by microorganisms to form aggregates that can be more easily separated through sedimentation or flotation.

7.3 Risk of Inaction

Upon diagnosing a potential cyanoHAB, state agencies often suggest posting advisories and closing public water access to warn people and their domestic pets to avoid the water (US EPA 2019). Although this may offset some routes of exposure, there are still potential exposures and impacts of the toxins to wildlife within and outside the water resource (Briand et al. 2003; Moy et al. 2016). Water resource owners and managers need to consider these potential risks and liability associated therewith. Typically, not intervening at early bloom stages allows the bloom to continue to produce more total toxin and ultimately may increase the amount and duration of total and dissolved toxin exposure (Watanabe et al. 1992; White et al. 2005; Lehman et al. 2007). With the increased awareness of the toxin impacts and unique exposure routes, this avenue may not be sufficient to offset risks. Blooms may alter the system directly and indirectly (Beversdorf et al. 2013; Chen et al. 2014) and become more entrenched to promote future blooms, including deposition of overwintering cells as a source of future blooms (Karlsson-Elfgren et al. 2003; Cirés et al. 2013). With no management, the potential health risks and aesthetic issues are often coupled with economic impacts from decreased property values, recreation, and tourism.

The effectiveness of any management strategy depends on how well it is matched to the specific characteristics of the site, the cyanobacterial assemblage, and prevailing environmental conditions. A technique that performs well in one system may provide little benefit in another, and approaches validated at bench or mesocosm scale do not always translate directly to field performance. The following considerations apply broadly across both proactive and reactive strategies and should inform method selection.

Characteristics of the water resource, such as flow, depth, volume, wind, wave action, mixing dynamics, relative depth, weather patterns, rough fish presence, and location of the bloom or proliferation, need to be understood to discern applicability of different management options. For example, internal nutrient mitigation may not be effective if large flushes of nutrients continually enter from the watershed or if substantial internal mixing from biota or anthropogenic activities occurs beneath the inactivation zone. In larger systems, a localized area may be prioritized for management (e.g., beach, marina, dog park, water intake or discharge structure) independent of implementing whole system management, though often requires more intensive and routine intervention due to bloom reintroduction and/or re-growth.

The problematic cyanobacteria at a specific site may be very dynamic. They can change location and characteristics rapidly even within a single 24-hour period. Understanding this constant variation and adapting management appropriately in real time can assist in achieving the desired level of control. Some key characteristics of the cyanobacteria species/assemblage that have shown to impact control include EPS content/bacterial consortium (Shen et al. 2011), mucilage (Tien 2002), single-cell/colony formation (Wu et al. 2007), genetic make-up (Harke and Gobler 2013), density/biomass (Bishop and Rodgers 2012), growth stage (Daniel et al. 2019), total algal assemblage composition (Weenink et al. 2021), buoyancy/location in water column/benthos, nutrient content (Jensen et al. 1982), toxin content (Schatz et al. 2007), and innate species or strain sensitivity (Lembi 2000; Garcıa-Villada et al. 2004).

Efficacy of the applied management technique may also be a function of the interaction with abiotic environmental conditions as well as how those impact the target cyanobacteria. Turbidity, temperature, nutrient concentrations, water chemistries, dissolved and particulate organic carbon, light intensity, etc. can all impact how a chosen management strategy would perform (US EPA 2003; Guasch et al. 2004; Piel et al. 2019). Some techniques may work better at a certain time of day or year, based on these factors and how they alter the exposure to the select strategy and the response of the target cyanobacteria. More studies need to be specifically designed to assess the impact of these abiotic and biotic factors on effectiveness of operational management programs for all control methods toward guiding selection and implementation aspects of management.

7.4 Practical Considerations in Selecting and Implementing Management Strategies

Management techniques and the research on how best to implement them are continually advancing, so it is important to evaluate current information prior to selecting an approach. Many techniques have shown efficacy at the laboratory or bench scale, although field validation is needed to confirm performance at operational scales. It's important to note that technologies may differ even within one specific management category, such as the amount of power or number of frequencies a sonication device may emit. Also, a specific formulation of an active ingredient could alter how it performs and whether it is granular or liquid and how concentrated or stable it is, etc. The application strategy and equipment used are also critical to getting the most efficiency out of a management strategy. Targeting a bloom in a specific location (e.g., benthic mats) can change the predicted efficacy of a method. A management framework to assist in selecting an appropriate technique for specific scenarios and designated use objectives is necessary to align viable management strategies.

8. Regulatory and Permitting Challenges

Even when an appropriate management strategy has been identified for a given site, implementation can be delayed or complicated by the regulatory and permitting landscape governing cyanoHAB control in the United States. Under the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA), HAB control agents classified as algaecides must undergo extensive registration processes before field application, with preliminary classification determinations alone extending beyond five months. In contrast, physical and mechanical approaches, such as aeration, artificial mixing, hypolimnetic oxygenation, and mechanical harvesting, typically fall under general operational or water management authority and face comparatively fewer regulatory barriers to deployment. However, a simpler regulatory pathway does not necessarily translate to greater effectiveness or appropriateness; the match between management strategy, bloom species, waterbody type, and designated use objectives remains the primary consideration in method selection regardless of permitting complexity. Concurrently, the National Pollutant Discharge Elimination System (NPDES) requires separate permits for chemical applications in aquatic environments, with some states necessitating submission of Notice of Intent documents and maintenance of Pesticide Discharge Management Plans prior to algaecide treatments (Calomeni et al. 2017). For agricultural operations, Concentrated Animal Feeding Operations (CAFOs) face additional regulatory burdens under the Clean Water Act, with over 15,500 facilities requiring NPDES permits and implementation of nutrient management plans to address water quality impacts (Centner 2004). The fragmented regulatory framework is further complicated by food safety considerations, as the Federal Food, Drug, and Cosmetic Act requires tolerance setting for any HAB control chemical residues that may enter food or drinking water supplies used for livestock watering, crop irrigation, or aquaculture production (US EPA 2015). For aquaculture specifically, regulatory compliance costs can reach millions of dollars annually, with complex permitting requirements creating substantial barriers to implementing timely HAB control measures that are critical for preventing catastrophic fish kills, livestock poisoning from contaminated water sources, and associated economic losses throughout the food production chain (Engle et al. 2023; Datta et al. 2025). These regulatory delays disproportionately impact smaller agricultural operations that lack specialized regulatory affairs resources, often extending project timelines by months or

years when rapid intervention is essential for protecting drinking water sources, preventing animal poisoning, and maintaining food production systems.

9. Conclusions and Future Directions

CyanoHABs are an expanding threat to freshwater resources across the United States and globally, affecting drinking water supplies, agricultural and livestock uses, aquaculture, recreation, and ecosystem health. Their increasing frequency and severity, driven by nutrient loading and changing weather patterns, mean that proactive and reactive management must become standard practice rather than crisis response. Addressing cyanoHABs at the scale and pace required will demand sustained collaboration among scientists, water resource managers, agricultural producers, regulators, and policymakers.

Future efforts should focus on:

1. Continued support for the interagency Cyanobacteria Assessment Network (CyAN) to provide near real-time data on HABs in large lakes throughout the US and expansion of CyAN to include smaller lakes and rivers as higher spatial and temporal resolution satellite data (and potentially drone and aerial survey data) become more widely available (including mission support for new/improved satellite missions and sensors). Share and promote use of CyAN-developed algorithms internationally to improve human health globally and increase our understanding of cross-border HABs and global HAB trends.

2. Supporting applied research on new or improved low-cost HAB and toxin sensors as management tools for pond and lake managers and to improve HAB early warning monitoring networks and forecasting efforts.

3. Developing and/or improving predictive models of HABs and toxin production to enable short-term forecasts (days) of geographic distribution, intensity, toxicity, and bloom transport, as well as longer-term (weeks to seasonal) projections to aid in planning efforts and investing in forecasting and monitoring infrastructure in priority areas (drinking water sources, large and heavily-used recreational area, etc.).

4. Continued and additional support for long-term nutrient use efficiency and nutrient loss reduction strategies to support reduction in cyanoHABs.

5. Expanded support for research, development, and field testing of emerging control strategies that are scalable, acceptable, and effective at mitigating cyanoHABs with negligible impacts to beneficial species or human uses.

6. Development of standardized protocols for monitoring benthic/periphytic proliferations and support on the description of novel taxa and/or novel toxins (toxic bioactive compounds) these may produce.

7. Determining and/or revising acute and chronic levels of toxicity of different cyanotoxins on animals, including humans, as well as in crops, food, food supplements, and aerosols.

Several federal programs currently support development and testing of cyanoHAB control strategies, including the USACE HAB Demonstration Program (Section 128 and the HAB Research and Development Initiative), the NOAA Prevention, Control, and Monitoring (PCM) program, the HAB Control Technologies Initiative (CTI), and USACE Aquatic Nuisance Species and Aquatic Plant Research Programs. Sustained and expanded investment in these programs is essential to moving the most promising control strategies from demonstration to operational use.

Continued research and development activities are needed, along with funding support to test the most promising emerging strategies at larger scales. While some emerging strategies show promise, limited and inconsistent effectiveness has been reported for many approaches. Ultimately, comprehensive technical assessments regarding efficacy, ecotoxicity, social acceptance, cost, scalability, and operational feasibility are required prior to wide-scale implementation of emerging techniques. The agricultural, water management, and public health communities cannot wait for perfect science to act—the tools and knowledge to reduce cyanoHAB impacts are available now, and applying them requires commitment, coordination, and sustained resources at every level from the farm field to federal policy.

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