Cyanobacterial blooms and Cyanotoxins: Occurrence and Detection

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Abstract

Enormous increase in anthropogenic activities results in nutrient loading into the environment causing eutrophication of aquatic bodies. The increased eutrophication of freshwater and marine water bodies has intensified the algal growth which is commonly known as algal blooms. Prokaryotic blue green algae/cyanobacteria are one of the most common bloom causing algae in aquatic ecosystem, commonly known as cyanobacterial harmful algal blooms (CHABs). Some cyanobacteria can produce toxins called as cyanotoxins, which not only hinder recreational use of water bodies but also adversely affect microalgae,

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S. K. Mandotra et al. (eds.), *Algae*, https://doi.org/10.1007/978-981-15-7518-1_15

invertebrates, fish, birds, plants, and mammals. The current chapters offer an overview of occurrence of CHABs and their toxins. Further, emphasis has been given on types of cyanotoxins, their measurement and removal from aquatic ecosystem.

Keywords

Algal bloom · Aquatic ecosystem · Bloom management · Cyanobacterial harmful algal blooms (CHABs) · Cyanotoxins

15.1 Introduction

Harmful algal blooms (HABs) comprise of phytoplankton which naturally produce bio-toxins that have harmful effects on resident population, as well as human beings (Carpenter et al. 1998; Harrness 2005). HABs can alter food chains, release potent toxins, and disrupt ecosystems (Paerl 1988). They broadly cause death of aquatic organisms either due to their toxins or by depleting the nutrients for other neighboring organisms. Despite knowing these familiar characteristics, HABs vary in terms of organisms causing bloom formation, type of impact, and bloom dynamics.

Cyanobacteria, one of the major contributors of HABs are ubiquitous and therefore found commonly in lakes, rivers, and other surface waters. Few examples of bloom forming cyanobacteria are *Lyngbya wollei*, *Cylindrospermopsis raciborskii*, *Anabaena bergii*, *Raphidiopsis curvata*, *Aphanizomenon flos-aquae*, *Anabaena lapponica*, and *Microcystis aeruginosa*. Like other algal species, cyanobacteria multiply rapidly in aquatic ecosystem and result in bloom formation when conditions are favorable. In freshwater systems, cyanobacteria are the major cause of HABs (Anderson et al. 2002). Their fast growing property leads them to occupy water surfaces and thereby impeding the sunlight from reaching other co-occurring photosynthesizing organisms (Horne 1972; Huisman et al. 1999) and resulting into enhanced pH levels far from the tolerable limit to other phytoplankton (Mogelhaj et al. 2006). The dominating cyanobacterial harmful algal blooms (CHABs) replace the more diverse and nutritious phytoplankton (Bernardi and Giussani 1990; Müller-Navarra et al. 2004). Depending on nutrient levels and light conditions, some cyanobacteria can float to different levels of water surface due to their feature of having gas filled cavities. This also helps cyanobacteria to establish themselves in the water body, causing "scum formation."

Various abiotic and biotic factors that influence CHAB formation and its persistence include intensity of light, availability, and type of nutrient (mainly phosphorus), pH, water temperature, and precipitation. Though the seasonal and yearly fluctuations in the cyanobacteria levels are the result of interrelationship of these factors but the major cause of the extensive proliferation of CHABs among all the factors is considered to be the eutrophication of aquatic bodies (Steffen et al. 2014; Gobler et al. 2016; Ndlela et al. 2016; Miller et al. 2017).

In present chapter we are providing an overview of cyanoblooms and cyanotoxins in terms of their occurrence and detection.

15.2 Toxic CHABs and Cyanotoxins

Historically, evidence of toxic blooms of cyanobacteria persists in Europe for over five hundred years (Codd and Beatie 1991). The first report of CHAB in killing livestock by toxic algae in lakes of South Australia was published in Nature (Francis 1878). Recurrent and acute CHABs have been reported world-wide over past one fifty years (Paerl and Huisman 2009). Different cyanobacterial genera are found in different continents of the world (Table 15.1), making algal bloom as a worldwide phenomenon. The dominance of CHABs in the different part of the world is mainly contributed by the presence/release of their toxins.

Cyanobacteria/BGA produce various types of cyanotoxins, which has been structurally divided into three major groups such as alkaloids (anatoxin-a, cylindrospermopsin, saxitoxins, and lyngbiatoxin-a), cyclic peptides (microcystin and nodularin), and lipopolysaccharides. However, on basis of biological response, the cyanotoxins can be majorly grouped into four categories: cytotoxins, hepatotoxins, neurotoxins, and dermatotoxins, (Kaebernick and Neilan 2001; Codd et al. 2005). Among them hepatotoxins and neurotoxins are very common. Hepatotoxins include microcystin, cylindrospermopsin, and nodularin. However, cylindrospermopsin has both neurotoxic and cytotoxic potentials (Corbel et al. 2014; Kaplan et al. 2012; Kaebernick and Neilan 2001), whereas anatoxins and saxitoxins are neurotoxins by different cyanobacterial species (Neilan et al. 2013).

15.3 Ecological Factors

The growth of CHABs is affected by many ecological factors like temperature, pH, intensity of light, and nutrient conditions. Among them quality of light and its intensity are among the vital factors in the growth of phytoplankton. The cyanobacteria being prokaryotic contain phycobiliproteins as light harvesting mechanism, which allows light absorption from wider spectrum of light (Oliver et al. 2012). Apart from light intensity and quality, temperature is one of the major factors that promotes cyanobacterial bloom formation and plays an essential role in toxins production and assimilation of nutrients (Davis et al. 2009; Mowe et al. 2015; Wang 1974). For example, after examining one hundred forty three lakes along latitude from subarctic part of Europe to southern area of South America Kosten et al. (2012) found that for the formation of cyanobacterial biomass, temperature and total nitrogen (TN) concentrations were the most important variables. Likewise Beaulieu et al. (2013) examined the proliferation of cyanobacterial species in 1147 freshwater bodies in the USA and showed that the linear regression model with multiple variables was best indicated by temperature and TN of the water bodies. Therefore, with increasing global warming, temperature of water will be increased, and cyanobacteria will gain an advantage over other phytoplankton and flourish in the water bodies.

The higher diversity of non-nitrogen fixers (*Microcystis* sp.) can be found with higher pH, while nitrogen fixers dominate at low pH (Whitton and Potts 2012). The

Table 15.1 List of dominant CHABs found across the world

Continent	Dominant cyanobacterial species	References
Africa	*Microcystis flos-aquae*, *M. wesenbergii*, *Dolichospermum* sp., *Oscillatoria* sp., *Anabaenopsis* sp., *Lyngbya* sp.	Ndlela et al. (2016), Mowe et al. (2015), Codd et al. (2005), Blaha et al. (2009)
America	*M. aeruginosa*, *Cylindrospermopsis* sp., *Dolichospermum* sp., *Lyngbya* sp., *M. viridis*, *M. wesenbergii*, *Aphanizomenon schindleri*, *D. flos-aquae*, *D. planctonicum*, *D. lemmermannii*, *D. smithii*, *D. viguieri*, *D. circinale*, *C. raciborskii*, *Nodularia* sp., *P. rubescens*, *Lyngbya majuscula*, *L. wollei*, *Phormidium* sp., *Woronichinia naegeliana*	Paerl and Otten (2013), Mowe et al. (2015), Codd et al. (2005), Blaha et al. (2009), Schanz et al. (1979), Pick (2016), Nguyen-Quang et al. (2018)
Antarctica	*Oscillatoria* sp., *Phormidium*, *Nostoc commune*, *Aphanocapsa hyalina*, *Aphanocapsa holastica*, *Arthronema* sp., *Geitlerinema deflexum*, *Nodularia harveyana*, *Oscillatoria subproboscidea*, *Phormidium murrayi*, *Phormidium pseudopriesteyi*, *Calothrix* sp.	Pandey et al. (2004), Taton et al. (2006)
Asia	*Aphanizomenon ovalisporum*, *Planktothrix rubescens*, *P. agardhii*, *M. aeruginosa*, *Dolichospermum* sp., *Nodularia spumigena*, *Synechocystis* sp., *Aphanizomenon* sp., *Cylindrospermopsis* sp., *Planktothrix* sp., *Microcystis* sp., *Merismopedia* sp., *Nostoc* sp.	Codd et al. (2005), Blaha et al. (2009), Paerl and Otten (2013), Meriluo et al. (2017)
Australia	*Chrysosporum ovalisporum*, *Anabaena circinalis*, and *Lyngbya majuscula*	John et al. (2019), Mitrovic et al. (2011), Paul (2008)
Oceania	*M. aeruginosa*, *Aphanizomenon tenuicaulis*, *C. raciborskii*, *A. ovalisporum*, *A. issatschenkoi*, *P. rubescens*, *Kamptonema formosum*, *M. panniformis*, *D. planctonicum*, *D. circinale*	Mowe et al. (2015), Codd et al. (2005), Blaha et al. (2009), Meriluo et al. (2017)
Europe	*Gloeotrichia* sp., *Cylindrospermopsis* sp., *Microcystis* sp., *Dolichospermum* sp., *Aphanizomenon* sp., *Planktothrix* sp., *Nodularia* sp., *Phormidium* sp., *Anabaenopsis* sp.	Paerl and Otten 2013, Meriluo et al. 2017, Codd et al. (2005), Svirčev and Simeunović (2007)

formation of bloom also depends upon the complex structure of the lake. Therefore, a thorough study of individual water body has to be done to study the toxic bloom formation as all these factors need extra attention to make water body exclusive.

The toxin content in some marine harmful cyanobacteria (Stolte et al. 2002; Glibert and Burford 2017) under nutrient limiting conditions was higher. On the

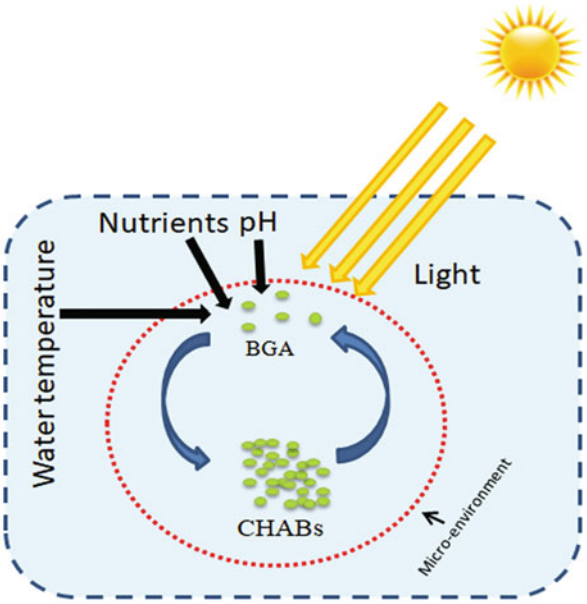

Fig. 15.1 Different ecological factors responsible for CHABs formation. Abbreviation: *BGA* blue green algae, *CHABs* cyanobacterial harmful algal blooms

basis of rigorous experimental evidence, it has been shown that phosphorus limitation controlled the release of allelochemicals externally in the cyanobacterium *Trichormus doliolum* (Von Elert and Jüttner 1997). There was an increase in production of microcystin and nostophycin by toxic *Nostoc* sp. under stress conditions of temperature, light, phosphate, and nitrate (Kurmayer 2011) (Fig. 15.1).

Since last few decades anthropogenic activities are increasing tremendously that causes the loading of nutrient in water bodies. Therefore, it is highly important to understand the effects of one or more environmental factors such as nutrients which drive the formation of CHABs.

15.3.1 Nutritional drivers of CHABs

The most studied environmental factor associated with CHABs is the natural and anthropogenic influx of nutrients into the freshwater ecosystems. The formation of CHABs was supposed to be mainly because of concentration of the nutrients (Piehler 2008). Although it is well known that nutrient input plays a symbolic part in proliferation of CHABs, still the type of nutrients is under debate (Piehler 2008).

In one of the primarily done extensive CHAB studies, (Smith 1983) while on his study on 17 lakes worldwide, interpret that CHAB formation and the TN: TP ratio are firmly associated and found that blooms do not favor higher ratios of TN: TP to multiply in water bodies. On same hand, Trimbee and Prepas (1987) analysis on 16 lakes of Canada supported the fact of low TN: TP concept. They found that TP

alone is the most potent predictor of cyanobacterial biomass than the total nitrogen to total phosphorus ratio.

Several studies depicted significant association between cyanobacterial harmful algal bloom proliferation and the availability of nutrients. Jacoby et al. (2000) reported that bloom formation and high TP concentration are strongly associated, while conducting his study on formation of cyanobacterial harmful algal blooms in Steilacoom Lake, Washington. Similarly, Anderson et al. (2002) in his investigation supported the association between influx of phosphorus and freshwater harmful blooms of cyanobacteria as well as between influx of nitrogen and marine CHABs. Correspondingly a positive relationship was analyzed between cyanobacterial biomass formation and TN:TP concentration (Giani et al. 2005). While investigating San Francisco Estuary, Lehman et al. (2005) also found the association of TN and TP with cyanobacterial biomass. While observing the 28 year old data set of Floridian lake, Havens et al. (2003) concluded that over the period of study total nitrogen to total phosphorus ratio declined from 30:1 to 15:1 corresponding an increase in cyanobacterial biomass.

Fisher et al. (1992) found that the nutrients for phytoplankton biomass in estuaries deviate from silicon and phosphorus limitation during spring season to nitrogen during summers. Maximum freshwater runoff during winter and summer precipitation drives the estuary towards cyanobacterial biomass controlled by phosphorus as in freshwater system, whereas the estuary has nitrogen-correlated algal biomass during low summer precipitation typical of a marine ecosystem. A study conducted on Western Lake Erie shows that increasing concentration of non-nitrate N over the last few decades (Spearman's rank correlation coefficient (ρ) = 0.68, p = 0.001) is significantly responsible for cyanobacterial bloom biomass (Newell et al. 2019).

15.3.2 Nutrient Drivers for Release of Extracellular Metabolites/ Toxins

The nutrient availability is recognized as one of the important components to control algal biomass and growth. Therefore proliferation of a specific species, while forming harmful algal bloom, is its ability to compete for limiting nutrients. The ability to compete for the nutrients available in the water body leads to dominance of particular species and thereby release of toxins in that environment.

Increase in release of extracellular compounds may occur under nutrient limiting conditions (Von Elert and Jüttner 1997). Grosse et al. (2018) observed that nitrogen limited communities exhibited substantially slower production of essential amino-acids, while with addition of nutrients in short-term experiments, this trend was contrary to previous result immediately after N addition to the levels found under not limiting conditions.

However, reports about relations between concentrations of nitrate and microcystin production have provided conflicting results. Einhellig (1995) concluded that limiting amount of distinct resource results in increasing allelochemical production. Ginn et al. (2010) explained that the N-limitation leads

to expression of *ntcA and mcy*B in *M. aeruginosa* (microcystin producer). Tonk et al. (2008) in the study conducted bring about the effect of N presence on MC production as addition of leucine and arginine increased the synthesis of microcystin LR and microcystin-RR, respectively, in *Planktothrix agardhii*. Van de Waal et al. (2009) also observed *Microcystis* blooms capable of producing microcystin-RR variants at higher levels mainly due to CO_2 and nitrogen enrichment. Cyanobacterial community structure consisting of *M. wesenbergii*, *Aphanizomenon flos-aquae*, and *M. aeruginosa* producing MC-LA, MC-YR, and MC-RR, respectively, was influenced by different forms of nitrogen source determining the toxicity of the bloom (Monchamp et al. 2014).

Nodularia spumigena blooms were reported to dominate the water body under conditions with higher phosphorus but low N:P and moderate salt concentrations (Mazur-Marzec et al. 2006). Similarly, Lehtimaki et al. (1997) examined that the synthesis of NOD is influenced by concentrations of nitrogen and phosphorus. While higher concentration of phosphorus (200–5500 μg L^{-1}) enhances the synthesis of nodularin but NOD production got inhibited by higher salinity and inorganic nitrogen concentrations.

Inconsistency in studies was also reported regarding cylindrospermopsin (CYN) production and different N-sources (NO_3^-, N_2,NH_4^+). Saker and Neilan (2001) were the first ones to start an investigation in *C. raciborskii* to study the correlation among CYN and type of N source for which *C. raciborskii* cultures were grown in absence of a fixed source of nitrogen resulting into slower growth rate but increased CYN while with changed nitrogen source in the form of NH_4^+, CYN was less and growth rate was higher. CYN production also depends upon phosphate limitation but contradictory reports regarding the same are found in literature. The decreased and enhanced expression of CYN secretion in *Aphanizomenon ovalisporum* have been observed under phosphate limitation in separate studies conducted by Bacsi et al. (2006) and Bar-Yosef et al. (2010), respectively. These studies clearly indicate that various environmental factors affect the production of CYN in several cyanobacteria.

Anatoxins (ATXs) synthesis was reported to vary with different factors like nutrient limitation, light, temperature, and different phases of growth (Kaebernick et al. 2000; Peary and Gorham 1996; Gupta et al. 2002; Rapala et al. 1993; Bumke-Vogt et al. 1996). Like MC, the growth of cell and ATX production were not related to each other in the study conducted by Long et al. (2001). N limitation could raise ATX production just like other cyanotoxins as already mentioned above (Neilan et al. 2013).

Saxitoxin (STX) production in cultures of *C. raciborskii* got influenced with N:P ratio as treatment with higher ratio resulted into increased STX production when compared to treatment with low N:P (Chislock et al. 2014). However, concentrations of nitrogen had reverse effect as with higher N concentrations, a lower amount of STX secretion has been found in *Raphidiopsis brookii* (Yunes et al. 2009).

It is evident that toxicity increases under nutrient stress and the activity of the toxins under such conditions provides us an advantage to suspect that allelopathic compounds play an important role in the growth and biology of toxic algae.

15.4 Methods of Detection

In order to measure the presence of cyanotoxins, various methods are available in the literature such as bioassays, molecular analysis, biochemical and chemical assays (Fig. 15.2). Enzyme-linked immunosorbent assay (ELISA) test kits are distinctive and accepted test methods to detect cyanotoxins (Gaget et al. 2017), as extensive training or expensive equipment are not required. ELISA kits can detect microcystin-LR, saxitoxin, and cylindrospermopsin precisely, while for anatoxin-a detection, a more rapid receptor-binding assay kit is available. Although they provide rapid results, there are certain limitations associated with ELISA kits as they are not congener specific.

LC/MS or liquid chromatography with mass spectrometry can precisely analyze specific congeners of microcystin with the use of available standards; this method in particular has been designed in a way to reduce matrix interference. In HPLC-PDA methods the quantification of toxin is trickier mainly because of less specificity and interference by matrix and are therefore less efficient than LC/MS methods. However, standards available for analytical toxins confirmation could assess the resolution of the congeners present.

15.4.1 Sample Handling

To ensure reliable results, samples must be handled properly. Guidelines for design and sampling for cyanobacterial toxin and taste-and-odor studies in lakes and reservoirs (2008) provided by The United State Geological Survey (USGS)

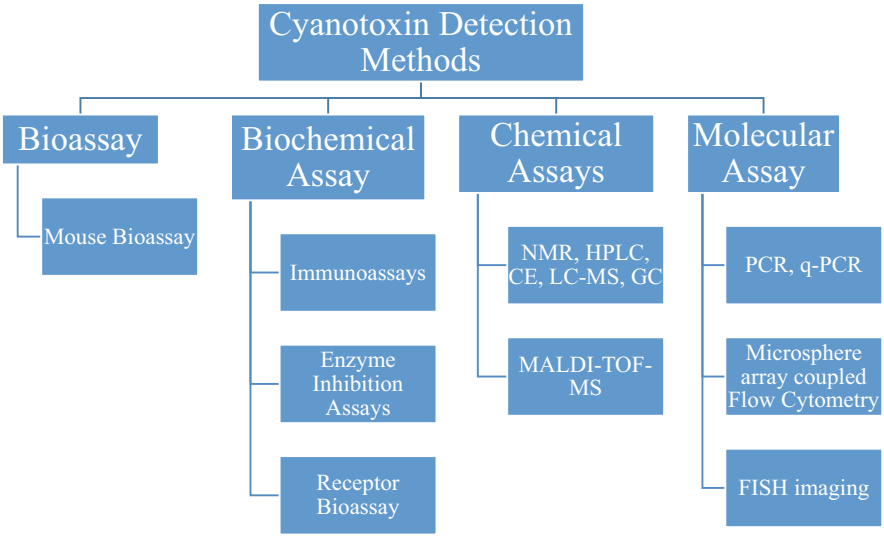

Fig. 15.2 Overview of Methods available for Cyanotoxin detection

sampling protocol can be consulted for establishing such procedures. The three most important sample handling consideration steps are (1) collection of samples, (2) quenching of samples using appropriate quenching agents, and (3) chilling of samples till further analysis at the laboratory.

15.4.2 Sample Analysis

While estimating both intracellular and extracellular toxins, cell lysis is generally done to rupture the cyanobacterial cells and to damage the cell wall and secrete the toxins into the solution. Most commonly used lysing technique is freeze/thaw cycling, though various other approaches such as sonication, bead beating, lyophilization are also used depending on analytical methods (Kim et al. 2009). The effectiveness of raw-water lysing using microscopic examination for intact algal cells is yet to be confirmed by analysts.

Variety of different extraction techniques and cell disruption methods are available for cyanotoxin detection from various cyanobacteria. Generally following steps of protocol are followed on algal samples: Extraction method, Selection of Solvent, Cell Disruption method, Centrifugation and Cyanotoxin detection.

15.5 Cyanotoxin Treatment and Bloom Management

Cyanobacteria and cyanotoxins identified in the surface water can be removed or inactivated in many different ways. After identification of cyanobacterial species that dominates the bloom and understanding its growth pattern as well as the properties of its intracellular and extracellular cyanotoxins, suitable treatment processes will help in employing adequate management schemes. As observed by Kim et al. (2018), oxidation of microcystin depends on temperature, pH of the water. Applying the wrong treatment process could damage the cells causing cell rupturing and release of cyanotoxins rather than their removal.

Table 15.2 compiles different types of methods for treatment of water to remove intracellular and extracellular toxins along with intact cells of most important cyanobacteria.

15.5.1 Developing an Exigency Strategy

Concerned authorities should develop effective strategies to get rid of cyanobacterial harmful bloom occurrence. The planning methods should approach various ways to rule out the possible risk involved with each action to eradicate algal bloom as all blooms are not toxic. Successful application of such planning involves many factors such as monitoring programs to determine sampling sites, frequency of sampling, sample volume, sampling methods for both cyanobacterial cells and specific

Table 15.2 Cyanotoxin treatment methods

Treatment method	Efficacy
Intracellular cyanotoxins	
Pre-treatment oxidation method	Causes cell lysis of cyanobacterial cells releasing the toxin into the surrounding water. Prefer lower doses of an oxidant (potassium permanganate). Otherwise, higher doses may destroy total toxins present
Coagulation	When cells which are assembled in sludge are confined from the plant
Membrane method	Study data limited. Ultra and microfiltration are useful when cells do not assemble on membranes
Flotation method	Dissolved Air Flotation (DAF) is most effective as most of the toxin producing cyanobacteria are buoyant
Extracellular cyanotoxins	
Membrane method	Based upon quality of water and pore size of membrane. Nanofiltration and reverse osmosis filtration are most efficient for removal of extracellular microcystin and cylindrospermopsin, respectively
Addition of Potassium Permanganate	Efficient method for oxidation of extracellular anatoxins and microcystins
Ozone method	Mainly to oxidize extracellular microcystin, anatoxin-a, and cylindrospermopsin
Chlorination method	Adequate method below pH 8 and not effective for anatoxin-a
Ultraviolet Radiation method	Degrade microcystin and cylindrospermopsin at higher application
Addition of activated carbon	Powdered activated carbon (PAC) and Granular activated carbon (GAC). Effectiveness of the method depends on carbon type and pore size. Microcystin are best adsorbed by wood-based activated carbons but carbon cannot adsorb saxitoxin

cyanotoxins, analytical screening method to be used, and appropriate conditions to send samples to laboratory for affirmation.

15.6 Future Prospects and Conclusion

With the growth of industrialization and uncontrolled use of natural resources, the healths of water bodies are severely affected in terms of biotic and abiotic factor. These imbalances are creating the bloom formation in water bodies, which eventually affect the survival/health of aquatic organisms. Therefore, it is very important to get a holistic overview of events/factors which control the bloom formation. Attempts have been made to do it but they are not quite enough to tackle this problem. In nut shell the time has come to make interdisciplinary efforts by ecologist/chemist/algologist for comprehensive understanding as well as to find out novel approaches to deal with this social issue worldwide.

References

Anderson DM, Glibert PM, Burkholder JM (2002) Harmful algal blooms and eutrophication nutrient sources, composition, and consequences. Estuaries 25:704–726

Bacsi I, Vasas G, Suranyi G et al (2006) Alteration of cylindrospermopsin production in sulfate- or phosphate-starved cyanobacterium *Aphanizomenon ovalisporum*. FEMS Microbiol Lett 259:303–310

Bar-Yosef Y, Sukenik A, Hadas O et al (2010) Enslavement in the water body by toxic *Aphanizomenon ovalisporum*, inducing alkaline phosphatase in phytoplanktons. Curr Biol 20:1557–1561

Beaulieu M, Pick F, Gregory-Eaves I (2013) Nutrients and water temperature are significant predictors of cyanobacterial biomass in 1147 lakes data set. Limnol Oceanogr 58:1736–1746

Bernardi R, Giussani G (1990) Are blue-green algae a suitable food for zooplankton? An overview. Hydrobiologia 200:29–41

Blaha L, Babica P, Marsalek B (2009) Toxins produced in cyanobacterial water blooms—toxicity and risks. Interdiscip Toxicol 2:36–41

Bumke-Vogt C, Mailahn W, Rotard W, Chorus I (1996) A highly sensitive analytical method for the neurotoxin anatoxin-a, using GC-ECD, and first application to laboratory cultures. Phycologia 35:51–61

Carpenter SR, Caraco NF, Correll DL et al (1998) Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecol App l8:559–568

Chislock MF, Sharp KL, Wilson AE (2014) *Cylindrospermopsis raciborskii* dominates under very low and high nitrogen-to-phosphorus ratios. Water Res 49:207–214

Codd GA, Beattie KA (1991) Cyanobacteria (blue-green algae) and their toxins: awareness and action in the United Kingdom. Public Health Laboratory Service. Microbiol Digest 8:82–86

Codd GA, Morrison LF, Metcalf JS (2005) Cyanobacterial toxins: risk management for health protection. Toxicol Appl Pharm 203:264–272

Corbel S, Mougin C, Bouaicha N (2014) Cyanobacterial toxins: modes of actions, fate in aquatic and soil ecosystems, phytotoxicity and bioaccumulation in agricultural crops. Chemosphere 96:1–15

Davis TW, Berry DL, Boyer GL, Gobler CJ (2009) The effects of temperature and nutrients on the growth and dynamics of toxic and non-toxic strains of *Microcystis* during cyanobacteria blooms. Harmful Algae 8:715–725

Einhellig FA (1995) Allelopathy: current status and future goals. In: Inderjit, KMM D, Einhellig FA (eds) Allelopathy: organisms, processes, and applications, ACS symposium series, vol 582, pp 1–24

Fisher TR, Peeler ER, Ammerman JW, Harding LW (1992) Nutrient limitation of phytoplankton in Chesapeake Bay. Mar Ecol Prog Ser 82:51–63

Francis G (1878) Poisonous Australian Lake. Nature 18:11–12

Gaget V, Lau M, Sendall B (2017) Cyanotoxins: which detection technique for an optimum risk assessment? Water Res 118:227–238

Giani A, Bird DF, Prairie YT, Lawrence JF (2005) Empirical study of cyanobacterial toxicity along trophic gradient of lakes. Can J Fish Aquat Sci 62:2100–2109

Ginn HP, Pearson LA, Neilan BA (2010) NtcA from *Microcystis aeruginosa* PCC 7806 is autoregulatory and binds to the microcystin promoter. Appl Environ Microbiol 76:4362–4368

Glibert PM, Burford MA (2017) Globally changing nutrient loads and harmful algal blooms: recent advances, new paradigms, and continuing challenges. Oceanography 30:58–69

Gobler CJ, Burkholder JM, Davis TW et al (2016) The dual role of nitrogen supply in controlling the growth and toxicity of cyanobacterial blooms. Harmful Algae 54:87–97

Grosse J, Brussaard CPD, HTS B (2018) Nutrient limitation driven dynamics of amino acids and fatty acids in coastal phytoplankton. Limnol Oceanogr 64:302–316

Gupta N, Bhaskar ASB, Rao PVL (2002) Growth characteristics and toxin production in batch cultures of *Anabaena flos-aquae*: effects of culture media and duration. World J Microbiol Biotechnol 18:29–35

Harrness (2005) In: Ramsdell JS, Anderson DM, Glibert PM (eds) Harmful algal research and response: a national environmental science strategy 2005–2015. Ecological Society of America, Washington, DC

Havens KE, James RT, East TL, Smith VH (2003) N:P ratios, light limitation and cyanobacterial dominance in a subtropical lake impacted by non-point source nutrient pollution. Environ Pollut 122:379–390

Horne AJ (1972) Nitrogen fixation in Clear Lake, California. II. Synoptic studies on the autumn *Anabaena* bloom. Limnol Oceanogr 17:693–703

Huisman J, Zonneveld C, Weissing FJ (1999) Competition for light between phytoplankton species: experimental test of mechanistic theory. Ecology 80:211–222

Jacoby JM, Collier DC, Welch EB et al (2000) Environmental factors associated with a toxic bloom of *Microcystis aeruginosa*. Can J Fish Aquat Sci 57:231–240

John N, Baker L, Ansell BRE, Newham S et al (2019) First report of anatoxin-a producing cyanobacteria in Australia illustrates need to regularly up-date monitoring strategies in a shifting global distribution. Sci Rep 9:10894

Kaebernick M, Neilan BA (2001) Ecological and molecular investigations of cyanotoxin production. FEMS MicrobiolEcol 35:1–9

Kaebernick M, Neilan BA, Börner T, Dittmann E (2000) Light and the transcriptional response of the microcystin biosynthesis gene cluster. Appl Environ Microbiol 66:3387–3392

Kaplan A, Harel M, Kaplan-Levy RN et al (2012) The languages spoken in the water body (or the biological role of cyanobacterial toxins). Front Microbiol 138:1–11

Kim IS, Nguyen GH, Kim SY et al (2009) Evaluation methods for cyanobacterial cell lysis and toxin (Microcystin LR) extraction using Chromatographic and Mass Spectrometric Analysis. Environ Eng Res 14:250–254

Kim SM, Lee HJ, Lee KM et al (2018) Oxidation of microcystins by permanganate: pH and temperature-dependent kinetics, effect of DOM characteristics, and oxidation mechanism revisited. Environ Sci Technol 52:7054–7063

Kosten S, Huszar VLM, Bécares E et al (2012) Warmer climates boost cyanobacterial dominance in shallow lakes. Global Change Biol 18:118–126

Kurmayer R (2011) The toxic cyanobacterium *Nostoc* sp. Strain 152 produces highest amounts of microcystin and nostophycin under stress conditions. J Phycol 47:200–207

Lehman PW, Boyer G, Hall C, Waller S, Gehrts K (2005) Distribution and toxicity of a new colonial *Microcystis aeruginosa* bloom in the San Francisco Bay Estuary, California. Hydrobiologia 541:87–99

Lehtimaki J, Moisander P, Sivonen K, Kononen K (1997) Growth, nitrogen fixation, and nodularin production by two Baltic Sea cyanobacteria. Appl Environ Microbiol 63:1647–1656

Long BM, Jones GJ, Orr PT (2001) Cellular microcystin content in N-limited *Microcystis aeruginosa* can be predicted from growth rate. Appl Environ Microbiol 67:278–283

Mazur-Marzec H, Meriluoto J, Plinski M, Szafranek J (2006) Characterization of nodularin variants in *Nodularia spumigena* from the Baltic Sea using liquid chromatography/mass spectrometry/mass spectrometry. Rapid Commun Mass Spectrom 20:2023–2032

Meriluo J, Blaha L, Bojadzija G et al (2017) Toxic cyanobacteria and cyanotoxins in European waters-Recent progress achieved through the CYANOCOST. Action and challenges for further research. Adv Oceanogr Limnol 8:161–178

Miller TR, Weirich C, Bartlett S (2017) Cyanobacterial toxins of the Laurentian great lakes, their toxicological effects, and numerical limits in drinking water. Mar Drugs 15:160

Mitrovic SM, Hardwick L, Dorani F (2011) Use of flow management to mitigate cyanobacterial blooms in the Lower Darling River, Australia. J Plankton Res 33:229–241

Mogelhaj M, Henriksen P, Lundholm N (2006) High pH and not allelopathy may be responsible for negative effects of *Nodularia spumigena* on other algae. Aquat Microb Ecol 43:43–45

Monchamp ME, Pick FR, Beisner BE, Maranger R (2014) Nitrogen forms influence microcystin concentration and composition via changes in cyanobacterial community structure. PLoS One 9: e85573

Mowe MAD, Mitrovic SM, Lim RP (2015) Tropical cyanobacterial blooms: A review of prevalence, problem taxa, toxins and influencing environmental factors. J Limnol 74:205–224

Müller-Navarra DC, Brett MT, Park S et al (2004) Unsaturated fatty acid content in seston and tropho-dynamic coupling in lakes. Nature 427:69–72

Ndlela LL, Oberholster PJ, Van Wyk JH, Cheng PH (2016) An overview of cyanobacterial bloom occurrences and research in Africa over the last decade. Harmful Algae 60:11–26

Neilan BA, Pearson LA, Muenchhoff J et al (2013) Environmental conditions that influence toxin biosynthesis in cyanobacteria. Environ Microbiol 15:1239–1253

Newell SE, Davis TW, Johengen TH et al (2019) Reduced forms of nitrogen are a driver of non-nitrogen-fixing harmful cyanobacterial blooms and toxicity in Lake Erie. Harmful Algae 81:86–93

Nguyen-Quang T, Fraser H, Hushchyna K et al (2018) Continuation of the systematic study (2nd year – 2017) of toxic algal blooms in McLaughlin and Irishtown Reservoirs to add to the water quality program of the City of Moncton—New Brunswick. Technical Report submitted to Government of New Brunswick, Environmental Trust Fund, Environmental and Local Government, Canada

Oliver RL, Hamilton DP, Brookes JD, Ganf GG (2012) Physiology, blooms and prediction of planktonic cyanobacteria. In: Whitton BA (ed) Ecol. cyanobacteria II their divers. Space time. Springer, Dordrecht, pp 155–194

Paerl HW (1988) Nuisance phytoplankton blooms in coastal, estuarine, and inland waters. Limnol Oceanogr 33:823–847

Paerl HW, Huisman J (2009) Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. Environ Microbiol Rep 1:27–37

Paerl HW, Otten TG (2013) Harmful cyanobacterial blooms: causes, consequences, and controls. Microb Ecol 65:995–1010

Pandey KD, Shukla SP, Shukla PN et al (2004) Cyanobacteria in Antarctica: ecology, physiology and cold adaptation. Cell Mol Biol 50:575–584

Paul VJ (2008) Global warming and cyanobacterial harmful algal blooms. In: Hudnell HK (ed) Cyanobacterial harmful algal blooms: state of the science and research needs. Springer, Cham, pp 239–257

Peary JA, Gorham PR (1996) Influence of light and temperature on growth and toxin production by *Anabaena flos-aquae*. J Phycol 2:1–3

Pick FR (2016) Blooming algae: a Canadian perspective on the rise of toxic cyanobacteria. Can J Fish Aquat Sci 73:1149–1158

Piehler MF (2008) Watershed Management strategies to prevent and control cyanobacterial harmful algal blooms. AdvExp Med Biol 619:259–273

Rapala J, Sivonen K, Luukkainen R, Niemelä S (1993) Anatoxin-a concentration in *Anabaena* and *Aphanizomenon* under different environmental conditions and comparison of growth by toxic and non-toxic *Anabaena*-strains—a laboratory study. J Appl Phycol 5:581–591

Saker ML, Neilan BA (2001) Varied diazotrophies, morphologies, and toxicities of genetically similar isolates of *Cylindrospermopsis raciborskii* (nostocales, cyanophyceae) from Northern Australia. Appl Environ Microbiol 67:1839–1845

Schanz F, Allen ED, Gorham PR (1979) Bioassay of the seasonal ability of water from a eutrophic Alberta lake to promote selective growth of strains of *Anabaena flos-aquae* and other blue-green algae. Can J Bot 57:2443–2451

Smith VH (1983) Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science 221:669–671

Steffen MM, Belisle BS, Watson SB et al (2014) Status, causes and controls of cyanobacterial blooms in Lake Erie. J Great Lakes Res 40:215–225

Stolte W, Karlsson C, Carlsson P, Graneli E (2002) Modelling the increase of nodularin content in Baltic Sea *Nodularia spumigena* during stationary phase in phosphorus-limited batch cultures. FEMS Microb Ecol 41:211–220

Svirčev Z, Simeunović J, Subakov-SimićG, et al (2007) Freshwater cyanobacterial blooms and cyanotoxin production in Serbia in the past 25 years. Geogr Panon 11:32-38.

Taton A, Grubisic S, Balthasart P et al (2006) Biogeographical distribution and ecological ranges of benthic cyanobacteria in East Antarctic lakes. FEMS Microb Ecol 57:272–289

Tonk L, Van de Waal DB, Slot P et al (2008) Amino acid availability determines the ratio of microcystin variants in the cyanobacterium *Planktothrix agardhii*. FEMS Microbiol Ecol 65:383–390

Trimbee AM, Prepas EE (1987) Evaluation of total phosphorus as a predictor of the relative biomass of blue-green algae. Can J Fish Aquat Sci 44:1337–1342

Van de Waal DB, Verspagen JMH, Lürlin M (2009) The ecological stoichiometry of toxins produced by harmful cyanobacteria: An experimental test of the carbon-nutrient balance hypothesis. Ecol Lett 12:1326–1335

Von Elert E, Jüttner E (1997) Phosphorus limitation and not light controls the extracellular release of allelopathic compounds by *Trichormus doliolum* (Cyanobacteria). Limnol Oceanogr 42:1796–1802

Wang WC (1974) Effect of turbidity on algal. Growth. Circular 121. State of Illinois, Department of Registration and Education, pp 1–12. ISWS-74-CIR121

Whitton BA, Potts M (2012) Introduction to the cyanobacteria. In: Whitton BA (ed) Ecol. cyanobacteria II their divers. Space time. Springer, Dordrecht, pp 1–13

Yunes JS, de la Rocha S, Giroldo D (2009) Release of carbohydrates and proteins by a subtropical strain of *Raphidiopsis brookii* (cyanobacteria) able to produce saxitoxin at three nitrate concentrations. J Phycol 45:585–591