Can Algicidal Bacteria be the Solution to Successfully Manage Freshwater Algal Blooms?

Wendy Wang[1] and Alirio Melendez Romero[2]*

Department of Research Project Qualifications, Shenzhen College of International Education, 518040, Shenzhen, China

***Corresponding author**

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ABSTRACT

Eutrophication is a phenomenon that can occur in any water body, caused by an excessive input of nutrients, particularly nitrogen and phosphorus. This causes the rapid growth of primary producers (usually an algae bloom), which depletes other nutrients in water and can cause disruption of the local ecosystem. The algal bloom, pollute drinking water, wildlife water reservoirs, and collapse ecosystems. Eutrophication has increased in recent years due to anthropogenic climate change and increased nutrient loading from agriculture and industrial wastewater. In freshwater, the most common bacterium causing algal blooms are Cyanobacteria, such as *Microcystis*. Current management strategies have focused on reducing phosphorus, however in eutrophic freshwater, harmful algal blooms are mostly the result of *Microcystis*, a genus of cyanobacteria that is unable to fix its own nitrogen. Thus, managing aquatic nitrogen will become crucial in eutrophic freshwater bodies. A variety of physical, chemical, and biological methods have been proposed and implemented to reduce algal blooms at all stages, however each method has its limitations. A particularly novel line of management is microbial management, taking advantage of the high specificity and lower cost of microbial mediation. This paper review the current understanding of eutrophication-related algal blooms and their effects, discuss current management techniques for freshwater algal blooms, and evaluate the validity of using algicidal bacteria to combat *Microcystis* algal blooms.

INTRODUCTION

For many years it has been known that excess phosphate input into freshwater lakes and reservoirs causes explosive algal growth, leading to harmful algal blooms that can pollute drinking water, poison local wildlife through bioaccumulating up the food chain, and disrupt local ecosystems (Denchak and Sturm, 2019). Consequences of leaving algal blooms unchecked include long term loss of biodiversity in the area, economic losses in the fishing industry (leading to food insecurity), and losses in tourism-related industries (Paerl et al, 2016).

Cultural eutrophication is eutrophication accelerated by human nutrient inputs such as nitrogen (in the form of nitrate) and phosphorus (in the form of phosphate), both commonly used in NPK fertilizer. These may come from improperly managed wastewater from urban or agricultural land, run-off from fertilized fields, or from rivers and estuaries leading into a stagnant body of water. Eutrophication can occur in both freshwater and marine environments, however the composition of the resulting algal bloom is different, with freshwater algal blooms being mainly caused by Cyanobacteria, while in marine algal blooms dinoflagellates and diatoms make up a significant proportion, depending on environmental conditions like wind and water temperature. In both freshwater and marine environments, the excess nutrient input causes the rapid growth of primary producers, which then take up dissolved oxygen as they grow and decompose, creating a hypoxic zone. This results in the death of other aerobic organisms, creating a “dead zone”. One example is the dead zone in the Gulf of Mexico, which forms every summer and ranges from less than 5,000 to over 20,000 km2 in size (Bowman, 2023). This dead zone grows off the 100 million kilograms of nitrogen fertilizer used in the Mississippi River watershed to grow (mainly) corn (Reed, 2007). Corn is a “leaky” crop, which absorbs less nitrogen fertilizer per acre, thus requiring farmers to add an excess of fertilizer, which is then carried into aquatic ecosystems through surface run-off. The National Oceanic and Atmospheric Administration (NOAA) estimates the cost of the Gulf of Mexico hypoxic zone to be 82 million USD annually, stemming from losses in the seafood and tourism industries (NCCOS, 2011).

Algal blooms can be a natural occurrence (NOAA, 2016). However, many water bodies now have harmful algal blooms (HABs) far beyond the magnitude of regular algal blooms. HABs make up around 1% of all algal blooms, but even normal algal blooms can create hazards, for example creating hypoxia when algal cells die and decompose. Recurring harmful algal blooms usually have an increased frequency, duration, and intensity, and can contaminate drinking water, causing losses in the fishing and tourism industries as well as being a public health concern (Denchak and Sturm, 2019). For example, in Lake Erie, harmful algal blooms now recur around the summer months, taking advantage of the warm weather and plentiful sunlight. The *Microcystis* blooms in 2011 and 2014 were estimated to cost 71 and 65 million USD respectively (Paerl et al, 2016). One factor is the 11,000 tons of phosphorus (mostly artificial fertilizer from nearby agriculture) loaded into Lake Erie, but another is the human-caused internal loading. The thermal stratification of large lakes such as Lake Erie allows the hypolimnion (lowest layer) to become hypoxic, typically in late summer. In hypoxic conditions, excess phosphorus (now stored in sediment) starts to leach out, and this results in internal loading of phosphorous (Orihel et al, 2017).

Due to global warming, the threat of algal blooms is only predicted to grow. While phosphorus is an important limiting factor in algal growth, the artificial input of nitrogen dwarves that of phosphorus, and increasingly, algal blooms are dominated by species (such as those of *Microcystis*) that are unable to meet their nitrogen needs from nitrogen fixation (Harke et al, 2019). Therefore, the primary objectives of the present study are to discuss the current understanding of eutrophication and microbial communities in water bodies, current management strategies, and the potential of using nitrate-reducing bacteria to control freshwater algal blooms.

METHODOLOGY

This study seeks to analyse and synthesise current knowledge on freshwater algal blooms in general and specifically on those by Microcystis in eutrophic conditions and examine the potential application of algicidal bacteria as a sustainable management option. The approach is to carry out a comprehensive and systematic analysis of public databases and international organisations to identify, source, and critically review relevant research literature.

Search Strategy

A thorough search across several scientific databases including PubMed, and Google Scholar, to identify and retrieve relevant peer-reviewed research articles, review papers, and authoritative reports. The search used various combinations of keywords and phrases-relevant to the study, which include but are not limited to: "eutrophication" ; "freshwater algal blooms"; "harmful algal blooms (HABs)"; "Microcystis"; "cyanobacteria"; "algal bloom management strategies"; "nutrient reduction;" "phosphorus control; nitrogen management; "algicidal bacteria"; "bacterial algicides"; "anammox;" "quorum sensing"; "microcystins"; and "bioremediation of algal blooms." Identified publications including original articles, review articles and relevant publications from government or international organisations, were reviewed to capture the most relevant studies.

Inclusion and exclusion criteria

Studies were included in the following areas:

1. Causes, ecological impacts, and consequences of freshwater eutrophication and algal blooms.

2. Specific characteristics, frequency, and toxicity of Microcystis in freshwater systems.
3. Descriptions and reviews of existing and proposed physical, chemical, and biological measures in managing algal blooms and nutrients inputs.
4. Research on the mechanisms and efficacy of algicidal bacteria and other microbial interventions facing Microcystis and other cyanobacteria, specificity, and environmental implications.
5. Nitrogen and phosphorus in the perspective of dynamics in algal bloom and the related management obstacles.
6. Grey literature (e.g., reports of government agencies like NOAA, EPA) was also taken into consideration for contextual information, economic impact data, and policy relevance in cases where peer-reviewed studies were limited.

Excluded were studies that dealt exclusively with marine algal blooms, or those not clearly relevant to the management of Microcystis blooms in freshwater ecosystems.

Data Extraction and Synthesis

Systematic extraction from the whole cohort of literature selected with regard to:

1. Drivers of eutrophication including nutrient loading and climate change impacts.
2. Ecological consequences of algal blooms, hypoxia, and disruption of ecosystems.
3. Characteristics of Microcystis blooms plus microcystin production.
4. Operational principles, advantages, disadvantages of different management strategies, and present-day applicability of all management approaches of algal blooms (physical, chemical, biological).
5. Specific types of bacteria possessing anti-cyanobacterial capabilities, their modes of action (e.g. direct attack, indirect chemical attack, quorum sensing disruption, nutrient cycling by means of anammox), and potential use in bloom control and toxin degradation.

The extracted data underwent critical evaluation and synthesis to identify common themes and emerging trends or gaps in knowledge. Specific comparative evaluations on the effectiveness, environmental specificity, and cost-efficiency of such approaches, particularly in terms of providing unique benefits and challenges of microbial-based solutions, were, however, emphasised.

Structure of the study

In summary, the first part of this study deals with basics of eutrophication and its ecological impacts. Thereafter, management technologies already available are reviewed according to their mode of action, nutrient input reduction or direct disruption of the bloom. Following next is a section that specifically elaborates on algicidal bacteria, with Microcystis as the major target, the character of microcystins, and the different ways through which bacteria could mitigate algal blooms. Finally, it ends up with conclusions summing up findings, as well as future prospects and challenges that might accompany the use of algicidal bacteria in freshwater algal bloom management.

Thermal stratification of water bodies and microbial community

In large, deep-water bodies, there is varying thermal stratification, separating the lake into distinct layers by temperature. The topmost, warmest layer is the epilimnion, and the lowest layer is the hypolimnion, with the metalimnion in between. Algal blooms can bloom even when nutrient loading is low by drawing on refluxed nutrients from the hypolimnion (Stauffer and Lee, 1973). In addition, this thermal stratification allows the hypolimnion to become hypoxic more easily and is a cause for the internal loading of phosphorus (Orihel et al, 2017).

The microbial community of a lake's epilimnion is dependent on the trophic state. For mesotrophic to oligotrophic lakes, there is a more diverse microbial community, while in eutrophic lakes *Microcystis* is usually the most abundant. In eutrophic lakes, the dominant taxa display more potential genes for aerobic carbon fixation, methanogenesis, and fermentation, while displaying less genes for nitrogen fixation, aerobic respiration, and CO oxidation. This shows that the heavy nitrogen input is responsible for the dominance of cyanobacteria unable to meet their own nitrogen fixation needs (Shen et al, 2019).

How has anthropogenic climate change indirectly increased eutrophication?

The influence of climate can affect which minerals are most responsible for eutrophication, and thus which management strategies will be most effective. Algal blooms can block out sunlight for bottom-dwelling primary producers, reducing their populations and increasing their own, especially in calm waters. Many artificial reservoirs created for hydroelectric power or irrigation are thus most susceptible to algal blooms, such as the Hartbeespoort reservoir in South Africa (Atta et al, 2020). The recent increase in intensity and duration of algal blooms can also be attributed to climate change. Global warming and the consequent warming of bodies of water increases the growth rate of algae, allowing them to rapidly proliferate and form blooms (Denchak and Sturm, 2019). Furthermore, warm water is unable to hold as much dissolved oxygen, meaning that aquatic ecosystems are more at risk of becoming hypoxic. More extreme weather, in the form of droughts and extreme storms, can increase soil erosion and surface run-off, carrying the nutrient-rich topsoil horizon into bodies of water, creating an excess of nutrients. In addition, the increase in atmospheric carbon dioxide increases the rate at which algae grow and die.

Problems with current management strategies

Most management strategies have focused on reducing phosphates. This is due to the ability of certain algae (known as nitrifying bacteria) to fix nitrogen into nitrates, and past research that has previously identified phosphate as being the main cause of algal blooms, at least in temperate freshwater lakes. However, more recent research has shown that nitrates and phosphates act in conjunction to increase algal growth, and climate may affect which minerals are more available for algal growth (Paerl et al, 2016). One crucial difference between management of phosphorus and nitrogen is the differences in their nutrient cycles; this has led to neglect in management of nitrates. In addition, harmful algal blooms in recent years have seen a shift in the dominant species, from microbes able to meet their biological needs for nitrogen through nitrogen fixation alone, to microbes unable to fix enough nitrogen for themselves, instead relying on anthropogenic input. While nitrates can be removed from an aquatic ecosystem by denitrifying bacteria as N_2 or NO_x, phosphates are more likely to become sediment and thus persist longer than nitrates. Thus, different management techniques must be applied to effectively reduce both nitrogen and phosphorus.

What are the effects of eutrophication?

The direct result of eutrophic aquatic ecosystems is increased primary productivity, resulting in an algal bloom. The growth and decomposition of the algae takes up dissolved oxygen, creating hypoxic conditions, defined as when dissolved oxygen (O_2) falls to below 2mg/L. In hypoxic zones, larger wildlife such as fish and aquatic invertebrates will start seeking zones with higher dissolved oxygen (DO), and if DO drops below 0.5mg/L, mass mortality occurs. Any motile organisms will have fled as far as possible, and immobile organisms will perish (Diaz and Rosenberg, 2008). On the microbial scale, anaerobic microorganisms begin to take up a larger proportion of the population, while facultative aerobes will switch to other sources to reduce, for instance sulphates, iron, or nitrates. Sulphate reduction in particular can stress organisms even further, as hydrogen sulphide is toxic to larger organisms.

Current management strategies

Current management strategies can be divided into reducing nutrient inputs and clearing algal blooms. This can be split further into the physical, chemical, and biological methods.

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Methods of reducing nutrient input

Phosphate stripping

Phosphate stripping is a chemical method of reducing nutrient loading, specifically phosphorus. It is a form of sewage treatment, precipitating phosphorus out of effluent sewage water, by using iron salts like iron (II) ammonium sulphate, or calcium hydroxide (Ca(OH)2) (Atta et al, 2020). As the phosphorus cycle is more geochemical than biological, physical and chemical methods are most effective at reducing phosphorus loading. While this method can remove 95% of phosphorus from wastewater, it has not yet become widely applied due to the costs of the chemical reagents.

Buffer zones

Buffer zones are a long term biological method of reducing nutrient input, by planting a section of vegetated land about 20-30m wide that can absorb effluent nitrogen by absorption or denitrification, sequester phosphorus, and stabilize river banks while preventing soil erosion (B. -M.Vought et al, 1995). Varying studies show that riparian buffer zones can reduce at least 76% of incoming nitrogen and 51% of incoming phosphorus, however these zones are only effective in narrow rivers (Jiang et al, 2020). For already eutrophic lakes and reservoirs, this method is not feasible.

Wetlands

A reconstructed wetland can be a biological method to reduce nutrient loading. For example, in Egypt, a reconstructed wetland at Lake Manzala has been trialled to treat effluent wastewater. The wastewater is diverted into sedimentation basins where larger sediments settle out of the wastewater, then flows into secondary wetland ponds. These ponds are highly active biologically, with rapid nutrient cycling from macrophytes which host denitrifying bacteria, and rapid sequestration of nitrogen into biomass (over 95% efficiency), which can then be used industrially or as fuel. The denitrifying bacteria convert nitrates to nitrogen, which is a harmless gas in the atmosphere (El-Refaie, 2010). However, the plants (such as water hyacinth, *Eichhornia crassipes*) used are usually invasive, because the plants are chosen for growth rates and invasive species grow at a rapid pace, posing a risk of releasing invasive species into local ecosystems. In addition, the removal efficiency varies greatly between seasons. For example, the removal efficiency of total suspended solids was 95% in February and 58% in July, showing an inverse relationship to temperature. Furthermore, this method requires a significant amount of land.

Evaluation of methods used to reduce nutrient input

The most successful methods for removing phosphorus are geochemical in nature, as the phosphorus cycle itself is physical than biological. However, physical methods of removing nitrogen are rarer and less effective. To develop a new method to control nitrogen inputs, it would be effective to revisit the wetland strategy and focus on the denitrifying bacteria, that can naturally remove nitrates from water.

Methods used to disrupt algal blooms Flushing

By flushing a lake with “new” water, it is possible to decrease the residence time of an established algal bloom. In Lake Taihu, horizontal flushing was shown to reduce bloom development time, resulting in an overall bloom residence time, from 365 days to 200 days annually. However, this process is “wasteful”, requiring large amount of water for large water bodies. Likewise, it is not feasible in areas that are prone to drought (Harke et al, 2015).

Vertical disruption

Vertically stable water columns favour the development of cyanobacteria over eukaryotes, and in Lake Niuwe Meer in the Netherlands, vertical disruption through bubbling was able to reduce *Microcystis* dominance and shift the summer microbial community to a mixed group of flagellates, green algae and diatoms (Visser et al, 1996). However, because the algal cells and bubbles have a net negative charge, it is difficult to reach a high efficiency of algae removal (greater than 90%) as the algae cells do not always attach themselves to the bubbles (Zeng et al, 2023). Moreover, this approach is not feasible in large water bodies.

Clay flocculation

Clay flocculation is a physical method of clearing algae blooms, and it has been used in East Asia with success. By sprinkling clay particles over the algal bloom, algae cells flocculate around the clay particle and fall to the bottom of the lake as clay/cell flocs, where the algae cells die of light deprivation or get buried beneath sediment. In addition, clay capped with zeolite can absorb ammonia and phosphates due to ion exchange and promote sequestration of P and removal of N (Chen et al, 2018). In South Korea, yellow loess is used for this purpose. However, this method can allow algae to escape, and the death of algae can also cause problems with the nutrient cycles.

Water treatment

Copper sulphate has been shown to be toxic to algae, inhibiting bacterial growth and replication. However, studies have shown that at concentrations of 0.5mg/L less than 40% of the total bacterial cells reached the end point of death (membrane loss). In addition, the lysis of bacterial cells could release more toxins from the lysed cells, contaminating drinking water further. In water samples, it has been estimated around 76% of total microcystin content is stored in algae cells. In addition, other bacteria that could potentially biodegrade the microcystins are usually also killed by the copper treatment. H2O2 is another chemical toxic to algae, however it requires UV radiation to significantly reduce algae populations. Chlorine and potassium permanganate also show promise as pre-treatment oxidants (Fan et al, 2014). These treatments can effectively reduce *Microcystis* and oxidize microcystins in drinking water, however implementing them in large water bodies would not be cost-effective and would have unpredictable effects on the wider microbial community and ecosystem.

Mechanical salvage

The simplest method to remove algae is by using a power device to mechanically salvage as much algae as possible to directly remove algal concentration in the water body. This method removes a lot of water from the lake itself, making subsequent treatments more difficult. In addition, this method requires significant manpower and is difficult to implement in larger water bodies (Zeng et al, 2023).

Ultrasonic treatment/Sono-degradation

Ultrasonic waves, which are sound waves from 20kHz to 1MHz, can be used to disrupt algal blooms. These waves can cause cavitation in the air bubbles that aquatic microbes use to regulate their vertical position in water, causing them to sink or rupture. In addition, the rupturing of the air bubbles may produce free radicals due to the high pressure inside the bubbles. This method can eradicate algal blooms, but it is highly non-specific, damaging other aquatic microbes such as *A. flosaquae*, members of the *Chlorophyceae* species, and *S. suspicatus* even more than the target microbe *M. aeruginosa*. Thus, it is unsuitable to be used in lakes and reservoirs directly. However, it has been shown that ultrasonic waves can degrade microcystins, so this may be a viable way to treat water for human use (Dehgani, 2016).

Evaluation of methods used to disrupt existing algal blooms

The physical methods of reducing algal blooms are usually only fit for smaller lakes and cannot handle the persistence and scale of notable blooming sites such as Taihu and Lake Erie. Chemical methods would work for treating water intended for human use, however the chemicals used would have unpredictable effects on local wildlife, including microorganisms like zooplankton. A similar argument can be made for sono-degradation. A biological approach that could modulate microbial community interactions while reducing N would be the optimal solution in both reducing nutrient inputs and established algal blooms.

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Algicidal bacteria

Microcystis: our main algae of interest Freshwater algal blooms are mostly made up of cyanobacteria such as *Microcystis*. The name "algal bloom" is a misnomer, as algae refers to plant cells with chlorophyll but no stems, roots, or leaves, and many "algal" blooms are made primary of Microcystis. Microcystis is a genus of

cyanobacteria that makes up most freshwater HABs and is of note due to the abilities of certain strains to produce cyanotoxins such as microcystins, hepatotoxins, and neurotoxins. In addition, in-situ mesocosm trials run in Taihu, China, show that even in highly favourable conditions, N2-fixing bacteria such as *Anabaena*, *Aphanizomenon*, and *Cylindrospermopsis*, are still unable to compete against an established *Microcystis* bloom. Thus, in highly eutrophic ecosystems, it is crucial to control both N and P to reduce algal blooms. *Microcystis* blooms and their toxins have been detected in over 79 countries, making it a global microbe of interest (Harke et al, 2019).

Microcystins

Microcystins are hepatotoxins produced by a range of bacteria such as *Microcystis* and *Anabaena*. Once known as "Very Fast Death factor", microcystins are monocyclic heptapeptides containing 7 amino acids. Microcystins have been identified as potential carcinogens. 75 variants have been documented, with the microcystin leucinearginine variant being most common. Microcystins are thermostable, posing a challenge to water treatment, though they break down slowly in direct sunlight (Fan et al, 2014). The second most affected organ in humans is the testis, shown to be able to cross the blood-testis barrier and increase expression of proto-oncogenes and oxidative stress. Microcystin lowers sperm motility and affects morphology, as well as disrupting the male hormone system (Lone, Koiri, and Bhide, 2015). Exposure can be from recreational activities like swimming, or contamination of drinking water, both of which can cause acute and chronic symptoms. Acute symptoms resulting from short term exposure can cause symptoms such as rashes, headaches, hay fever-like symptoms, pneumonia and diarrhoea (US EPA, 2018). In addition to the threat they pose to human health, sublethal extracts of microcystins has been shown to cause severe developmental abnormalities in zebrafish, such as reduced later life swimming performance, and vertebral abnormalities in the form of extra neural and haemal processes (Orfanakis et al, 2022).

What microorganisms have shown anti-cyanobacterial capabilities?

About 50 genera of bacteria belonging mainly to *Pseudomonadota, Actinomycetes,* and *Bacteroidetes,* have been shown to demonstrate anti-cyanobacterial behaviour. The most well studied and widespread anti-cyanobacterial bacteria belong to *Pseudomonadota*, a phylum noted for having many nitrogen-fixing bacteria. While fungi have also been demonstrated to produce anti-cyanobacterial chemicals, much of the current literature has been concentrated on bacteria for their effectiveness and ubiquity (Kong et al, 2022).

How can bacteria disrupt algal blooms in freshwater?

There are many modes of action for bacterial algicide. For example, *Paucibacter* is shown to be capable of physical attachment to *Microcystis* and secretion of algicidal chemicals (Le, 2022). Other bacteria may be able to indirectly reduce algal blooms by reducing dissolved nitrogen to atmospheric nitrogen (such as anammox bacteria), while others may be able to mediate cell signalling cascades that can lead to cell death.

Quorum sensing

Quorum sensing (QS) is a cell density dependent cell signalling system. By controlling the concentration of autoinducers, cells can detect the concentration of other cells and adjust gene regulation, accordingly, allowing the cell to perform energy-intensive processes only when it is beneficial to the colony as a whole (Rutherford and Bassler, 2012). In the case of HABs, microcystin production is increased in biofilms, and microcystin could be a signal to initiate biofilm formation in response to a stressor (Rzymski et al, 2020).

M. aeruginosa has been shown to exist as both free-living cells and biofilm aggregations. The aggregation of *M. aeruginosa* poses a greater risk for ecosystems, by blocking out light for aquatic photo synthesisers. The dense mats produced can wash ashore and dry, forming a dry patch of “algae” with high microcystin content, posing risks for wildlife or pets that consume it (Denchak and Sturm, 2019). Like many other Gram-negative bacteria, *M. aeruginosa* has been shown to use quorum sensing (Zhai et al, 2012). QS may be implicated in microcystin production, biofilm formation, and understanding the effect of QS systems on the formation of algal blooms will provide key insights on how to reduce the magnitude and toxicity of algal blooms (Pimentel and Giani, 2014). Microcystin production is significantly increased at higher cell density, showing that controlling algal blooms will also control water toxicity (Wang et al, 2021). An addition of microcystin into cultured *M. aeruginosa* cells leads to formation of colonies as well as general cell density increase. Microcystin is stored intracellularly, and its release signals a range of biotic and abiotic stressors, promoting aggregation and biofilm formation (Rzymski et al, 2020).

Anaerobic ammonium oxidizing bacteria (anammox)

Anammox bacteria are a recently discovered group of bacteria with the ability to anaerobically reduce ammonia to nitrogen, removing bioavailable nitrogen from aquatic systems (Kuenen, 2008). The currently discovered species Anammox bacteria reduce ammonia and nitrite, both bioavailable forms of nitrogen, to inorganic N2 gas. This is done through the oxidation of ammonia by nitrite to hydroxylamine, and subsequent formation of dinitrogen gas. Notable genera include *Brocadia* and *Kuenenia* (both freshwater), however no pure culture has been found yet, so all 10 species currently discovered are given as “Candidatus” species (Kartal et al, 2013). Anammox bacteria are unique in that they possess an anammoxosome, which is made of ladderane lipids. The anammoxosome is an organelle that catalyzes the reaction between ammonia and nitrite to form nitrogen gas and water. The ladderane lipids are crucial to the anammoxosome, as an intermediate of the anammox reaction is hydrazine, which is toxic to all living organisms. The ladderane lipids prevent hydrazine leakage and serve as a method of identifying anammox organisms, due to the rarity of ladderane in nature (Boumann et al, 2009). While anammox bacteria are strict anaerobes, they may be able to tolerate low oxygen levels by attaching themselves to suspended particles, securing an anaerobic environment in addition to sources of nitrogen. The anaerobic nature of anammox bacteria suggests a negative feedback loop between blooms and anammox bacteria; the hypoxic conditions caused by the bloom allow the anammox to proliferate, reducing the bloom until DO increases to toxic levels for the anammox. Hence, anammox bacteria are usually found in the hypolimnion of lakes. A study done in 2017 in Xidong reservoir, China, showed that during a cyanobacterial bloom, anammox accounted for 27.3% of N2 formation from surface sediments, while the usual proportion is around 20%, showing that anammox bacteria may play a significant part in reducing dissolved nitrogen during algal blooms (Xue et al, 2017).

Algicide: chemical/indirect attack

Both fungi and bacteria are able to synthesize a range of anti-cyanobacterial compounds. However, many of the algicidal compounds produced are unable to be fully purified and isolated. The 5 general classes of anticyanobacterial compounds are alkaloids, protein/amino acids, fatty acids/cyclic peptides/peptide derivatives, enzymes, and others (Kong et al, 2022). It is estimated that indirect attack is responsible for about 70% of algicide mediated by bacteria (Le, 2022). Some of these compounds can be highly specific; for example, L-lysine works specifically on *Microcystis aeruginosa*, due to *M. aeruginosa* being unable to efficiently export or degrade lysine. This can then cause lysine to be incorporated into bacterial peptidoglycan, preventing transpeptidation, resulting in leaky peptidoglycan walls. This causes irreversible damage to membrane integrity and photosynthetic machinery (Kim, Kim and Park, 2023). Other amino acids, for example tryptoline, may show up to 100 ± 2% effectiveness at eradicating *M. aeruginosa*, but this effect is quickly lost as the amino acids are degraded or used by other organisms. Alkaloids, such as nuciferene and capsaicin, may also be used to inhibit algal blooms. While some alkaloids can affect a wide range of microorganisms, other display selectivity and may also increase microbial diversity and homogeneity. These may be secreted by plants into the surroundings, or they may be synthesized by other aquatic microbes. Nuciferene in particular shows high specificity and the ability to reduce superoxide dismutase, catalase, and ascorbic acid concentrations in *M. aeruginosa* cells, resulting in oxidative damage and subsequent cell death (Zhao et al, 2022). Certain strains of bacteria are able to conduct both indirect and direct attack against algal cells with high specificity (Le et al, 2022).

Algicide: direct attack

bacteria such as *B. cereus* have been shown to exhibit direct attack against a variety of microbes, including

M. aeruginosa. This mode of attack is responsible for around 30% of algal cell death (Le et al, 2022). After contact with the attacking microbe, the attacked algal cells show cyst-like growths within the cell, speculated to be a defense mechanism as the attacking cell ruptures the cell wall of the algal cell. One mechanism of direct attack is by disrupting the electron transport chain in photosystem I of the algal cell, leading to peroxidation of the phospholipid bilayer and subsequent cell death (Zhang et al, 2021). *M. aeruginosa* strains that produce microcystin are shown to produce lower levels of thioredoxin and peroxiredoxin, showing that toxic *M. aeruginosa* strains are more vulnerable to oxidative stress (Schuurmans et al, 2018).

Microcystin release:

The major problem with using bacteria to control algal blooms is the issue of microcystins. The subsequent lysis of algal cells could release toxic levels of microcystins into the water (Schuurmans et al, 2018). In addition, the lysis of one cell releasing microcystins may cause remaining cells to undergo biofilm formation in response to a stressor, potentially increasing microcystin production (Rzymski et al, 2020). The tradeoff between algal cell removal and microcystin removal can be balanced by utilizing strains of bacteria able to degrade microcystin and trigger cell death, one strain of which has been identified by Le et al in 2022.

CONCLUSION

Notwithstanding every management technique, the overarching problem leading to the increase of Harmful Algal Blooms (HABs) is still effluent, nutrient-rich water. Without legislation to control the application of artificial fertilizers and agricultural runoff, HABs will continue to increase in frequency in the wake of global warming. However, in the short to midterm, biological methods of algal bloom control show many benefits over chemical and physical methods. The advantages of being highly specific and not releasing secondary pollutants, as well as being low-cost and effective, puts bacterial methods at the forefront of algal bloom control. Bacteria are able to control the formation of algal blooms at every level, from the initial eutrophic state to the established bloom state, to the removal of residual toxins. However, they are limited by the lack of large-scale studies done, and the uncertainty of the dynamic responses of the microbial community. It would require a significant input of bacteria into existing water bodies to achieve the same concentrations used in laboratory studies, and the problem of large-scale implementation still affects bacterial methods. One solution could be to use bacterial methods as a “clean-up” method, after physical methods have already reduced the concentrations of algal cells; this would prevent a rapid regrowth of Cyanobacteria. Thus, current studies strongly suggest that these new biological technologies could have a significant impact on reducing algal blooms and remediating the disrupted nutrient cycles of aquatic ecosystems.

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