

A Review of Biological Control of Cyanobacterial Harmful Algal Blooms

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Abstract

The eruption of cyanobacterial blooms, as a global environmental issue, has severely impacted the health of aquatic ecosystems and posed a direct threat to the safety of drinking water. In recent years, owing to the dual advantages in economic and environmental aspects, biological methods in this field have increasingly become a focal point of academic research. This paper provides the most comprehensive review of the current prevalent biotechnological algae control techniques, encompassing microbial, plant-based, and animal-based approaches. The article delves into the details of the sub-methods under these categories, exploring their underlying mechanisms, respective advantages and challenges faced, and assesses the potential feasibility of these methods. Given the ongoing evolution of research in this field, the authors conclude with profound guidance and recommendations, aimed at steering future efforts in the realm of biological algae control towards achieving higher efficacy and broader applicability.

Keywords: Cyanobacterial blooms; biological algal control; algicidal effect; allelopathic effect.

Introduction

The persistent exacerbation of climate change in tandem with eutrophication has led to the proliferation of blue-green algal blooms, positioning them as a salient issue within the realm of global water environmental concerns^[1-2]. Furthermore, the steady increase in temperature and partial pressure of carbon dioxide (pCO₂) owing to the presence of higher levels of carbon dioxide in the atmosphere (attributed to global warming) also contributes to the significantly increased intensity, frequency, and duration of cyanobacterial blooms in eutrophic waters^[3]. Predominant genera responsible for these blooms encompass *Aphanizomenon*, *Cylindrospermopsis*, *Dolichospermum*, *Microcystis*, *Nodularia*, *Planktothrix*, *Trichodesmium*, and *Oscillatoria*^[1,4]. In environments abundant in nutrients, concomitant with conducive temperature and ample light, blue-green algae can undergo rapid replication, attaining significant biomass. Various biotic (e.g., zooplankton predation, microcystin toxins) and abiotic factors (e.g., temperature, nutrients, metal ions) can lead these organisms to cluster, forming colony cells and subsequent surface blooms^[5-7]. The ecological ramifications of such blooms are two-fold: the predominant proliferation of blue-green algae undermines aquatic algal diversity, while the

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attenuation in water clarity and ensuing oxygen depletion (anoxia and hypoxia) perturb the benthic living milieu, culminating in extensive fish and crustacean mortality^[8-9]. Additionally, these expansive blooms can induce heightened turbidity, secretion of mucilaginous compounds, and emission of malodorous substances, thereby obstructing water utility and encumbering sectors like fisheries and tourism^[10-12]. Of paramount concern is the fact that certain cyanobacterial taxa secrete toxins, which can deleteriously impinge upon the physiological processes of avifaunal and mammalian organisms, possessing the potential to bioaccumulate in *Homo sapiens*, thus indirectly imperiling human health trajectories^[13-15].

Currently, methodologies aimed at curtailing blue-green algal blooms bifurcate into three primary domains: physical, chemical, and biological approaches. The physical dimension leverages machinery or engineering techniques, encompassing strategies like dredging, water substitution, ultrasonic intervention, UV exposure, and lacustrine agitation^[16-18]. While devoid of engendering secondary pollution and alien species intrusion, these techniques necessitate rigorous equipment, are labor-intensive, and carry a substantial economic burden^[19]. The chemical paradigm employs either indigenous or synthesized compounds for algal mitigation, chiefly algicides and flocculants. These agents either deter algal growth or induce aggregation for removal. Though expedient and efficacious in the short-term, their transient efficacy, potential for toxin release, and occasional toxicity to coexisting aquatic entities raise concerns^[20-22]. Biological strategies pivot on the nutrient competition and predation dynamics within aquatic ecosystems. By recalibrating the aquatic community structure and fortifying the ecological trophic chain, they aim to restore the equilibrium and salubrious cycling of aquatic ecosystems^[23]. Given their environmental benignity, specificity, cost-effectiveness, and proficiency in mitigating fine particulate blue-green algae, biological strategies are gaining traction among water environment researchers and exhibit promising application horizons. This manuscript delves into the triad of primary biological algal intervention techniques: microbial, botanical, and aquatic faunal, elucidating their respective algal mitigation mechanisms and appraising their merits and drawbacks. The ultimate aim is to furnish insights for the efficacious management of lacustrine and reservoir-based blue-green algal blooms.

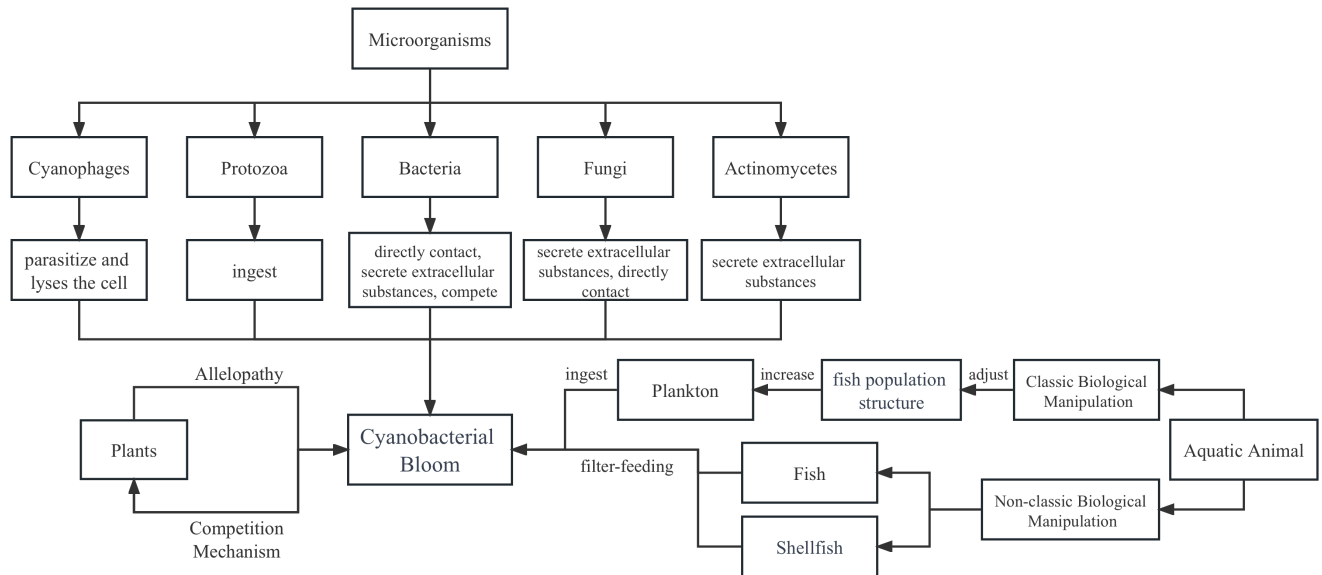


Figure. 1. Illustration of Biological Control of Cyanobacterial Blooms

1 Microbial Methods

Microbial strategies to mitigate the impacts of cyanobacterial harmful algal blooms pivot around three primary mechanisms. Initially, a direct action is taken against the cyanobacteria by certain microorganisms. These organisms either mount a direct assault on cyanobacterial cells or secrete extracellular compounds to disrupt their structural integrity. In some cases, these microorganisms also hinder the photosynthesis processes of the cyanobacteria, thereby curbing their growth and expansion^[24]. Secondly, there are microorganisms that play a role in the assimilation and decomposition of excess nutrients within the water bodies. By consuming these excess nutrients, they indirectly limit the proliferation of the blooms, as these nutrients are vital for their rapid growth^[25]. The third mechanism, bioflocculation, is where certain microbial agents induce the clumping together of algal cells. This clumping makes it easier to then remove these cells from the water column, reducing the overall density of the bloom^[26]. Currently, the principal microbial entities recognized for their algal control potential encompass cyanophages, protozoa, bacteria, fungi, and actinomycetes (Refer to Figure 1 for an illustrative overview).

1.1 Cyanophages

Cyanophages are a specialized group of viruses that have a strong affinity for cyanobacterial hosts, with the ability to modulate their photosynthetic processes. They are widespread across both marine and freshwater ecosystems^[27]. A considerable number of these viruses belong to the *Caudovirales* order, characterized by their linear, double-stranded DNA structure (dsDNA)^[28]. Their genomes range in size from 18-500 kb, encoding between 27-600 genes^[29]. Due to their significant abundance and pronounced genetic diversity, cyanophages play a vital role in influencing the dynamics of aquatic microbial communities^[30].

Historically, cyanophage research began in 1963 when Safferman et al. isolated LPP-1, a groundbreaking cyanophage capable of targeting *Lynbya*, *Plectonema*, and *Phormidium* strains^[31]. Subsequent research over the following decades has revealed many cyanophages, enriching our understanding of their complex genomic landscapes and key genes for host-pathogen interactions^[32-34]. Recent advances in freshwater cyanophage research have highlighted new isolates like Lbo240-yong1^[35] and MaMV-DH01^[36].

Cyanophages demonstrate varying levels of host specificity. They can infect a single strain within a species or spread across multiple genera^[37]. This suggests that cyanophages could potentially control harmful cyanobacterial blooms. For instance, the *Heterosigma akashiwo* virus clone 01(HaV01) can target *H. akashiwo* H93616 without affecting other organisms^[38]. The infection life cycle starts when the cyanophage attaches to a compatible host, enabling cellular invasion and utilizing the host's machinery for replication. When a certain intracellular viral density is achieved, the host cell lyses, reducing the cyanobacterial population. The newly formed cyanophages then infect nearby susceptible cyanobacterial cells^[39]. However, it is imperative to underscore that such specificity does not invariably translate to efficacy in algal bloom control, given that cyanophages typically do not impact cyanobacterial species originating from disparate locales, even when the species are congruent^[40]. Despite viral-induced reductions in specific cyanobacterial abundances, alternate cyanobacterial species may facilely assume their ecological niches^[41].

In addition to the potential drawbacks associated with the specificity of cyanophages, employing these viruses for aquatic ecosystem management is fraught with numerous challenges. Initially, a variety of factors including cation concentrations^[42], photodynamics (encompassing solar irradiance levels and pigments)^[43-48],

the metabolic state and resistance of the host, temperature^[44-45], as well as nutrients such as nitrogen and phosphorus^[37,44,48] play significant roles in influencing their infectivity. Moreover, it is imperative to acknowledge that specificity is not a unique characteristic of cyanophages; the emergence of phage-resistant phenotypes in host populations adds complexity to their application^[49-50]. Although some studies have demonstrated that infectivity can be maintained in certain scenarios^[51], and the potential for genetic engineering to enhance cyanophage traits, thereby increasing their adaptability to environmental changes and amplifying their prospective practical applications, it is important to highlight that these strategies may not be feasible in the immediate future. Last but not least, the current limited understanding of complex interactions between cyanophages and cyanobacteria, including aspects related to cyanophage propagation and biokinetics, further complicates the practical implementation of cyanophages in aquatic environments^[48-49,52].

1.2 Protozoa

Within the aquatic food web, protozoa play a crucial role, primarily utilizing algae to fulfill their energy needs and support growth and replication. A large number of protozoan species rely heavily on algae to satisfy their energetic and material needs for both growth and reproduction. Protozoa also play a significant role in managing cyanobacterial harmful algal blooms, demonstrating several unique characteristics:

1) Diverse Dietary Preferences: Protozoans exhibit a wide range of feeding behaviors, notably preying on various algal groups including diatoms, green algae, filamentous algae, and especially, microcystin-producing cyanobacteria. For instance, the species *Blepharisma americanum* has been highlighted due to its ability to consume *Microcystis*, demonstrating its potential as a biocontrol agent in the mitigation of algal blooms^[53]. In another example, the ciliate grazer *Furgasonia blochmanni* has been observed to prey on *Phormidium*^[54]. Additionally, there are various other documented instances of protozoans feeding on algae, further enriching the body of research in this area^[55-56].

2) Intensive Grazing: Protozoan populations, when flourishing and reaching substantial densities, can significantly lower algal cell concentrations through intense grazing^[57]. An example provided by Wang Jin et al.^[58] illustrates this phenomenon, where a flagellated protozoan, *Kinetoplastida*, was isolated from a pond experiencing an algal bloom. This protozoan demonstrated an extraordinary ability to ingest microcystins, consuming more than 10 algal cells at once. In Lake Constance, protozoa were found to consume about 14% of the primary production during a bloom event, showing a stronger grazing impact and quicker adaptability to increased food availability than larger planktonic organisms^[59]. Their rapid replication, especially in conditions conducive to microcystin proliferation, is vital in substantially reducing algal biomass.

3) Adaptive Resilience: Protozoans showcase remarkable survival strategies, particularly in low-algae conditions, where they resort to encystment, creating a dormant refuge. With the return of favorable conditions and algal abundance, these encysted forms reactivate and resume grazing. This adaptive resilience is evident in the fluctuating algal blooms in Lake Cubria, UK, where protozoan dynamics and morphological changes appear closely tied to algal bloom cycles^[60].

4) Ease of Cultivation: Protozoans are amenable to large-scale in-vitro propagation, positioning them as potential agents for controlled biocontrol strategies. Additionally, they can be easily cultured in large numbers indoors.

Recent experiments demonstrating *Ochromonas*' ability to reduce *Microcystis* prevalence and increase green algae and diatoms are promising, which suggests a potential role for protozoa in shaping phytoplankton

community structure and mitigating harmful blue-green algae in freshwater environments^[61]. However, more detailed scientific research is required to fully understand the implications, considering the chosen protozoan species, their feeding efficiency, environmental conditions, and the types of algae involved. Additionally, the potential lack of specificity of protozoa for harmful algae must be considered, as they might prefer non-harmful algae, inadvertently promoting harmful algal blooms. In conclusion, employing protozoa for algae control necessitates a comprehensive application of various control methods and further investigation into the impacts on blue-green algae populations, while maintaining a critical perspective on the method's true effectiveness.

1.3 Bacteria

In 1942, Geitler^[62] made a pioneering discovery by identifying the alga-lysing myxobacterium *Polyangium parasiticum*, which exhibited lytic activity against *Cladophora*. This groundbreaking work opened the doors to extensive research, leading to the discovery of a diverse array of alga-lysing bacteria. Among the prominent genera identified are *Myxobacter*, *Bacillus*, *Alteromonas*, *Pseudomonas*, *Pseudoalteromonas*, and *Vibrio*, to mention just a few^[63]. Predominantly, these bacteria are Gram-negative and have been isolated from areas affected by water blooms or red tides, though some have also been found in terrestrial soils. It is noteworthy that the host range of algicidal bacteria varies; while many exhibit a broad spectrum of activity, certain algalytic bacteria, such as *Pseudomonas fluorescens*^[64] and *Shewanella* sp. (*Gammaproteobacteria*)^[65], display a more selective activity towards different algae, showing species- or genus-specificity^[66]. Instances of high randomness and unexplained specificity in their actions have also been recorded^[67]. The mechanisms through which these algal-lytic bacteria exert their effects can be categorized into direct and indirect actions.

Direct lytic mechanisms predominantly entail contact-mediated and parasitic lysis. The contact-mediated lysis necessitates an intimate interaction between the bacterial entity and the algal cell, culminating in the secretion of hydrolytic enzymes that specifically target and degrade the algal cell wall, which is composed of cellulose. This process ultimately leads to cellular lysis and death^[68-69]. An illustrative example is provided by *Chitinimonas prasina* LY03, a strain identified by Li et al.^[70] in the proximities of Xiamen. This bacterium establishes attachment to the algal cells of *Thalassiosira pseudonana* via its flagellar structures and secretes chitinase, thereby facilitating the breakdown of the algal cell wall and subsequently leading to cell lysis.

On the other hand, certain bacterial species adopt an intracellular parasitic strategy, infiltrating the algal cells and exploiting their nutrient reserves. This infiltration results in a disruption of the algal cells' metabolic processes, culminating in cell lysis. Burnham et al.^[71] provide an exemplary case of this phenomenon.

Indirect mechanism refers to the phenomenon where bacteria compete with algal species for limited nutrients, or exert algicidal effects through the secretion of extracellular bioactive compounds^[72]. Exemplary bacteria within this category include *Pseudomonas*^[73-74], *Pseudoalteromonas*^[75-76], *Vibrio*^[77-78], and *Bacillus*^[79]. The active compounds released by algicidal bacteria encompass -cyano-L-alanine^[80], the proteinaceous compound P7^[81], benzoic acid^[82], and novel L-amino acid oxidase^[83], among others. These compounds interact with algal cells in a multitude of ways, potentially disrupting photosynthesis, inhibiting pigment biosynthesis, inducing oxidative stress, blocking the respiratory chain, and reducing assimilation products, as well as disrupting intracellular ionic balance. All these interactions may culminate in algal cell lysis and death^[84-85]. A typical example of such compounds is the biosurfactant glycolipids produced by *Pseudomonas aeruginosa*, particularly the mixtures of Rha-Rha-C₁₀-C₁₀ and Rha-C₁₀-C₁₀, which exhibit high toxicity to

wards algal cells, leading to membrane rupture, internal damage, and eventual cell death^[86]. Additionally, Wang Qiong^[87] demonstrated the inhibitory effects of the sterile supernatant from *Bacillus laterosporus* SK-1 isolated from eutrophic aquaculture waters, in which a hydrophilic protein was identified as the main lysing agent. It is noteworthy to mention that there is a perspective considering that the presence of bacterial cells is imperative, and extracellular products alone are insufficient to induce lysis. For instance, in one study, bacteria inhibited the metabolic activities of cyanobacteria, such as nitrogenase activity and photosynthesis, resulting in the lysis of *Nostoc ellipsosporum*^[88].

Moreover, some bacteria influence algae indirectly through competition for nutrients. For instance, bacteria from the genus *Acinetobacter* actively compete with algae for essential nutrients in aquatic environments, potentially leading to algal death due to nutrient deficiency, especially under conditions of limited external nutrient availability^[89].

Compared to viruses, algicidal bacteria are more suitable as biocontrol agents, as bacteria can survive on alternative food sources during non-bloom periods, and mutation within the host is not an issue, as bacterial predation does not rely on unique attachment receptors^[66]. However, the use of algicidal bacteria also presents challenges; firstly, they cannot completely clear blooms, as they somewhat rely on the presence of algae for the organic carbon provided^[90]; secondly, successful cyanobacteria lysis only occurs when the predator-prey ratio reaches or exceeds a critical threshold, which might necessitate the adoption of enhanced biocontrol approaches^[91].

In addition to conducting further research to unveil the mechanisms of host specificity and identify the actual molecular targets of algal toxins, it is crucial to extend the studies on using algicidal bacteria for controlling harmful algal blooms to field trials. Primarily, most of the current studies assessing the impact of algicidal bacteria on natural communities are conducted under controlled laboratory conditions, as cited in^[92-93]. However, bacteria that exhibit algicidal activity in laboratory cultures may not respond to algal blooms in natural environments^[94]. Secondly, exploring the interactions between algicidal bacteria, target algal species, and environmental microbial communities is vital for determining the potential roles these bacteria might play in regulating the growth and termination of cyanobacterial blooms^[94-96]. It is also necessary to determine which mechanisms, such as contact dissolution, lytic enzyme production, extracellular product release, parasitism, or endophytic/exophytic associations, may be applicable for large-scale application^[91]. Moreover, analyzing the impact of environmental factors, such as temperature, pH, and nutrient limitations, on the efficacy of biological control is of utmost importance^[97].

1.4 Fungi

Fungi exhibit a notable ability to inhibit or lyse algae, primarily facilitated by the secretion of extracellular compounds. Fungal genera such as *Acremonium* and *Emericellopsis* produce the compound cephalosporin C. This particular molecule targets and inhibits the synthesis of peptidoglycan in cyanobacterial cell walls, thus compromising their structural integrity and leading to cellular lysis^[98].

In a comprehensive study, Zuo Jincheng et al. conducted an exhaustive screening of 28 symbiotic fungi associated with macroalgae. Out of these, 4 strains demonstrated significant potential, where their crude extracts substantially curtailed the proliferation of cyanobacteria, specifically targeting *Microcystis aeruginosa*. Subsequent investigation into their secondary metabolites unveiled 32 distinct monomeric compounds, each exhibiting algal inhibitory properties^[99].

Moreover, research spearheaded by Jia et al.^[100] uncovered direct algal lytic mechanisms exhibited by certain fungi. The fungus *Trichaptum abietinum* 1302BG provides a quintessential example. This fungal species establishes contact with *Microcystis aeruginosa* cells via its mycelial structures. Post-contact, within a span of 48 hours, the fungus envelopes these algal cells with an external mucous membrane. This encapsulation leads to a subsequent dissolution of the algal cells.

While experimental and field research in this area is currently limited, exploring the use of fungi as a method to control cyanobacterial blooms holds promise as a potential research avenue. For example, a study by Bruno Kenji Ortiz-Canavate et al.^[101] convincingly demonstrated that fungal parasites act as natural antagonists against cyanobacteria in their natural habitats. Additionally, another study found that using *Trichaptum abietinum* 1302BG to treat various phytoplankton species resulted in a suppression rate 2-10 times faster than that achieved by algicidal bacteria^[100].

1.5 Actinomycetes

Actinomycetes, a diverse class of branching bacteria known for forming hyphae and sporangia, are ubiquitously distributed across various ecosystems. Particularly noteworthy in the context of algal inhibition are strains from the *Streptomyces* genus, including *S. microflavus*, *S. globisporus*, *S. gancidicus*, and *S. griseinus*^[102-104]. These actinomycetes often exert their inhibitory effects on algae through the secretion of extracellular compounds. For instance, *Streptomyces neyagawaensis* isolated from Juam Lake in Korea by Cho et al.^[105] manifested a remarkable 84.5% inhibition rate against bloom-forming cyanobacteria. Additionally, this strain displayed inhibitory activities against both cyanobacteria and diatoms. In a parallel investigation, Xu Yaobo et al.^[106] identified *Streptomyces malaysiensis* F913 from eutrophic pond soil. The fermentation broth of this strain exhibited substantial inhibitory prowess against *Microcystis aeruginosa* FACHB-905.

2 Plant Method

The plant-based approach for managing cyanobacterial blooms primarily employs allelopathy and competition. Allelopathy involves the release of allelochemicals by plants during various growth phases to inhibit algal proliferation, while competition focuses on the utilization of aquatic plants to contest with harmful algae for vital resources like nutrients, light, and oxygen.

2.1 Allelopathy

Plants mitigate the growth and metabolic activities of proximal algae through the secretion of allelochemicals via various mechanisms, such as volatilization, leaching, root exudation, and plant residue decomposition. Managing cyanobacterial blooms using plant allelopathy encompasses three primary strategies:

- 1) Deploying live aquatic plants in afflicted water bodies and leveraging compounds like phenols, low molecular weight organic acids, and terpenoids they release to deter harmful algal proliferation^[107]. For instance, Nakai et al.^[108] demonstrated that allelochemicals from *Myriophyllum*, under optimal nutrient and light conditions, could effectively counteract *Microcystis aeruginosa* growth; *Peridinium bipes* was proven to have the same effect in another study^[109], causing the leakage of phycobilines from *Microcystis aeruginosa* within 1 h of incubation. Such allelochemicals can rupture algal cell membranes, leading to the disassembly of phycobiliproteins on thylakoid membranes and an increase in plasmalemma permeability, ultimately

impeding their photosynthetic machinery, or inhibit specific enzymatic activities, curtailing their biomass expansion^[109-110].

2) Introducing dried plants into water bodies, exploiting the inhibitory compounds they release post-immersion. Su Wen’s^[111] research revealed that rice straw soaking solution could selectively target specific toxic and non-toxic cyanobacterial strains, with the former demonstrating higher sensitivity.

3) Extracting allelochemicals from aquatic plants and incorporating them into cyanobacterial bloom waters. He Liansheng et al. determined that water extracts from lotus stems and leaves could hinder *Microcystis aeruginosa* growth, with leaf extracts exhibiting superior efficacy^[112]. Nonetheless, the volatility and transient nature of these extracts, combined with steep extraction costs, have impeded their widespread application^[113].

2.2 Competition Mechanism

Large aquatic plants and harmful algae share aquatic ecosystems, engaging in competition for essential resources such as nutrients and light. Aquatic plants’ ability to predominantly absorb nutrients serves multiple purposes: it attenuates water eutrophication, curtails the proliferation of planktonic algae, and enhances water quality^[114]. Furthermore, the metabolic activities of these plants can modulate factors like water transparency, pH, and alkalinity, indirectly influencing the aquatic ecosystem’s structure and acting as a deterrent against algal blooms^[115].

A significant strategy in algal bloom management leveraging this competition is the implementation of plant floating beds. Introduced primarily in European and American regions since the 1980s, this approach has gained traction as an effective tool for water pollution control and aquatic ecosystem restoration, yielding positive outcomes. The design typically incorporates plants characterized by extensive root systems, adaptability, and economic significance^[116]. Renowned species employed include *Vetiveria zizanioides*, *Iris pseudacorus*, and *Apium graveolens*. These floating beds excel in extracting nitrogen and phosphorus from the water, diminishing nutrient availability for algae. Concurrently, they foster piscine growth, bolstering the count of algal predators and impeding algal bloom incidents^[116].

3 Aquatic Animal Approach

Aquatic animals, including fish, zooplankton, and benthic creatures, can influence cyanobacterial blooms through their feeding behaviors. This control can be classified into classic and non-classic biological manipulation techniques (Figure 1).

3.1 Classic Biological Manipulation

Shapiro et al.^[117] introduced the classic biological manipulation method in 1976, emphasizing the regulation of fish populations. The strategy either introduces carnivorous fish or eradicates those preying on zooplankton. By adjusting the fish population, it diminishes herbivorous zooplankton’s natural predators, augmenting their biomass. Consequently, this exerts increased predation on algae, reducing algal biomass. This “top-down effect” seeks to mitigate cyanobacterial blooms by leveraging the ecological role of zooplankton, impacting algae by manipulating their predators higher in the food chain. This methodology is now standard in managing water quality across numerous European and American lakes.

286 However, while effective in modulating plankton levels in certain water bodies, the classic approach has
 287 inherent limitations. Zooplankton populations are typically small, and their plankton consumption capacity
 288 is limited. Their selective feeding habits can leave certain algae uneaten, potentially precipitating subsequent
 289 algal bloom events. Liu Jiankang et al.^[118] observed that zooplankton often neglect filamentous and colony-
 290 forming algae, leading to a swift rise in the biomass of the untreated algae over time. Furthermore, aquatic food
 291 webs exhibit complex trophic relationships. McQueen^[119] quantified the top-down effects across trophic levels:
 292 piscivorous fish to planktivorous fish at 100%, planktivorous fish to zooplankton at 88%, and zooplankton to
 293 phytoplankton at 64%. Thus, relying solely on the top-down effect to regulate plankton populations may not
 294 always yield the anticipated results.

295 3.2 Non-classic Biological Manipulation

296 Given the challenges of the classic biological manipulation approach, Liu Jiankang et al.^[118] introduced a
 297 non-classic method leveraging plankton-feeding fish and mollusks for direct algae control. Successfully tested
 298 in East Lake, Wuhan, this strategy can filter algae at the millimeter scale. Additionally, harvesting these
 299 organisms extracts nutrients from the water, enhancing water quality. The method currently utilizes various
 300 filter-feeding fish and mollusk species.

301 3.2.1 Filter-feeding Fish

302 Prominent in bloom control, the Silver carp and Bighead carp have been extensively studied. Experiments
 303 in East Lake indicated successful bloom control at a carp density of 50 g/m³^[118]. In a separate study at
 304 Yuqiao Reservoir, Zheng Jun et al.^[120] found a 45%~50% removal rate of dominant *Microcystis* species
 305 during summer, with a fish density of ≥ 10 g/m³ and a stocking ratio of 2:2:1 for Silver carp, Bighead carp,
 306 and Grass carp.

307 These fish possess unique filter-feeding organs, enabling them to process algae larger than their gill slits.
 308 While large zooplankton filters sub-40 μ m plankton, Silver and Bighead carp can handle plankton ranging
 309 from 10 μ m to several mm^[121]. These carps also exhibit tolerance to algal toxins. Xie et al.^[122] demonstrated
 310 that Silver carp can withstand significant daily toxin intakes for up to 80 days.

311 However, these fish do not digest all ingested cyanobacterial cells. Zhang Guohua et al.^[123] noted a
 312 digestion rate of justb 25%~30%. Wang Yiping et al.^[124] argued that the once-filtered *Microcystis* cells
 313 don't sustain lethal damage. Excreted algal cells can even see an uptick in photosynthetic activity due to
 314 overcompensatory growth, which might further stimulate bloom occurrences.

315 3.2.2 Filter-feeding Bivalves

316 In recent years, there have been numerous reports on the manipulation of bivalves to biologically control
 317 cyanobacteria and other planktonic algae blooms. Among them, Western countries have used Zebra mussels
 318 (*Dreissena rostriformis bugensis*) to regulate cyanobacterial blooms in inland waters and have achieved good
 319 results. For instance, Waajen et al.^[125] conducted a 14-day experiment in a eutrophic pond in Breda, the
 320 Netherlands. The results showed that after adding Zebra mussels, the total chlorophyll a and cyanobacterial
 321 chlorophyll a levels (2.4 and 1.0 μ g/L, respectively) were significantly lower than in the control group without
 322 the mussels (84.1 and 7.3 μ g/L, respectively). Water clarity significantly improved, with the treated group

reaching over 0.8 m, while the control group was only 0.57 m. The introduction of Zebra mussels effectively improved the water environment and suppressed the development of blooms.

In China, more studied bivalves for algae control include *Lymnaea sp.*, *Bellamya aeruginosa*, *Corbicula fluminea*, and *Hyriopsis cumingii* Lea. Ouyang Shan et al.^[126] pointed out that bivalve mollusks can directly filter algae in water, such as *Hyriopsis cumingii* Lea, which can consume most of the algae in eutrophic ponds through filter-feeding. Pan Jianlin et al.^[127] set up 20 enclosures in Meiliang Bay of Taihu Lake and studied the algae-controlling effects of indigenous Taihu bivalves *Cristaria plicata*, *Hyriopsis cumingii* Lea, and *Bellamya dispiralis*. The results showed that all three species could significantly reduce water chlorophyll a concentration. 108 hours after the start of the experiment, the water clarity in the test groups increased on average to 2.3 times that of the control group. The test groups did not exhibit blooms, while about 1/10 of the water surface in the control group did. The *Cristaria plicata* treatment group showed a significant decline in cyanobacteria, especially *Microcystis* biomass, and blooms were significantly suppressed.

However, this method shares the same problem with controlling blue-green algae through filter-feeding fish: bivalves cannot fully digest the blue-green algal cells. Qu Mingzhi and others^[128] pointed out that the *Bellamya aeruginosa* expels undigested algal cells enveloped in feces. Upon examination, it was found that *Microcystis*, which has typical physiological structures and is active, accounted for 93% of the fecal volume. When the feces decompose, the surviving *Microcystis* re-enters the water, potentially causing a second outbreak of algal blooms. However, if there is a certain amount of sediment in the water, the sediment will envelop the feces. Due to the strong binding nature of the sediment, only half of the feces will decompose after 70 hours. By then, most of the *Microcystis* in the feces would have either died or become inactive, reducing the likelihood of a secondary outbreak. At the same time, the *Hyriopsis cumingii* also cannot fully digest the ingested algae. Their digestion rates for *Microcystis*, Cryptophyta, and Chrysophyta are 63.8%, 41.1%, and 46.5% respectively^[129].

Conclusion

(1) Microbial Interventions in Cyanobacterial Bloom Management: Microbial strategies for the mitigation of cyanobacterial proliferation present a highly specific and ecologically benign approach, commonly devoid of ancillary contamination. The pronounced reproductive proficiency of microbes allows for substantial cultivation. Yet, the heterogeneous resilience of these microbes under unfavorable conditions limits their ubiquitous applicability in natural aqueous settings for bloom control. Current experimental paradigms suggest avenues for exploration, including: 1) Deployment of autochthonous algae-inhibitory microbes, sourced from impacted aquatic ecosystems, to leverage their inherent environmental compatibility; 2) Acclimatization of lab-propagated microbes, ensuring their aptitude in real-world aquatic ambiances prior to release; 3) Employing genetic modifications to foster directed mutations, perpetually refining these microbes for augmented ecological adaptability, thus fortifying their potential in practical bloom management scenarios.

(2) Phytological Methods in Cyanobacterial Bloom Control: Phytological techniques hinge on the physiological dynamics of plants to deplete aqueous nutrients, thereby curbing algal proliferation. Furthermore, they exude allelopathic entities that inhibit algal dominance. The inhibitory potential via allelopathy is intrinsically linked to parameters such as allelochemical dispersal proficiency, aqueous concentrations of said compounds, their chemical characteristics, the precise toxicodynamic mechanisms at play, and the taxonomic

specificity of the cyanobacteria under consideration. Regarding nutrient competition, prevalent phytological floating platforms are susceptible to attrition, hindering prolonged nutrient extraction. Their detachment or degradation can compromise their efficacy. Given these extant challenges, prospective investigations in phytological intervention strategies could dwell on: 1) Amplifying the allelochemical dispersal rates; 2) Augmenting natural aquatic concentrations of allelopathic entities; 3) Delving into the bio-chemo-toxicological aspects of these allelopathic compounds; 4) Unraveling the interaction dynamics between allelochemicals and target cyanobacterial taxa; 5) Crafting advanced carriers for phytological flotation systems.

(3) Zooplankton, Ichthyological, and Mollusk-Driven Cyanobacterial Bloom Mitigation: Methods utilizing zooplankton, piscine species, and mollusks exhibit convergence in their ability to eliminate and metamorphose cyanobacterial cells through foraging, albeit with incomplete cellular digestion. A critical biomass threshold in the aquatic milieu is essential to exert discernible bloom regulation. Variabilities in size and trophic preferences among these biotic regulators stipulate differences in their filtration spectra and the cyanobacterial species they target. Notably, in the Chinese context, documentation regarding zooplankton-mediated control remains scant, whereas mollusk and piscine interventions are more extensively reported. Addressing the pervasive challenge of incomplete algal digestion necessitates exploring strategies to manage undigested remnants and to harness novel bio-regulators, prioritizing endogenous aquatic entities. Such strategies may bolster consistent algal reduction while curbing potential bioinvasions.

In summation, an exclusive reliance on singular biological modalities for bloom suppression may offer circumscribed results. Consequently, emergent research should pivot towards the synergistic application of diverse biological mechanisms, striving for holistic solutions to cyanobacterial bloom challenges.

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