Review

Incorporating Microbial Species Interaction in Management of Freshwater Toxic Cyanobacteria: A Systems Science Challenge

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Abstract: Water resources are critically important, but also pose risks of exposure to toxic and pathogenic microbes. Increasingly, a concern is toxic cyanobacteria, which have been linked to the death and disease of humans, domesticated animals, and wildlife in freshwater systems worldwide. Management approaches successful at reducing cyanobacterial abundance and toxin production have tended to be short-term solutions applied on small scales (e.g., algaecide application) or solutions that entail difficult multifaceted investments (e.g., modification of landscape and land use to reduce nutrient inputs). However, implementation of these approaches can be undermined by microbial species interactions that (a) provide toxic cyanobacteria with protection against the method of control or (b) permit toxic cyanobacteria to be replaced by other significant microbial threats. Understanding these interactions is necessary to avoid such scenarios and can provide a framework for novel strategies to enhance freshwater resource management via systems science (e.g., pairing existing physical and chemical approaches against cyanobacteria with ecological strategies such as manipulation of natural enemies, targeting of facilitators, and reduction of benthic occupancy and recruitment). Here, we review pertinent examples of the interactions and highlight potential applications of what is known.

Keywords: cyanotoxin; harmful algal bloom (HAB); mycotoxin; non-target effect (NTE); phycosphere
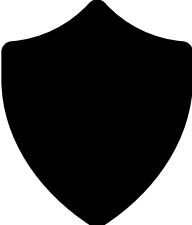
1. Introduction

Cyanobacteria are a diverse group of bacteria whose members have been found almost everywhere on Earth, from literally the deepest seas [1] to the driest deserts [2]. Evidence suggests that cyanobacteria were not only among Earth's earliest lifeforms and the first to be able to photosynthesize but also the ancestors of the chloroplasts within plants [3]. Cyanobacteria comprise much of the base of the food web in aquatic systems, supporting aquatic biodiversity and ecosystem resilience [4]. However, certain cyanobacteria are toxic to humans and other animals [5–8] and proliferate to nuisance abundances in many parts of the world. When this proliferation occurs in a place and time that makes it an immediate threat to human health and the environment, the event is referred to as a Harmful Algal Bloom (HAB). HABs have been reported in all 50 states of the US and may become more frequent and severe over time due to factors such as nutrient pollution and global climate change [9]. They may also act synergistically with other anthropogenic stressors, such as microplastics, to dampen the effectiveness of toxic cyanobacteria control [10].

In inland freshwater lakes, the most common constituents of HABs are toxic cyanobacterial species within the genera *Dolichospermum*, *Aphanizomenon*, *Microcystis*, *Planktothrix*, and *Raphidiopsis* [11,12]. The ability of these species to dominate phytoplankton communities during HABs is often attributed to intrinsic competitive advantages, such as the ability to fix nitrogen and tolerate higher temperatures [13], adjust their vertical positions within the water column [14], or escape predation [15]. Factors such as large rainfall events [16] and ballast water exchange [17] may, in addition, promote the species' movement and establishment across landscapes [18–22]. In this review, we discuss current methods of control

for HABs and identify and synthesize pertinent examples of microbial interactions, which can be applied to not only avoid adverse outcomes but also to develop novel strategies based on systems science that enhance the management of HABs and freshwater resources (Table 1).

Table 1. How cyanobacterial interactions with other aquatic microbes pertain to HABs management.

Microbial Relationship	Microbial Mechanism	Management Implications
Protection	• Support nutrient uptake and colony formation (construction of phycosphere and mucilage). • Solubilize phosphorus and decompose hydrogen peroxide. • Confer oxidative stress resistance. • Directly or indirectly deter grazers.	• Resistance to algaecides, disinfectants, and other control methods. Cyanobacteria Promotion
Antagonism	• Confer toxin resistance to cyanobacteria grazers. • Trigger compensatory feeding in grazers. • Limit nutrient availability through remineralization. • Reduce ability to deal with osmotic stress by metabolizing osmoprotectants of cyanobacteria. • Interfere with signaling compounds. • Disrupt nutrient uptake. • Directly consume or compete with cyanobacteria.	• Microbes can be used for biological control. Cyanobacteria Inhibition

2. Control Methods

The current knowledge of cyanobacterial traits and putative environmental drivers has inspired various methods of controlling HABs that fall roughly within the categories of physical, chemical, and biological. Physical control entails the mechanical inhibition, removal, or elimination of toxic cyanobacteria [23]. The use of plankton nets, hand-removal, and coagulants falls within this category [24,25], as do dam operations in reservoirs (hydrologic control, flushing [20,26]). Physical control methods also include alteration of the habitat to make it unfavorable for cyanobacterial survival and proliferation. For instance, artificial shading [24,27], pressurization [28], and physical aeration, nanobubble ozonation, or sonication/ultrasound/acoustic cavitation [29–31] can be used to physically suppress or damage cyanobacterial cells, and the capping and dredging of aquatic soil and sediment can be used to reduce pre-existing nutrient loads and viable toxic cyanobacterial dormant stages [32–34]. Potentially, these methods can be automated or otherwise improved using recent advances in robotic technology and artificial intelligence, such as low-cost unmanned surface vehicles equipped with active suction pumps and mesh-based algae filtration systems [35].

Chemical control entails the application of compounds that are harmful to toxic cyanobacteria [36]. Artificial compounds such as commercial copper salt solutions [37,38] are often used, but natural compounds such as methanolic allelochemicals of seaweed are also available [39]. The modes of action of these chemical control agents can be direct or indirect. Direct modes include cell lysis and blockage of metabolic processes such as photosynthesis [40]. Indirect modes include photosensitivity induction [41], removal of growth-limiting nutrients (e.g., with flocculants such as aluminum sulfate to bind growth-limiting nutrients [42]), and impedance of colony formation (e.g., with iron reducers such as humic [43]).

Biological control entails the use of living organisms to keep toxic cyanobacteria in check. These organisms may be brought in from outside the system or manipulated within the system. They may include competitors of toxic cyanobacteria (e.g., green algae and diatoms), which consume cyanobacterial resources and might directly interfere with cyanobacterial survival and reproduction through allelopathy or overgrowth [44–46]. The organisms may also include predators, parasites, or pathogens of toxic cyanobacteria, such as planktivorous fish and arthropods [47,48]. Alternatively, organisms can be installed or manipulated at the edge of the habitat afflicted with toxic cyanobacteria (or in a connected habitat that is upstream) to modify environmental conditions. Examples of this include the planting of cover crops to reduce soil erosion in agricultural systems [49], the construction of riparian buffer zones and floating wetlands to curb or counteract influx of nutrients and cyanobacteria from terrestrial sources [49,50], and the seeding of lake habitats or adjacent riparian buffer zones with organisms capable of diverting, eliminating, or mineralizing nutrients (e.g., submerged aquatic vegetation and filter-feeding bivalves [51,52]).

Despite there being a broad array of physical, chemical, and biological control options for managing toxic cyanobacteria, the problem of HABs persists [19,53]. Contributing to the challenge of resolving this problem are factors such as the spatial and temporal heterogeneity within and among the habitats where HABs occur [54], along with the variability among the differing species, morphospecies, and strains of cyanobacteria in toxicity, morphology, patterns of growth, and physiological tolerance [55]. Furthermore, methods to control toxic cyanobacteria can sometimes affect non-target organisms as well. Commonly employed algaecides, for example, have been shown to have lethal and sublethal effects not only on toxic cyanobacteria but also on zooplankton, fish, and the more nutritious cyanobacteria and algae that support the food web [37,40,56–58]). Similarly, the use of barley straw to reduce light penetration through the water column and to chemically inhibit cyanobacteria via its subsequent decay can prevent HABs [59], but also it reduces light availability to beneficial phytoplankton and aquatic plants and to visual aquatic animals that rely on light to locate food and mates and avoid predators [60,61]. The straw can also deoxygenate the water as it decays, which can cause fish death [62]. Non-target organisms might also add complexity to the challenge of HABs management by providing the toxic cyanobacteria with protection against the method of control. To assess and mitigate the risks of non-target effects in managing freshwater HABs, a deeper understanding of the microbial ecological interactions underlying these effects is required.

3. Interactions of Toxic Cyanobacteria with Other Aquatic Microbes

3.1. Protection and Promotion

Aquatic microbes that consistently benefit toxic cyanobacteria include various species of heterotrophic bacteria and fungi (HBF). Some HBF share intimate and often mutually beneficial symbioses with toxic cyanobacteria. Many of these inhabit the "phycosphere", the region that immediately surrounds individual cyanobacterial cells [63,64]. Differing strains of toxic cyanobacteria are known to have distinct HBF assemblages residing in their phycospheres that vary in composition with environmental conditions [65]. A study conducted in western Lake Erie, for example, revealed that phycosphere communities of *Microcystis* sp. differ from both the microbial communities detected in the surrounding water and those detected in the phycospheres of co-occurring phytoplankton species [66].

Microbial interactions in the phycospheres of well-characterized phytoplankton such as *Microcystis* have been extensively studied in laboratory settings and, to a lesser extent, in the field, and could have significant implications for how we manage cyanobacteria [67–69]. In some cases, HBF symbionts are so critical to the ability of toxic cyanobacteria to survive and grow that culturing the cyanobacteria axenically requires special effort [70,71].

While the precise mechanisms have yet to be resolved, phycospheric heterotrophic bacteria such as in the genus *Aeromonas* have been found to induce and support colony formation in *Microcystis aeruginosa* via secretion of signaling compounds and extracellular polymeric substances [70,72,73]. These compounds are crucial in colony formation, which entails the aggregation, functional arrangement, and adherence of cells, along with the construction of surrounding mucilage. The process provides cyanobacteria not only with improved nutrient uptake efficiencies [73] but also with resistance to algaecides [74] and disinfectants [75]. Similarly, heterotrophic bacteria within the genus *Rhizobium* stimulate the growth of *M. aeruginosa* by solubilizing phosphorus and decomposing hydrogen peroxide [76,77], with the latter being both a natural toxic byproduct of aerobic photosynthesis [78] and an algaecide used by humans to control HABs [79].

Fungi beneficial to toxic cyanobacteria are commonly known to be part of terrestrial symbioses such as toxin-producing lichens [80,81], but have not often been reported in equivalent symbioses with toxic cyanobacteria in aquatic systems (meaning, in relationships that are protracted, coevolved, and reliant on spatial or temporal proximity). This may be because fungal benefits that enable cyanobacteria to thrive on land (e.g., hyphal substrate degradation and increased desiccation tolerance [82]) are less useful to cyanobacteria in water. Nevertheless, there is evidence, both experimentally created [83] and observed [84,85], of fungi within the genus *Aspergillus* providing cyanobacteria within the genus *Nostoc* with benefits that include oxidative stress resistance comparable to the previously mentioned (bacteria-conferred) protection against hydrogen peroxide. Moreover, free-living "white-rot" fungi have been shown to drive transformations of common herbicides such as diuron and atrazine, rendering the herbicides subsequently non-lethal to cyanobacteria [86].

HBF can also promote and/or benefit from toxic cyanobacteria via food web interactions. For example, by infecting grazers of cyanobacteria, pathogenic or parasitic HBF can lower the grazers' ability to withstand cyanobacterial toxins and lack of nutritional value [87]. Similarly, they can benefit from their hosts becoming immunocompromised due to exposure to HABs [88–90]. HBF that are decomposers or necrotrophic may capitalize on the mortality caused by HABs (including the subsequent abundance of lysed cyanobacteria arising as the HABs dissipate) and simultaneously benefit toxic cyanobacteria by renewing the availability of nutrients that promote cyanobacterial growth and reproduction [91,92].

3.2. Antagonism and Inhibition

Although interactions with other aquatic microbes can be beneficial to toxic cyanobacteria, as described in the previous section, they can also be detrimental. Pathogens and parasites of grazers can increase, rather than decrease, consumption of toxic cyanobacteria by conferring toxin resistance to their hosts [93] or force their hosts to feed more frequently and less discriminately to compensate for the losses of nutrients and energy associated with their infection [94]. Decomposers can constrain, rather than promote, HAB formation, either by remineralizing nutrients instead of recycling them so that they are less available to cyanobacteria [95–97] or by metabolizing cyanobacterial osmoprotectants (chemicals that enable microbes to cope with osmotic stress [98]) and signaling compounds (chemicals that enable microbes to send and receive information about their respective internal and external conditions to and from one another, including for the purpose of quorum sensing [99]). The latter, in the cases of dimethylsulfoniopropionate (osmoprotectant) and dimethylsulfide (signaling compound), not only interferes with cyanobacterial use and retention of sulfur but also prevents various micronutrients from traversing cyanobacterial cell membranes [100,101].

Various microbes have also been found to cause direct harm to toxic cyanobacteria as predators, parasites, or allelopathic competitors, and have subsequently garnered attention as prospective biological control agents against HABs. Theoretically, these species would be better equipped to keep up with the growth, mutation, and dispersal rates of toxic cyanobacteria than most macroscopic control agents, since they, as fellow microbes, are more like the cyanobacteria in each of these respects. Moreover, their size, capacity for asexual reproduction, and relative metabolic flexibility would make them more amenable to being grown in large batches, transported, and dispensed where needed. Candidate microbial biological control agents include cyanophages (host-specific viral pathogens of cyanobacteria such as LPP-1 [102–106] and microzooplankton (unicellular and meta-zoan eukaryotes less than 200 μm in size that feed on other organisms, which include protozoan nanoflagellates [107,108]), as well as several kinds of HBF. The potential efficacy and limitations of each of these groups as biological control agents have been thoroughly reviewed elsewhere [20,109–111], with their major strengths including tailorable specificity (from strain-specific to phylum-specific) and useable sublethal effects (e.g., reduction in mechanical stiffness, inhibited growth, and impaired or dysregulated photosynthesis) and their major weaknesses including lack of scalability from laboratory to field settings given present technology and vulnerability to abiotic extracellular conditions (e.g., pH, tempera-ture, and solar radiation) and biological factors such as bacterial restriction endonucleases and exopolysaccharides, and competing pathogens or virophages (viruses that obligately coinfect hosts with other viruses).

Among heterotrophic bacteria, predators of cyanobacteria include members of the phyla Proteobacteria, Bacteroidetes, and Firmicutes. Although, in most cases, the details of their predatory feeding strategies are unresolved, there are some that are relatively well-known. The mode of feeding of *Bdellovibrio bacteriovorus* is to enter and consume its prey from the inside, and that of *Myxococcus xanthus* is to overwhelm prey defenses via coordinated offenses akin to pack-hunting [112]. Bacterial pathogens of cyanobacte-ria include *Alcaligenes denitrificans*, which surrounds and penetrates host cells to initiate pathogenesis [106]. Bacterial allelopathic competitors include the sand-filter-prevalent manganese-oxidizing *Pseudomonas* sp. QJX-1, which has been found to inhibit the growth of *Microcystis aeruginosa* via its release of 2,4-di-tert-butylphenol [113]. The best-known antag-onists of toxic cyanobacteria among the fungi are chytrids. Zoosporic parasites/pathogens (e.g., strains of *Phanerochaete chrysosporium*) infiltrate cyanobacterial cells and initiate patho-genesis from within [114]. Mohamed et al. (2021) highlighted numerous other fungal species that not only selectively inhibit the growth of cyanobacteria (without affecting that of other phytoplankton) but also efficiently lyse cyanobacterial cells and degrade the cyanobacterial toxins released from the cells after decay [115].

4. Prospects for Incorporating Microbial Species Interactions into the Management of Toxic Cyanobacteria

The intricacies of the ecological interactions described above and how they may influence the effectiveness/applicability of control measures against toxic cyanobacteria underscore the need for systems science (non-reductionist) perspectives and approaches in managing HABs. Even where microbial exchanges constitute significant obstacles to the control of toxic cyanobacteria, there may be opportunities for refining existing methods and developing new strategies grounded in ecological theory [116]. The following are some prospective means by which microbial species interactions can be incorporated into the management of toxic cyanobacteria, based on current approaches, as well as precedents set in ostensibly analogous systems.

4.1. Non-Targeted Approaches

Toxic cyanobacteria, pathogenic enteric bacteria, toxic fungi, and parasitic protozoa often display similar distribution patterns and responses to environmental conditions, including correlative associations with factors such as agricultural and wastewater runoff [117,118]. As such, carefully designed runoff and wastewater management interventions may be sufficient to address all or most of these microbial threats simultaneously [119–121]. Where landscape development is feasible, these might include the creation or restructuring of bioswales [122] and urban greenspace [123] to reduce nutrient pollution and fecal contamination. As previously stated, reducing nutrient inputs from agricultural runoff, sewage, and sediment erosion to the system is widely considered the most effective of all current methods of controlling HABs but is generally challenging due to spatial and socioeconomic constraints. This includes the challenge of addressing legacy nutrients and natural contributions to eutrophication in aquatic ecosystems, which can continue to fuel HABs even if point and non-point sources are fully addressed [53,124,125].

Sterilization with broad-spectrum antibiotics or antibiotic "cocktails" might also be viable in addressing multiple microbial threats simultaneously. However, in the case of these, best management practices may need to be further developed and enforced to prevent the spread of antimicrobial resistance among pathogens [126] and the loss of treatment effectiveness to higher-order drug interactions [127]. As it is, residues of antibiotics contaminating aquatic systems may already be generating these problems and having differential impacts on separate microbial species [128]. Furthermore, they may be promoting/perpetuating HABs by altering the microbiota of zooplankton such as *Daphnia magna* that would otherwise be enabled by their microbiota to adapt to toxic cyanobacteria [129,130].

Where landscape development and broad-spectrum antibiotics are not applicable or less cost-effective than targeted interventions against individual kinds of microbes, the preference should be for ones that minimize non-target effects. A surprisingly household prospective chemical control agent that fits this description in the case of the toxic cyanobacterium *Microcystis* sp. is simple tea extract, which reportedly inhibits the growth of the cyanobacterium without initially affecting that of co-occurring algae and cladocerans [131].

4.2. Targeting of Facilitators

Targeting of facilitators to manage toxic cyanobacteria would be a variation on the theme of classical biological control, wherein, instead of introducing or promoting species that are antagonistic to toxic cyanobacteria (at carefully selected times and locations), one would neutralize the species responsible for the cyanobacteria's vitality and resistance to targeted intervention. It could entail using antimicrobial substances or natural enemies that harm the facilitating associates of toxic cyanobacteria where circumstances prevent the application of algaecides or cyanobacteria-specific control methods. The reported effectiveness of fungicides for controlling cyanobacterial outbreaks on Bermuda grass putting-green surfaces might be viewed as evidence of this principle having already been applied [132]. However, a study by Lu et al. (2019) pertaining to natural aquatic systems reported, in contrast, that the common fungicide azoxystrobin can promote freshwater cyanobacterial dominance through growth inhibition of green algae and fungal competitors and parasites of cyanobacteria, indicating that system- and species-specific nuances need to be identified and elucidated [133].

More sophisticated techniques in the same vein would be to isolate and introduce quorum-silencing/quenching agents [134,135] that interfere with cyanobacteria-facilitator communication and exchange or to modify conditions in a way that "flips the switch" from facilitation to pathogenesis. Though not yet in the case of toxic cyanobacteria, the latter has been shown to be possible in the case of HAB-forming dinoflagellates. The toxic photoautotrophic dinoflagellate *Prorocentrum minimum* is reproducibly killed by its photoheterotrophic bacterial symbiont *Dinoroseobacter shibae* upon the removal of specific nutrients from its environment, offering a possible analog for inducing pathogensis in phycosphere-dwelling HBF facilitators of toxic cyanobacteria [136].

4.3. Reduction of Benthic Occupancy and Recruitment

In terrestrial systems, "seed banks" are the assemblages of plant seeds found in parts of the soil where seeds can safely remain dormant until there are signs of favorable growth conditions above-ground. Seed banks can enable terrestrial weeds to continuously re-infest habitats, even in the face of dedicated above-ground control efforts [137,138]. Methods involving manipulation of seed banks to control weeds include using (soil-applied) chemicals to stimulate premature germination, solarization (placement of a transparent tarp across a soil bed to desiccate weeds and seeds through the green-house effect), and introduction or stimulation of microorganisms that rapidly colonize and kill/impair seeds prior to germination via chemotaxis (direct movement in response to a gradient of increasing or decreasing concentration of a chemical cue, in this case the "scent" of the target seeds [137]). In aquatic systems, benthic sediments can house seed banks as well, comprising not only the seeds of submerged aquatic vegetation and other aquatic plants but also the dormant stages of phytoplankton, heterotrophic bacteria, and fungi (akinetes, heterocysts, and spores [139,140]. Overwintering and benthic recruitment from these aquatic seed banks are thought to be important origins of source populations for HABs and other large summer populations of cyanobacteria [141] and, in some cases, appear to be linked to toxicity [142,143].

While solarization of benthic sediment in situ would require substantial dredging and likely still be ineffective (due to the capability of various toxic cyanobacteria to survive for years in a desiccated state [27]), the other methods described above may be workable, as might physical alternatives to solarization such as the use of benthic weed mats [24], ultrasonication [30,144], hydraulic jet cavitation [29], and sediment capping [32,36]. It is uncertain at present what impact these methods have on HBF and other non-target aquatic organisms (e.g., phytoplankton, invertebrates, fish), but, since these methods predominantly disrupt light-dependent reactions (e.g., photosynthesis) and osmoregulation (control of the balance of flow of fluid and solutes across the cell membrane), it may be that they enable HBF to outcompete or opportunistically infect cyanobacteria in the benthic zone. Chytrid fungi in the genus *Rhizosiphon*, for instance, are specialist pathogens on akinetes (hardy dormant cells) of the cyanobacterium *Dolichospermum macrosporum* and have been found to exhibit higher incidences of infection at specific times seasonally [145]. Similarly, the sunlight cues that trigger germination of cyanobacterial akinetes and heterocysts can be manipulated or simulated via artificial shade and lighting or restoration of vegetated beds and surrounding landscape [139,146] to make cyanobacteria emerge prematurely or belatedly, thereby exposing them to unfavorable abiotic conditions or making them more vulnerable to HBF and to other microbial antagonists, such as predatory amoeba [147].

4.4. Manipulation of Natural Enemies

Natural enemies (predators, parasites, or pathogens) of weeds and pests are intuitive choices for use as biological control agents against these organisms but must be screened and employed carefully. Ideally, they are native to the habitat and specialized to feed on the target (prey-/host-specific), to avoid the possibility of they themselves becoming invasive or being ineffective in controlling their targets. The same principles apply in the case of biological control of toxic cyanobacteria. For example, free-living freshwater amoeba such as *Acanthamoeba castellanii* feed and grow efficiently on toxic cyanobacteria but are also

parasites of humans and potential reservoirs of opportunistic pathogens [148]. Additionally, even when the risk of the control agent becoming another problem is low, it is important for practitioners to understand and address why these specialist consumers have failed to control the target in the absence of human intervention prior to using them. Often, the issue pertains to differences in phenology (e.g., timings of emergence, periods of activity, life cycle phases, migration) or rates of reproduction and adaptation. Gregarious insect pests and mast-seeding weeds, for example, hatch (or germinate) simultaneously as a cohort, develop rapidly, and achieve juvenile and adult populations that overwhelm predator populations ("predator satiation" [149]). This type of barrier to natural top-down control can be overcome by rearing consumers to high abundance elsewhere in controlled settings and inundating the pests precisely when it allows the natural enemies to gain the upper hand. In the case of controlling HABs, culturable HBF that are antagonistic against toxic cyanobacteria would be conducive to this approach, given their handleability and rapid growth rates [150,151]. Similar applications of (beneficial) microbes have been utilized in contaminant remediations of soil and water [85,152].

To reduce the likelihood of toxic cyanobacteria adapting to individual control agents, two or more can be employed simultaneously or in sequence to create conflicting requirements for adaptation (opposing selection pressures). For example, planktivorous grazers deterred by cyanobacterial toxins, colony formation, or filamentous growth forms can be introduced in conjunction with HBF that disrupt these defense mechanisms. Some of these HBF may be beneficial symbionts of the grazers (gut microfauna or transient "probiotics" [153–155]). Others may be free-living HBF that reduce the "harmfulness" of HAB-forming cyanobacteria by degrading cyanobacterial toxins (e.g., microcystin-LR, cylindrospermopsin, and saxitoxin [156–158]). This would be akin to how indigenous soil bacteria such as *Pseudomonas putida* J1 are employed (via the aeration of the soil) to neutralize allelopathic compounds of terrestrial plants, such as the juglone exuded from the roots of black walnut trees [159].

Grazers that ingest large quantities of toxic cyanobacteria in short time periods but have low reproductive rates due to malnutrition (making them prone to predator satiation) might similarly have their populations and per capita feeding rates boosted by the introduction of alternative resources that either provide the missing nutrients or dilute the toxic/noxious effects of the target [160,161]. HBF have been shown in this way to sustain or increase the populations of zooplankton such as copepods and cladocerans during HABs of inedible cyanobacteria [162,163] and might therefore be amenable to this approach. There is also the possibility of taking the approach a step further so that the effect is sustained over time. One of the ways this is achieved in terrestrial applications of biological control is via the construction of banker plant systems, combinations of plants that provide nearby shelter and supplementary diets for biological control agents of target pests [164,165]. In principle, floating wetlands [166] and submerged aquatic vegetation [167] could be employed similarly to provide refugia for planktivorous fish, zooplankton, and HBF in HAB-dominated portions of lakes.

5. Future Research Directions for HABs Management

There are still research gaps that must be addressed before the incorporation of species interactions into HABs management. For instance, it is presently uncertain whether the combined effects of toxic cyanobacteria and other microbial threats to water quality, such as pathogenic enteric bacteria [168], toxic fungi [169], and parasitic protozoa [170], are generally additive. Studies suggest that feedbacks, synergies, and interferences do occur among them, which may create tradeoffs between the options for aquatic resource management. For instance, *Myxosoma cerebralis,* the fungal cause of Whirling Disease in fish, has been found to benefit from the conditions that arise when HABs collapse (and toxic cyanobacteria senesce) and is effectively immune to the algaecides most often used against toxic cyanobacteria [171,172]. Similarly, afflictions such as White Bacterial Disease [173] and fungal parasitism [174] have been shown to be less prevalent and less lethal in zooplankton

such as *Daphnia* spp. when the zooplankton are able to feed on toxic cyanobacteria such as *Dolichospermum* spp. and *Microcystis* spp. Attempting to target toxic cyanobacteria in isolation (e.g., with algaecides) may thus make aquatic species more vulnerable to pathogens and parasites in the same way that antibiotic treatments of bacterial infection can promote candidiasis (systemic yeast infection) in human patients [175,176]. Just as physicians evaluate risk factors such as age, body weight, immune status, and likelihood of exposure to opportunistic pathogens to avoid this scenario and select appropriate courses of treatment [177–179], water resource managers can utilize information regarding the aquatic system such as food web structure [180], spatial structure [181] and history of disturbance (including previous HAB events [182]) to select optimal methods for controlling toxic cyanobacteria. Considering such ecological complexities will reduce the potential for non-target effects and potentially increase the efficiency of these methods by helping to determine the appropriate combination and sequence for methods targeting the respective cyanobacterial and fungal threats. Furthermore, some of the underlying complexities could potentially be teased out via the use of mesocosm experiments [183] and ecological network models parameterized with field observations [184], as has been achieved to some extent in ocean systems.

Additionally, developing and implementing comprehensive HABs management strategies which account for and incorporate the effects of microbial species interactions depends on our ability to elucidate aquatic microbial community structure and dynamics. This, in turn, requires us to be able to adequately identify aquatic microbes and monitor their distributions, population dynamics, and activities. The advent of modern molecular techniques (e.g., DNA metabarcoding) has provided a platform to overcome historical limitations of microbial water quality monitoring. Unfortunately, most aquatic microbes are still poorly characterized, and it is well beyond the scope of most water quality assessment programs to collect high-resolution data regarding microbial biodiversity and ecology. Relevant insights can, nonetheless, be gleaned from established methodologies. Microbial water quality is typically assessed via the detection of a handful of cultivable biological indicators of fecal pollution assumed to correlate with the presence of waterborne pathogens. While this approach focuses on a small range of microbial targets (such that its value is limited to the narrow scope of public health risks these targets are associated with, i.e., gastrointestinal illness), it can still uncover clues regarding microbial dispersal and metabolic activity. Methods such as the use of high-throughput fluorescence (e.g., sonde measurements of chlorophyll-a and phycocyanin RFUs [185]) and fatty acid profiles [186,187] can similarly provide coarse estimates of total relative abundances of cyanobacteria, heterotrophic bacteria, and fungi in aquatic systems. Combined with environmental tracers (e.g., radiolabeled nutrients and toxins [188]), these methods may provide valuable insights into processes such as nutrient cycling and bioaccumulation in aquatic food webs [189,190].

6. Conclusions

Harmful algal blooms (HABs) of toxic cyanobacteria are a complex environmental issue, with far-reaching ecological, socioeconomic, and human health consequences that may be increasing in severity as time goes on. The fact that previous methodologies to resolve it have yielded mixed results suggests that there may be case-specific nuances to account for in every HAB-afflicted aquatic system and that novel approaches must be developed that incorporate them. However, it should not be forgotten that HABs of the same kind occur globally and are already a serious problem [191,192]. Even amidst the case-specific nuances and differences [193–195], there must be shared conditions and processes for the global patterns in HAB occurrence to be observed, perhaps most conspicuously within the dynamics of the ecological species interactions within these systems. As such, it remains appropriate to leverage what is known, refine and utilize all available tools, and develop appropriately multifaceted approaches to managing HABs across various systems. This includes consideration of the reality that, although faster, more aggressive control methods may thoroughly eliminate target species such as toxic cyanobacteria,

methods that allow the species to remain within the system and exhibit small-amplitude population cycles can be more cost-effective and more conducive to ensuring ecosystem resilience [196–198].

To further optimize HABs management strategies, various physical, chemical, and biological control methods such as those described in this review can be productively integrated and harmonized, as they are in the case of other pressing global environmental issues (e.g., the spread of invasive species and the spread of new and reemerging infectious diseases [199–203]). Most importantly, holistic perspectives can be brought to bear on the issue of HABs that recognize and utilize the fact that toxic cyanobacteria and other significant microbial threats to water quality do not occur and function in isolation but as part of intricate, dynamic, diverse, ecological communities.

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