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REVIEW ARTICLE

Biological control of Freshwater Cyanobacterial blooms; A Review

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Abstract: Outbreaks of cyanobacterial blooms in freshwaters have been increasingly reported worldwide during the last few decades. One of the major problems with cyanobacterial blooms is that some species can be toxic. Their toxins (cyanotoxins) can have mild to serious health effects on humans and animals due to direct contact or ingestion with drinking water and food. Due to the unavailability of efficient testing methods for cyanotoxins especially in developing countries, people may consume toxin contaminated water and foods. Non-toxic cyanobacterial blooms may cause other ecological and socioeconomic impacts. Therefore, physical and chemical control methods are currently being employed as direct control or removal of cyanobacterial blooms. However, due to some intrinsic adverse consequences of physical and chemical control of blooms on the ecosystem and high operational cost, biological control has gained attention as an alternative sustainable bloom management strategy. A diverse array of control agents such as viruses, bacteria, fungi, actinomycetes, protozoa, flagellates, and macrophytes with the potential to terminate or suppress the growth of cyanobacteria have been isolated and identified from freshwater bodies in different parts of the world. Among the controlling agents, heterotrophic bacteria in the aquatic environment are of high interest owing to their high specificity on the targeted cyanobacteria and high survival ability during non-bloom conditions. Heterotrophic bacteria antagonize cyanobacteria either through direct contact or indirectly by the secretion of allelopathic compounds. The mechanisms of antagonism are known to be physiological and metabolic dysfunctions and transcriptional regulation of genes. In addition, there are some evidence to show regulation of antagonism through cell density-dependent quorum-sensing (QS) mechanisms. In response, cyanobacteria induce defensive mechanisms such as alteration of colony morphology and activation of chemical defences against microbial antagonists. This review article aimed to encompass the current status of knowledge on the biological control of freshwater cyanobacterial blooms and to highlight the existing knowledge gap in the available literature. We highlight that although a large number of microbial antagonists have been isolated, identified, and demonstrated their cyanobacteria lytic activity in the laboratory, their field application is still challenging. Understanding the spatial and temporal variations in antagonists and cyanobacteria in a particular aquatic ecosystem is essential for planning an effective bloom management strategy. We also highlight the necessity in expanding research focus towards novel strategies to enhance application potential and overcome existing challenges.

***Keywords**: Biological control, cyanobacterial blooms, microbial antagonists, antagonistic mechanisms*

Introduction

Cyanobacteria are the predominant primary producers in aquatic ecosystems. Excessive growth of cyanobacteria on surface waters forms dense biomass known as a bloom. The frequency of cyanobacterial bloom outbreaks and their spatial coverage in freshwaters have increased in recent decades throughout the world (Paerl et al., 2011; Zhou et al., 2013; Van Wichelen et al., 2016). The major contributory factor associated with bloom formation appears to increase nutrient availability especially, phosphates, nitrates, ammonium, and trace metals entering into water bodies (Kulasooriya, 2017;

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Eckersley & Berger, 2018). As a consequence, dense and thick biomass of cyanobacteria is formed on the surface and sub-surface of water bodies. Cyanobacterial bloom has become a global concern due to its ecological and socio-economic impacts such as deterioration of water quality, physical interference to the water purification and drainage and declining of aesthetic value. Cyanobacterial biomass generates unpleasant taste and odour in water and increase biological oxygen demand which in turn reduces the availability of oxygen for other aquatic organisms and ultimately cause trophic shift and collapse of aquatic ecosystems (Falconer, 1999; Anderson, 2009; Rastogi et al., 2014; Ndlela et al., 2016; Demeke, 2016; Huisman et al., 2018). During the period of decaying cyanobacterial cell biomass, a wide range of cyanotoxins is released into the surrounding waters. Cyanotoxins that enter into drinking water supplies and accumulate in food chains are a risk to public health and animals (Codd, 1995; Carmichael et al., 2001). The most predominant cyanobacterial genera which contribute to the bloom formation in freshwaters include, *Anabaena* (*Dolichospermum*), *Aphanizomenon*, *Cylindrospermopsis*, *Gloeotrichia*, *Gomphosphaeria*, *Lyngbya*, *Microcystis*, *Nodularia*, *Nostoc*, and *Planktothrix* (Paerl et al., 2001). Further, most of these dominant bloom-forming cyanobacteria are known to produce intracellular or extracellular metabolites such as cyanotoxins, taste and odor causing substances, and other associated organic matters (AOMs) (Zhou et al., 2013). The frequency of occurring cyanobacterial blooms has increased during the last two decades due to climate change and global warming (Joehnk et al., 2008; Mowe et al., 2015b; Paerl et al., 2016). Cyanobacterial blooms could occur at alarming rates in the future as consequences of global warming and enrichment of water bodies with mineral nutrients through the expansion of modern agriculture.

Ensuring access to a safe and clean water supply is one of the sustainable development goals (SDG 6) that needs to be addressed by 2030 (Gain et al., 2016). To achieve this goal, sustainable management of freshwater reservoirs all over the world is vitally important. Hence, much of the scientific interest has been focused on seeking out effective and efficient strategies to control and minimize adverse impacts caused by harmful and nuisance cyanobacterial blooms. The aim of any such measure should be focused on the provision of hygienically safe water for all purposes, drinking, recreation, aquaculture, and industry with required standards (Jančula & Maršálek, 2011). The most appropriate long-term strategy to control cyanobacterial bloom is the restriction of excess nutrient inputs specifically, nitrogen (N), and phosphorus (P) into water bodies. However, this method has limited applicability in many countries due to economic constraints (Zhou et al., 2013). Short-term conventional remediation measures that include physical methods such as, filtration, electrolysis, and ultrasound sonication (Codd et al., 2005; Park et al., 2017; Zhao et al., 2017) and chemical methods such as application of copper sulphate, aluminium chloride, sodium hypochlorite, and hydrogen peroxide are widely applied (Codd et al., 2005; Merel et al., 2009; Jančula & Maršálek, 2011; Huh & Ahn, 2017). However, as these methods mainly focus on the removal or suppression of cell biomass, there are limitations such as, high investment and /or operational cost, low efficacy, and formation of harmful by-products that may have adverse effects on the environment (Maruyama et al., 2003; Dziga et al., 2013; Osman et al., 2017). Moreover, short-term methods do not aim for the removal of cyanotoxins. Hence, cyanotoxin-contaminated water that enters into purification plants may reach consumers without being treated since most drinking water treatment methods currently in use are incapable of complete removal of cyanotoxins (Schmidt et al., 2002; Merel et al., 2009). Although chlorination removes higher amounts of cyanotoxins, it requires to apply a higher dosage of chlorine while maintaining pH below 8. Therefore, it is not applicable to use in drinking water purification due to health concerns. On the other hand, undesirable chlorinated by-products can be formed as a result of the chlorination of algal cells (Merel et al., 2009). Therefore, widely accepted and sustainable remediation strategies are vitally important to control cyanobacterial blooms.

Biological control strategies including application of microorganisms (Kang et al., 2005; Gumbo et al., 2008), macrophytes (Zhou et al., 2014), and zooplanktons (Haney, 1987) have been tested to control dynamics and succession of algal blooms and their toxins. These techniques are popular among scientist nowadays due to its environmentally friendliness and cost-effectiveness (Eckersley & Berger, 2018; Sun et al., 2018). Therefore, many biological agents have been isolated from freshwaters to investigate their potential in cyanobacterial bloom management. Among those organisms, much attention has been paid to heterotrophic bacteria owing to their abundance and strong antagonistic interactions with cyanobacteria (Maruyama et al., 2003; Dziga et al., 2013; Osman et al., 2017). Some recent reviews have compiled both past and present successful research efforts on cyanobacterial cell lysis and underlying mechanisms (Pal et al., 2020;

Wang et al., 2020; Yang et al., 2020). Hence, this review article aimed to; (i) encompass recent advances achieved in biological control of freshwater cyanobacterial blooms, (ii) highlight the knowledge gaps based on the available literature, and (iii) suggest some innovative ideas to overcome challenges in field application. Therefore, this review will bring new insights into future research towards broadening the application potential of biological control of cyanobacterial bloom in both temperate regions and tropics.

Biological Control of Cyanobacterial Blooms

Control and/or removal of cyanobacterial blooms and their toxins have been tested with viruses (Tucker & Pollard, 2005; Yoshida et al., 2006; Manage, 2009; Yeo & Gin, 2013; Zhang et al., 2020), bacteria (Idroos & Manage, 2018; Zhang et al., 2019; Yang et al., 2020), fungi (Kagami et al., 2007; Zeng et al., 2015), actinomycetes, protozoa (Van Wichelen et al., 2016; Sun et al., 2018), and higher plants (Qiu et al., 2001; Wang et al., 2009). They provide a short-term measure to reduce or terminate cyanobacterial blooms. As reported by Sigee et al., (1999), the controlling agent should be a native species isolated from the bloom environment without undergoing either genetic modifications or enhancement. Further, the biological agent should be highly host-specific that do not cause impacts on other non-targeted organisms including human beings (Sigee et al., 1999). In addition, attributes such as adaptability to various physical conditions, capacity and ability to multiply, prey consumption, ability to capture prey, ability to survive in low prey densities, susceptibility towards a wide range of hosts, and ability to respond to changes in the host are considered in the selection of biocontrolling agent/s of blooms (Daft et al., 1985).

More often, blooms are biologically controlled through the regulation of the population density of cyanobacteria by associated microbial or other phytoplankton communities present in the freshwater environment (Manage et al., 2001; Yoshida et al., 2008; Manage, 2009; Zhang et al., 2012). A study conducted in Brazil provided an evidence for the natural control of *Cylindrospermopsis raciborskii* bloom in a freshwater reservoir (Bouvy et al., 2001). They have suggested that the bloom was controlled probably due to the breakage of *Cylindrospermopsis* filaments by some zooplanktonic species which then facilitated other zooplankton to feed on broken filaments. Further, they hypothesized that the population shift in zooplankton communities seemed to be associated with heterotrophic bacterial population density. Some field studies available in the literature provide evidences for different zooplankton-cyanobacteria interactions (Haney, 1987). It is clear that some interactions promoted the growth of colonial cyanobacteria by selective grazing of competitive phytoplanktons while filamentous cyanobacteria such as *Anabaena* and *Oscillatoria* inhibited zooplanktons through interfering filter-feeding behaviour of zooplanktons. Therefore, the co-existence of filamentous cyanobacteria with toxin-producing colonial cyanobacteria may cause detrimental effects on zooplanktons due to toxicity of cyanotoxins and deficiency in nutrients.

Over the past few decades, numerous experimental efforts have been taken to utilize the natural bloom control phenomenon as a strategy to control cyanobacterial blooms. Augmentation of a pre-adapted predator population of cyanobacteria maintained in nutrient-rich media was found to be an interesting strategy when the native populations are incapable of controlling blooms (Ndlela et al., 2016). This will be more advantageous as cultured organisms are highly specific to the targeted host species and are not expected to cause direct chemical pollution. However, the introduction of a non-native population may not always be successful due to the stressful environmental conditions and competition for resources that they may have faced in the new environment. On the other hand, it is undesirable to apply a non-native population to sensitive environments (Sigee et al., 1999; Gumbo et al., 2008). Furthermore, survival of the predator population in the newly introduced habitat could not always be guaranteed and therefore continuous reapplication may be necessary (Blakeman & Fokkema, 1982).

Biomanipulation

In the application of biomanipulation process, cyanobacterial blooms can be controlled by using aquatic organisms through the manipulation of the trophic cascade. The most commonly applied approach is enhancing the grazing pressure on phytoplankton while decreasing the same pressure on zooplankton (Sierp et al., 2009; Demeke, 2016). This approach was initiated in 1975 and since then, it is frequently practiced as a lake quality management method in many developed countries in temperate regions and subtropical regions of Australia. However, it is rarely practiced in tropical freshwaters (Yatigammana, 2013). Fish (piscivorous and filter-feeding planktivorous fish), Daphnia, bivalves, and

macrophytes are being widely used either alone or combinations in biomanipulation schemes (Triest et al., 2016). Sierp et al. (2009) have identified the potential use of native species, Murray cod (*Maccullochella peelii peelii*) in southern temperate Australia to control algal blooms. Moreover, Lu et al. (2006) have studied the potential use of Tilapia (*Oreochromis niloticus*) to eliminate *M. aeruginosa* bloom, through their ingestion and digestion mechanisms. Filter-feeding fish species, bighead carp (*Aristichthys nobilis*), and silver carp (*Hypophthalmichthys molitrix*) have a potential to remove *M. aeruginosa*, via the mechanism of grazing (Görgényi et al., 2016). Yatigammana (2013) has proposed the introduction of native snakehead *Channa striata* (Loolla) and large herbivorous zooplankton as a biomanipulation tool for controlling algal blooms in Sri Lankan freshwater reservoirs. Stocking of piscivorous eels (*Anguilla anguilla*) in reservoirs has been frequently practiced in Germany to increase the predation pressure on the planktivorous fish. This could negatively affect on the cyanobacterial bloom control (Schulze et al., 2004).

As an invertebrate group, the introduction of bivalves has deserved much attention. Bivalves, *Hyriopsis cumingii* and *Nodularia douglasiae* were identified as potential grazers against *M. aeruginosa* (Hu et al., 2016; Sugawara et al., 2021). Although there are some successful stories, the effectiveness of biomanipulation as a bloom control strategy has been limited in highly eutrophic water bodies where the total phosphorus concentration exceeds 100 µg/L (Demeke, 2016). However, it is effective for relatively smaller water bodies where the population of grazers can be manipulated continuously (Lazzaro, 1997). Moreover, problems encountered with stocking densities and removal of fish, changes in nutrients and pH status, and shifting of diet away from cyanobacteria are the major limitations that affect the success of biomanipulation.

Bacteria-mediated biological control

The interactions between freshwater cyanobacterial blooms and their associated bacteria play an important role in the regulation of cyanobacterial growth (Paerl, 1996; Rashidan & Bird, 2001; Eiler et al., 2006). Shi et al. (2012) have reported distinct changes in the structure and composition of free-living and attached bacterial communities associated with cyanobacterial blooms. Daft & Stewart (1971) reported cyanolytic bacteria as a commonly found group in aquatic environments with a high primary productivity. This was further confirmed by the findings of Rashidan & Bird (2001) in which they observed an increase in the number of lytic *Cytophage* sp. during the bloom and their density reached to the maximum after one week of bloom decline. According to the observations made by Daft et al. (1973), the number of cyanolytic bacteria associated with cyanobacterial colonies was higher than that of the surrounding water column, which is an indicator of their cyanolytic activity. Another study carried out to identify the bacterial composition associated with cyanobacterial blooms in Swedish lakes revealed the presence of novel bacterial taxa that are characteristic for cyanobacterial blooms (Eiler & Bertilsson, 2004). Further, 16S rRNA gene heterogeneity analysis indicated the existence of different bacterial community compositions in different cyanobacterial blooms even under similar environmental conditions (Eiler & Bertilsson, 2004). Cai et al. (2014) have reported that bacterial communities associated with *Microcystis* blooms were complex and highly organized. Large bacterial aggregates were able to degrade complex molecular weight compounds whereas small aggregates were able to degrade simple compounds. As a result, bacterial communities associated with cyanobacterial blooms coordinate recycling of organic matter, nutrients, and trace elements within the bloom and indirectly maintain cyanobacterial bloom dynamics in the reservoir. Therefore, owing to their highly specific composition and functionality, bloom-associated bacterial communities are considered as promising agents for controlling cyanobacterial blooms. The first knowledge on the bacteria-mediated cyanobacterial cell lysis dated back to 1967 (Shilo, 1967). Since then, several bacterial strains have been isolated from different parts of the world. These cyanolytic bacteria play an important role in regulation, termination, or/and suppression of the growth of harmful and nuisance cyanobacterial blooms (Meyer et al., 2017). Most of the reported studies have mentioned that the majority of algicidal bacteria belong either to the phyla Bacteroidetes or Gammaproteobacteria (such as *Alteromonas*, *Pseudomonas*, and *Pseudoaltermonas*). Further, Alphaproteobacteria have also been reported with algicidal activity (Goecke et al., 2013). In addition, few gram-positive bacteria belong to the phylum Actinobacteria and the genus *Bacillus* (Firmicutes) have algicidal activity (Mayali & Azam, 2004; Zhou et al., 2014). Moreover, the findings of (Daft et al., 1975) and (Rashidan & Bird, 2001) elaborated that the bacteria-mediated cyanobacteria lysis process is species or genus-specific. However, such kind of specificity was not observed in some other lytic bacteria of a single genus, where they were able to

lyse cells of several boom-forming cyanobacteria (Daft et al., 1975).

Bacteria play an important role as a biological controlling agent over other microorganisms due to their survival ability during non-bloom conditions by using alternate food sources, non-dependent bacterial predation on unique attachment receptors, and less chance of experiencing mutations within the host (Rashidan & Bird, 2001). Therefore, many studies have been conducted to isolate and characterize individual bacterial strains and bacterial communities associated with cyanobacterial blooms. However, most of the studies were limited to the temperate region while very few studies have been conducted in the tropics. Further, many of the extensive studies have been focused on *Microcystis* sp. due to its cosmopolitan distribution and being the most dominant or co-dominant species in most of the reported blooms (Paerl et al., 2014; Mowe et al., 2015a). For an example, bacterial strain SDK2, *Ochrobactrum* sp. isolated from a eutrophic water body had the potential to inhibit the growth of *M. aeruginosa* via an extracellular substance. A consortium of bacteria consisting of *Rhizobium* sp. (MF185100), *Methylobacterium zatmanii* (MF185099), and *Sandaracinobactor sibiricus* (MF185098) was capable of inhibiting the growth of *Microcystis* by 95% (Pal et al., 2018). Actinomycete, *Streptomyces amritsarensis* HG-16 has shown a high algicidal activity against *M. aeruginosa* cells and a strong inhibitory effect on MC-LR synthesis by secreting an extracellular algicidal substance (Yu et al., 2019). However, these interesting findings may make the pavement for controlling *Microcystis* bloom in the natural environment through augmentative biocontrol strategies. In previous studies, probiotic bacteria have been employed as a biological controlling agent to eliminate cyanotoxins and cyanobacterial blooms. Verschuere et al. (2000) have reported a variety of inhibitory compounds namely, antibiotics, bacteriocins, siderophores, and lysosomes which are synthesized by probiotic bacteria against cyanobacterial blooms in aquaculture. However, some of these substances have positive effects on the growth of other unicellular algae (Verschuere et al., 2000) and therefore gained limited interest as a biological control agent.

Virus-mediated biological control

Viruses that utilize cyanobacteria as their host are known as "cyanophages". Cyanophages influence the cyanobacterial community structure negatively by altering cyanobacterial metabolism (Xia et al., 2013). Therefore, the dynamics of cyanophages affect the abundance and composition of cyanobacterial blooms in waterbodies. Most cyanophages are highly specific towards several filamentous cyanobacteria including *Anabaena*, *Lyngbya*, *Plectonema*, *Phormidium*, and *Pseudanabaena* (Safferman & Morris, 1964; Liu et al., 2008; Yeo & Gin, 2013; Zhang et al., 2020). Rapid generation time (Sigee et al., 1999), undergoing host resistance mutations (Padan & Shilo, 1973), high degree of host specificity are the characteristics that make cyanophages an effective biocontrolling agent against cyanobacteria (Sigee et al., 1999). However, difficulty in producing large quantities of active inoculum limits its application (Sigee et al., 1999). Many studies have been carried out to identify cyanobacteria lysing viruses from eutrophic water bodies all over the world. A study done by Phlips et al. (1990) have discovered cyanophages that can kill *Lyngbya birgei*, *Anabaena circinalis*, *A. flos-aquae*, and *M. aeruginosa* from the freshwater environments. Later, several other researchers have isolated cyanophages or phage-like particles from freshwaters and demonstrated their lytic activity against *M. aeruginosa* and filamentous cyanobacteria (Manage et al., 2001; Tucker & Pollard, 2005; Yoshida et al., 2006; Jiang et al., 2019). Those studies have shown that the effects of cyanophages on the cyanobacterial population were sometimes cyanobacterial population density-dependent (Manage et al., 2001). Interestingly, the findings of Yoshida et al. (2008) highlighted the impacts of seasonal dynamics of the cyanophage community on the abundance and shifts in microcystin-producing and non-microcystin-producing populations. It indicated that the cyanophage assemblage has the potential to infect only a small percentage of the *M. aeruginosa* population. A short-tailed cyanophage, Ma-LEP isolated from Lake Eire showed a negative effect on the growth and photosynthesis of *M. aeruginosa* (Jiang et al., 2019). In some occasions, isolation method and assay procedure have shown a significant effect on the lytic activity of cyanophages towards cyanobacteria such as *Anabaena circinalis* and *Anabaena cylindrica* isolated from a tropical reservoir. Further, factors including the physiological condition of the host, nutrient concentration, and presence of divalent ions, magnesium ion (Mg^{2+}) or calcium ion (Ca^{2+}) were shown to influence on the isolation of cyanophages (Yeo & Gin, 2013). Putative cyanophages encompass a variety of morphotypes. The majority of them were tailed-phages (Yang et al., 2020). The first filamentous cyanophage was found to be infected on a broad range of host taxa including *Anabaena*, *Microcystis*, and *Planktothrix* (Deng & Hayes, 2008). In addition to the particle morphology, cyanophages seemed to be genetically diverse. The

genotypic characterizations revealed a high diversity of *Microcystis* lysing viruses in natural water (Honjo et al., 2006; Deng & Hayes, 2008) and sediments (Kate et al., 2013).

Fungi-mediated biological control

Many of the cyanobacteria are prone to be attacked by fungal parasites. The majority of the fungal parasites belong to the Chytridiomycota that attack filamentous cyanobacteria including, *Anabaena*, *Aphanizomenon*, *Cylindrospermopsis*, *Lyngbya*, and *Oscillatoria* (Kagami et al., 2007). They are involved in bloom termination by attacking cyanobacterial filaments (Sime-Ngando, 2012). Only a limited number of studies have been carried out to investigate the algicidal activity of non-chytrid fungi. Their antagonistic activity can be either direct or indirect. Fungi that directly attack cyanobacteria cause cell lysis or inhibition of growth through the secretion of mucus membrane (Jia et al., 2010a) while indirectly attack through the secretion of diffusible extracellular substances (Nakagiri & Ito, 1997; Jenkins et al., 1998). A white-rot fungus, *Phanerochaete chrysosporium* has shown its potential to attack algae directly by damaging cell membranes followed by cell death (Zeng et al., 2015). Another white-rot fungus, *Lopharia spadicea* has been reported to inhibit the growth of *Microcystis* (Wang et al., 2010b). *Trichaptum abietinum* which is also a white-rot fungus was able to inhibit the growth of four cyanobacterial species including three species of *Microcystis* and *Oocystis borgei* (Jia et al., 2010b). Further, the algicidal mechanism of *Trichaptum abietinum* was revealed to be a direct attack of algal cells by fungal mycelia through the secretion of mucous membrane (Jia et al., 2010a). Moreover, Jia et al. (2012a) reported the ability of this species to degrade MC-LR secreted by *M. aeruginosa* PCC7806. Thus, simultaneous effects on cyanobacterial cell lysis and degradation of MC-LR of the fungal strain *Trichaptum abietinum* are important in effective cyanobacterial bloom control. Further both *Trichaptum abietinum* and *Lopharia spadicea* were able to decrease the biomass of cyanobacterial bloom (Jia et al., 2012b). Mohamed et al. (2014) found that *Trichoderma citrinoviride* exhibited a species-specific growth inhibitory effect on *M. aeruginosa* and more importantly, it completely degraded Microcystins. *Emericellopsis salmosynnemata* and *Acremonium kiliense* have shown their potential to lyse *Anabaena flos-aqua* through releasing antibiotics β-lactam and cephalosporin (Redhead & Wright, 1980).

Other organisms-mediated biological control

In addition to viruses, bacteria, and fungi other organisms have also been reported to exhibit direct or indirect algicidal activities. Van Wichelen et al. (2016) reported the ability of several mixed trophic (*Ochromonas*, *Poterioochromonas*) and heterotrophic flagellates (*Monas*, *Paraphysomonas*, *Polytomella*, *Collodictyon triciliatum*, and *Diphylleia rotans*) to graze *Microcystis* and other nuisance algal blooms. The grazing effect and growth rates of flagellates when feeding on *Microcystis* cells have been investigated in previous studies (Kim et al., 2006; Baeka et al., 2009). The flagellate *Diphylleia rotans* has exhibited an active growth when fed on *M. aeruginosa*, but not on diatoms, *Cyclotella meneghiniana*, and *Stephanodiscus hantzschii*. Thus, the results infer microcystin dependence for the growth of *D. rotans* (Kim et al., 2006). A similar observation has also been obtained by Baeka et al. (2009) for the active population growth of *Ochromonas* sp. regardless of the toxicity of prey types. As reviewed by Van Wichelen et al. (2016), different *Microcystis*-grazing flagellates have exhibited similar patterns of ingestion and growth rates when feeding on *Microcystis* cells. Different abiotic factors such as temperature, nutrients, pH, and phase of the bloom development affect on grazing activity of flagellates (Kim et al., 2006; Yan et al., 2009; Zhang et al., 2009). For an example, the flagellate, *Diphylleia rotans* has shown substantial grazing pressure on *M. aeruginosa* at the beginning phase of their bloom. Besides to the abiotic factors, the colony morphology of different cyanobacteria also influenced to the grazing potential of flagellates. The flagellate *Ochromonas* sp. has induced colony formation of *M. aeruginosa* by deterring flagellate grazing (Yang et al., 2006). In addition, only a few grazers, *Poterioochromonas*, *Ochromonas* sp., *Diphylleia rotans* have been identified with the capability of degrading MCs and reducing the toxicity of MCs while feeding on *Microcystis* (Ou et al., 2005; Kim et al., 2006; Baeka et al., 2009; Mohamed & Al-Shehri, 2013). Haney (1987) reported that the susceptibility of colonial cyanobacteria to zooplanktons compared to smaller phytoplanktons highlighting an important trophic link in tropical lakes.

In addition, aquatic macrophytes directly inhibit the growth of cyanobacteria by the competition for acquiring light, nutrients, and space (Qiu et al., 2001; Wang et al., 2009) and indirectly inhibit by releasing allelochemicals (Nakai et al., 2000).

Potential mechanisms involved in biological control of cyanobacteria

Biocontrol agents either directly or indirectly lyse cyanobacterial cells or inhibit their growth (Mayali & Azam, 2004; Gumbo et al., 2008). Cell lysis that takes place due to the physical contact between lytic organisms and targeted cyanobacterial species is referred to as "direct attack" (Daft & Stewart, 1971; Rashidan & Bird, 2001). Excretion of extracellular substances responsible for the cell lysis of cyanobacteria without any physical contact is known as "indirect attack" (Imamura et al., 2000; Kodani et al., 2002). Thus, extracellular substances interfere with normal metabolism and impede the growth and reproduction of cyanobacterial cells (Zhou et al., 2016). Some cyanolytic bacteria exhibit both direct and indirect modes of attack. *Bacillus cereus* CZBC1 directly lyse cells of *Oscillatoria chlorina* and *O. tenuis* and indirectly lyse *O. planctonica* (Hu et al., 2019). According to the existing literature, it is clear that studies have mainly focused on understanding morphological and physiological mechanisms involved in cyanobacterial cell lysis (Figure 1). Therefore, less attention has been paid to understanding the genetics of interactions between cyanobacteria and biocontrol agents. It is important to identify functional genes involved in the interaction and their pattern of expression during the interaction. Further, understanding of the antagonistic behaviors of biocontrol agents during the suppression and responses exhibited by cyanobacteria and biocontrol agents under stress conditions is essential.

Direct attack of cyanobacterial cells

Biocontrol agents directly attack cyanobacterial cells through the establishment of cell-to-cell contact and penetration of cyanobacterial cell walls in order to reach cell contents for their nutritional and other requirements. This type of direct mode of attack is found in most viruses, certain bacteria, fungi, and flagellates (Table 1) (Manage et al., 2000; Jia et al., 2010a; Kim et al., 2006; Zeng et al., 2015). In addition, entrapment through the formation of aggregates has also been described for certain interactions (Burnham et al., 1981). However, the genetics of the direct attack of cyanobacterial cells by heterotrophic bacteria has been rarely studied.

A recent transcriptome profiles of algicidal bacteria, *Stenotrophomonas rhizophila*, *Pseudomonas putida*, *Acinetobacter beijerinckii* and *Delftia* sp. and cyanobacteria, *M. aeruginosa*, and *A. flos-aquae* identified differentially expressed genes in 24 h co-cultures (Osman et al., 2017). This study has been carried out under the predator-prey ratio of 1:1. Therefore, genes may have been differentially expressed due to the induced stress by both predator and prey. The most highly up-regulated genes in bacteria were related to cell motility, signal transduction, and putative lytic activity. Moreover, the only significant up-regulated lytic gene was L,D-transpeptidase in *Stenotrophomonas rhizophila*. In *M. aeruginosa* co-cultures, significant down-regulation of genes involved in photosynthesis has also been identified. Up-regulation of lytic genes and lytic activity in the biocontrol agent and down-regulation of photosynthesis which is a major physiological process in cyanobacterial counterparts provides evidences for an active antagonistic mechanism. Further, the study also mentioned an energy metabolic pathway shift in bacterial isolates due to nutrient-related stress. In addition, microscopic observations also provided evidence for the physical attachment of bacteria and cyanobacteria. Thus, this comprehensive study by Osman et al., (2017) provides a better understanding of the complex cell-to-cell interactions between cyanobacteria and their heterotrophic bacteria.

Indirect attack on cyanobacterial cells

Secretion of extracellular substances seems to be the main strategy of indirect attack in most predatory organisms including, bacteria, fungi, and other eukaryotes to kill cyanobacteria as a source of food or to reduce the competition for their survival. To date, many algicidal substances released by bacteria with the potential to decompose cyanobacterial cells have been isolated and identified. Most of the identified compounds are enzymes such as agarase, amino-peptidase, alkaline phosphatase, lipase, glucosaminidase, proteins, enzymes, protease, lipid peroxidases, antibiotics, biosurfactants, and bacillamides (Meyer et al., 2017). These algicidal substances can lyse or kill cyanobacteria due to membrane destruction through inhibition of the PSII photosystem and by the activation of antioxidant defense mechanisms (Harel et al., 2013; Shao et al., 2014). Different types of mechanisms responsible for cyanobacteria cell lysis through an indirect attack have been described in Table 02. As a response to the indirect attack, cyanobacteria activate a cascaded of reactions such as increasing enzyme activities (catalase, peroxidase), membrane lipid peroxidation, and increasing production and release of toxins by changing their physiology (Zhang et al., 2016; Zhou et al., 2016).

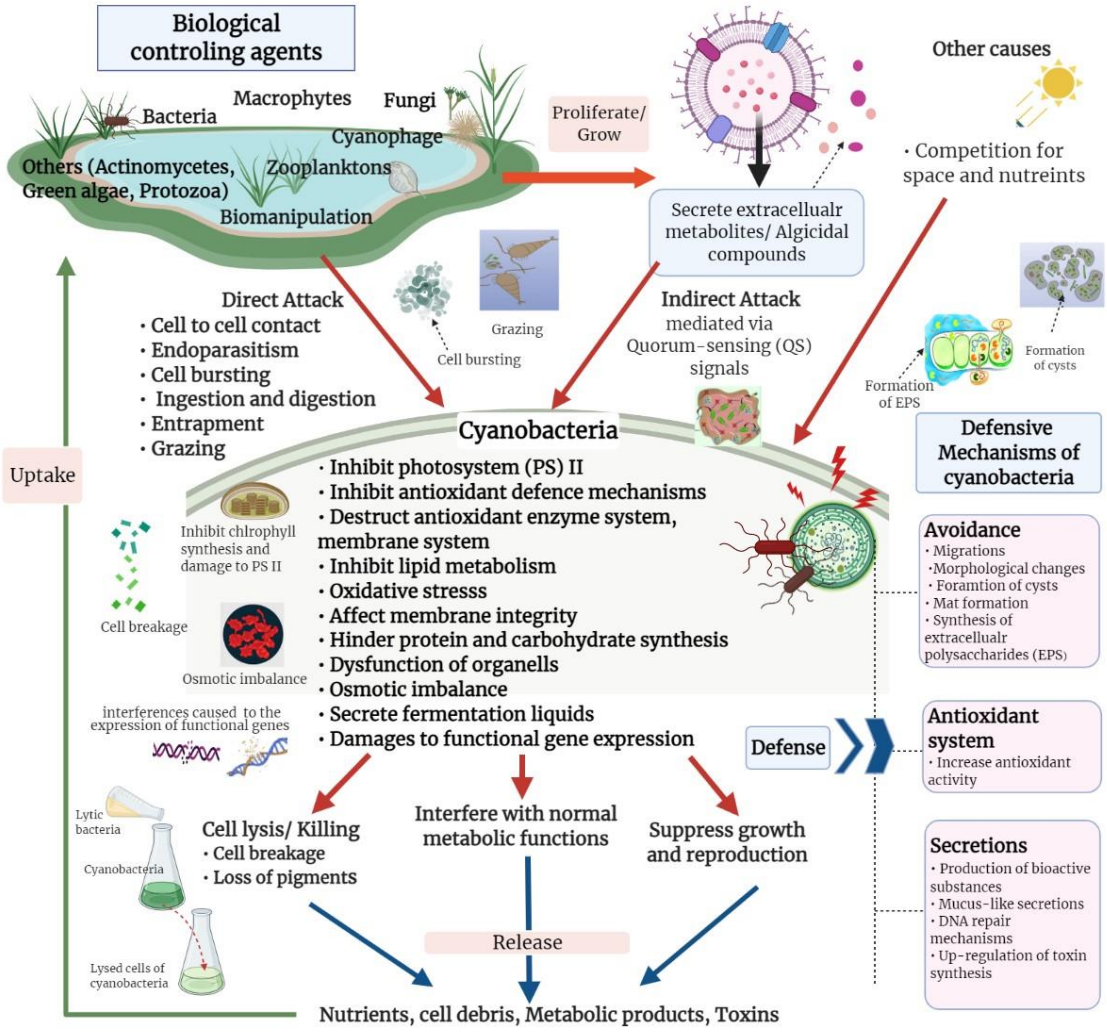

Figure 1: Conceptual diagram representing the mechanisms involved in cell lysis and suppression of cyanobacteria and adoption of defensive mechanisms against the damage in cyanobacteria

Table 1: Selected references on cyanolytic bacteria which cause cyanobacterial cell lysis via direct attack and their underlying mechanisms of cell lysis

Cyanolytic bacteria	Host cyanobacteria	Mechanisms of cell lysis	Reference
Myxobacter CP 1-4	More than 40 strains of cyanobacteria	Cell to cell contact	(Daft & Stewart, 1971)
Myxococcus xanthus PCO2	*Phormidium luridum*	Entrapment	(Burnham et al., 1981)
Bdellovibrio -like bacteria	*Microcystis aeruginosa*	Endo-parasitism (Breaking down cell structures after penetrating to the host cell)	(Caiola & Pellegrini, 1984)

Alcaligenes denitrificans	*M. aeruginosa*	Cell to cell contact by inhibiting the metabolic functions	(Manage et al., 2000)
Cytophaga	*Microcystis*	Cell to cell contact	(Rashidan & Bird, 2001)
Bacillus cereus	*Aphanizomenon flos-aquae*	Cell to cell contact by secreting slime extrusions	(Shunyu et al., 2006)
Saprospira sp. (Bacteroidetes)	*Anabaena*	Cell to cell contact (bacteria form bundle-like group structures)	(Shi et al., 2006)
Alcaligenes denitrificans	*M. aeruginosa*	Cell to cell contact at the individual level	(Manage & Premetilake, 2011)
Alcaligenes xyosoxydans			
Flavobacterium marinotypicum			
Streptomyces sp. L74	*A. flos-aquae*	Cell to cell contact	(Luo et al., 2013)
Bacterium DCJ-2	*Plectonema boryanum*	Cell to cell contact	(Liu et al., 2015)
Chryseobacterium species	*M. aeruginosa*	Cell to cell contact	(Zhang et al., 2019)

Further, Zhang et al. (2015) have reported that damages caused by the algicidal compound, 2′-deoxyadenosine on unicellular cyanobacterial cells and filamentous forms of cyanobacteria were distinct from each other. However, less/no damage has been observed on the morphology of the heterocysts of the filamentous forms. Therefore, the morphology of prey species may influence the lytic activity of the predatory bacteria. Moreover, the findings of Alamri & Mohamed (2013) highlighted selective inhibition of the growth of harmful cyanobacteria by some algicidal compounds released by predatory bacteria while there was no negative impact on other beneficial species of green algae. Therefore, utilization of such types of predatory bacteria for controlling cyanobacterial blooms would be more ecologically feasible. However, all cyanolytic bacterial species are not capable of degrading cyanotoxins and vice versa. Only a few strains of bacteria have been isolated with a potential to lyse cyanobacterial cells and degrade cyanotoxins. One example is *P. aeruginosa* PA14 which showed a fast cell lysis of *M. aeruginosa* and a slow degradation of MCs (Kang et al., 2012). Simultaneous application of *Microcystis* lytic bacteria and MCs degrading bacteria have been tested successfully in the laboratory to eliminate both *Microcystis* cells and their toxins (Lee et al., 2018).

As reviewed above, heterotrophic bacteria in aquatic environments have the potential to control or suppress cyanobacterial bloom-forming species either by direct or indirect attack. Lytic bacteria disrupt cellular structure through the disruption of the cyanobacterial cell wall, membranes, and thylakoids, interfere with physiological processes such as photosynthesis, antioxidant system, enzymatic activities, production of reactive oxygen species (ROS), and expression of genes related to cell division, photosynthesis, maintaining the integrity of membranes and synthesis of cyanotoxins (Wu et al., 2014; Demeke, 2016; Hu et al., 2016; Xuan et al., 2017; Liu et al., 2019; Yu et al., 2019). The majority of previous work provides evidence for an indirect mode of attack by secreting a wide range of metabolites while the direct attack of cyanobacteria has been less described.

Cyanobacterial defensive mechanisms during the lysis process

Similar to other organisms living in the environment, cyanobacteria also adopt defensive mechanisms to ensure their survival and to maintain population structure in the natural environment (Van Donk et al., 2011; Anderson et al., 2012). Cyanobacteria adopt mechanisms to survive under adverse environmental conditions by changing cell morphology, formation of colonies, spines, and thick cell walls migration, formation of cysts, and production of bioactive substances (eg: anti-microbial substances) (Van Donk et al., 2011). During active predation, colonies of *Microcystis* transform into high morphological variability and enlargement of

Table 2: Selected references on cyanolytic bacteria which attack cyanobacteria via an indirect mode and their underlying mechanism of cell lysis

Cyanolytic bacteria	Host cyanobacteria	Mechanisms of cell lysis	Reference
Streptomyces neyagawaensis	Not mentioned	Secretion of an extracellular algicidal substance after the close attachment between host and bacteria	(Choi et al., 2005)
Pseudomonas putida HYK0203-SK02	*Stephanodiscus hantzschii*	Secretion of an extracellular substance Suppress the growth of the host in all growth phases	(Kang et al., 2005)
Bacillus fusiformis (B5)	*Microcystis aeruginosa*, Other: *Chlorella* and *Scenedesmus*	Secretion of heat-stable (121 °C) extracellular substance	(Mu et al., 2007)
Pseudomonas putida	*M. aeruginosa* and wide range of phytoplankton	Secretion of an extracellular substance	(Zhang et al., 2011)
Exiguobacterium A27	Not mentioned	Secretion of many algicidal compounds which were unknown	(Tian et al., 2012)
Bacillus flexus EMGA5	Selective inhibition of the growth of harmful cyanobacteria, no impact to beneficial green algae	Secretion of an algicidal compound, b-carbolines (harmine and norharmane)	(Alamri & Mohamed, 2013)
Bacterial strain, TL	*M. aeruginosa*	Secretion of extracellular substances (non-proteins)	(Liu et al., 2013)
Streptomyces sp. L74	*M. aeruginosa*, *O. animalis*, and *Aph. flos-aquae*	Secreting an algicidal compound (triterpenoid saponin)	(Luo et al., 2013)
Serratia marcescens LTH-2	*M. aeruginosa*	Secretion of an extracellular substance, Prodigiosin ($C_{20}H_{25}N_3O$)	(Fei et al., 2013)
Brevibacillus laterosporus	*Oscillatoria*	Secretion of an extracellular substance (require high concentration of cell filtrate)	(Jia et al., 2014)
Shewanella sp. Lzh-2	*M. aeruginosa* 9110	Secretion of extracellular enzymes, S-2A (hexahydropyrrolo[1,2-a]pyrazine-1,4-dione) and S-2B (2, 3-indolinedione (isatin)	(Li et al., 2014)
Bacillus amyloliquefaciens FZB42	*M. aeruginosa*	Secretion of an algicidal compound, Bacilysin Suppress the growth and metabolism of host	(Wu et al., 2014)
Bacillus sp. Lzh-5	*M. aeruginosa* 9110	Secretion of two algicidal compounds, S-5A (cyclo[Gly-Pro]) and S-5B (cyclo[ProVal])	(Liu et al., 2015)
Streptomyces jiujiangensis JXJ 0074T	*M. aeruginosa* FACHB-905 *M. viridis* FACHB-1284	Secretion of an algicidal compound, 2′ deoxyadenosine	(Zhang et al., 2015)

	Nostoc punctiforme FACHB-252 *O. tennuis FACHB-247*		
Chryseobacterium sp.	*M. aeruginosa*	Secretion of extracellular substances	(Hong et al., 2016)
Achromobacter sp.	*M. aeruginosa*	Secretion of an algicidal compound Alter the morphology and physiology	(Wang et al., 2010a)
Streptomyces eurocidicus JXJ-0089	*Microcystis*	Secretion of two algicidal compounds, tryptamine, and tryptoline Alter the morphology and physiology	(Zhang et al., 2016)
Pseudomonas aeruginosa	*Microcystis aeruginosa*	Secretion of fermentation liquid Suppress the metabolism of the host	(Zhou et al., 2016)
Bacillus sp. AF-1	*Microcystis aeruginosa*	Secretion of an algicidal compound Alter the morphology and physiology of the host	(Xuan et al., 2017)
Bacillus cereus	*Oscillatoria chlorina*	Cell to cell contact	(Hu et al., 2019)
	Oscillatoria tenuis		
	Oscillatoria planctonica	Secretion of an extracellular substance	

colonies and increment of aggregation against predatory bacteria (Xu et al., 2012) and flagellates (Yang et al., 2009a; Yang et al., 2009b) probably to reduce predation risk. The presence of antagonists and accumulation of extracellular polysaccharides in the surrounding induce enlargement of colony size of *Microcystis* (Yang et al., 2009a; Yang et al., 2009b). In contrast, some predatory bacteria can reduce the colony size of *Microcystis* by altering their defensive mechanisms (Gumbo et al., 2010; Wang et al., 2013). Apart from morphological variability, a significant increase in the enzyme activities such as catalase (CAT) and peroxidase (POD) was observed in the cyanobacterial cells as defensive mechanisms against algicidal bacteria (Shao et al., 2012). For example, *Synechococcus* sp. BN60 showed weak algicidal activity (48.6%) against the algicidal bacterium, *Brevundimonas* J4 due to the inducible production of an antimicrobial-like compound when compared to the much stronger algicidal activity of J4, (91.8%) when co-cultured with *M. aeruginosa* 9110 which had no chemical defence against *Brevundimonas* J4 (Lin et al., 2014). Another study done by Yi et al., (2015) have identified a self-defensive mechanism of *M. aeruginosa* by secreting a mucus-like substance against an algicidal *Pedobacter* bacterial strain.

Regulations of algicidal interactions

Spatial and temporal changes in the aquatic environment may hinder or stimulate the algicidal activity of bacteria. Therefore, proper regulation of algicidal activity is required for bacteria to maintain an efficient algicidal activity throughout the process (Meyer et al., 2017). Thus, some cyanolytic bacteria find their host algae along a chemical gradient known as chemotaxis. This allows bacteria to move constantly and find their prey (Smriga et al., 2016). Quorum-sensing (QS) is a cell density-dependant mechanism that was earlier thought to play an important role in regulation of algicidal activity. However, only a few studies were able to prove the relation between algicidal activity and QS in gram-negative (Guo et al., 2016) and positive bacteria (Jiang et al., 2014; Wu et al., 2014).

In the QS mechanism, algicidal activity is mediated by key definite signalling molecules. In the algicidal gram-positive bacterium, *Bacillus* sp. strain S51107,

the production of high-molecular-weight algicidal substances against *M. aeruginosa* was regulated primarily by the NprR-NprX QS mechanism. It secretes NprX, a mature form of signalling peptide that specifically interacts with NprP forming NprR-NprX complex to activate the gene expressions responsible for various metabolic functions (Wu et al., 2017). Guo et al., (2016) have reported that N-butyryl-homoserine lactone (C4-HSL) mediated QS is involved in the production of two algicidal compounds by gram-negative *Aeromonas* sp. strain GLY-2107. Further, it was mentioned that the N-butyryl-homoserine lactone (C4-HSL) mediated QS mechanism positively regulates the synthesis of the algicidal compound 3-methylindole and negatively regulates cyclo(Gly-Phe) (Guo et al., 2016). In contrast, the production of two low-molecular-weight algicidal compounds, indole-3-carboxaldehyde and cyclo-(Pro-Phe) were not regulated by the QS mechanism (Wu et al., 2014). These contrasting findings highlight the presence of diverse QS-regulated algicidal mechanisms involved in bacteria. Therefore, manipulation of QS-mediated mechanisms will become a novel cyanobacterial bloom control strategy. However, further studies are necessary to fully understand the mode of regulation in QS.

Application potential, challenges and prospects of biological controlling of cyanobacterial blooms

Although laboratory experiments have demonstrated a high potential for biological control of cyanobacterial blooms, there are certain constraints that limit its environmental application. Major constraints are poor antagonistic capabilities of indigenous microbial communities at field conditions, spatial and temporal dynamics in cyanobacterial blooms, difficulties in scaling up from laboratory to field, and absence of benchmark values for identifying the most suitable/efficient controlling agent/s.

The efficacy of bloom lysis, suppression, or termination can be improved by using microorganisms having different metabolic and functional capabilities. Combinations of several strains with different cyanolytic and inhibitory modes of action would provide a selective advantage over single strains. Therefore, isolation and screening should focus on strains with efficient catabolic genes and enzymes, with high resilience to external stresses, and strains that are not human pathogens and not antibiotic-resistant. Lack of information on the population dynamics of the microbiome in natural water bodies and weak physiological control of catabolic gene expression in microorganisms under stress conditions have hampered the transition of microorganisms from the laboratory to the field environment. In many of the laboratory experiments, axenic cultures of cyanobacteria have been used to screen out antagonistic behaviors of biocontrol agents. Therefore, for field application, high competency in effective control of cyanobacterial blooms in the presence of a mixed population of aquatic life is vitally important. Hence, the selection of ideal consortia of antagonists that could successfully colonize and tolerate local stress conditions over other organisms will be more advantageous. However, it is important to understand that any selection may not be universal because of the highly dynamic nature of aquatic environments.

Application of algicidal compounds isolated from microbial strains also needs careful evaluation before being applied to the field. Biodegradability of algicidal compounds which were either isolated from nature or through chemical synthesis is an important factor that needs to be considered. Chemically synthesized algicides may additionally cause secondary pollution in aquatic ecosystems (Meepagala et al., 2005). Even though natural algicidal substances are biodegradable, rapid degradation may not provide an ideal condition for efficient control of cyanobacterial blooms because complete lysis may require certain concentration and time. Zhang et al. (2015) have reported complete degradation of an algicide, 2′- deoxyadenosine at 15 µg/mL concentration after 5 days of inoculation and had provided ample time for the lysis of cyanobacteria. Further, they have observed a continuation of cell lysis even after complete degradation of the algicidal compound due to irreversible cell damages caused by the compound. The effectiveness of most of the algicidal compounds identified to date has not been evaluated for the elimination of bloom biomass *in-vivo* and their impacts on non-targeted organisms. Further, forecasting the cyanobacterial bloom dynamics after removal of the targeted cyanobacteria would be essential to understand future events that could have been taken place. As far as we know, no study has yet been forecasted on the dynamics of non-targeted phytoplanktonic taxa after removal of targeted cyanobacteria/algae.

Apart from environmental concerns, cost-effectiveness of any biological method needs to be considered prior to the environmental application.

Conclusion

Many application potentials and challenges have been identified in the concept of biological control of cyanobacterial blooms. Although research on controlling cyanobacterial blooms with biocontrol agents have been initiated a few decades ago, present understanding of the mechanisms involved in cyanobacterial cell lysis, gene regulation, and the impact of environmental factors in bloom controlling potential are still in their infancy because of the complexity of aquatic ecosystems.Moreover, studies describing cyanobacterial bloom inhibition/cell lysis had not been conducted under similar experimental conditions and thus could not be compared with each other to select the most appropriate strain/s. At the same time, the feasibility of bringing laboratory-based systems to the natural environment remains the biggest challenge. Because a single species of cyanobacteria may interact either synergistically or antagonistically with thousands of other organisms inhabiting the same environment and vice versa. Therefore, we highlight that a much better understanding of the spatial and temporal variations in bloom-forming species, their antagonists, and antagonistic interactions in a particular aquatic ecosystem are essential for implementing effective bloom management programs. Therefore, researchers should step out from the laboratory to the field to elucidate the application potential of any biocontrol agent in nature. Further, expanding research focus towards novel strategies such as QS-mediated mechanisms, gene regulation, and manipulation of enzyme biosynthetic pathways may broaden application potential and facilitate overcoming challenges.

With the expansion of intensive agriculture and changes in global climate, it is expected that the present scenario of bloom proliferation and subsequent toxin release will be intensified in the near future. Therefore, improvements in water treatment technologies to minimize nutrient loading to the water bodies and efficient management of cyanobacterial blooms and their consequences such as deterioration of water quality and contamination with cyanotoxins should be minimized for maintaining social well-being and environmental sustainability.

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