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Interactions between macrophyte management and harmful algal blooms: Predictors of risk and proactive management strategies

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ABSTRACT

Management of invasive aquatic plants is necessary to maintain ecological functions and designated uses of water resources. However, a particular concern often shared by resource managers and stakeholders that has delayed macrophyte management is the potential for harmful algal blooms (HABs) to occur following plant die-off. Although concerns highlight the importance of this issue, there has been limited synthesis of peer-reviewed literature to comprehensively characterize and contextualize the current scientific understanding. Therefore, the objective of this scoping literature review was to summarize the scientific literature on the topic and to assess potential strategies and approaches that may help mitigate associated risks. Eleven relevant studies were identified: five were field monitoring assessments exploring the relationship between macrophyte management, water quality, and algal parameters; three were microcosm or mesocosm experiments focused on specific aspects of macrophyte-HAB interactions; and three were perspective or social science papers. Hypotheses derived from this literature review were that certain conditions, such as shallow waterbodies with a history of HABs, intensive management actions (e.g., whole-lake treatments), and nutrient-rich environments may promote conditions more favorable for HAB formation following macrophyte management. This paper aims to serve as a foundation to encourage future research and support decision making focused on practical solutions.

Key words: alternative steady state, eutrophic, harmful algal bloom, Hydrilla, invasive, nutrient

INTRODUCTION

Critical freshwater resources often require management of invasive aquatic plants to maintain navigation, flood risk mitigation capacity, power generation, water supply, and recreation (Cole 2006, Suedel et al. 2006, Wersal and Madsen 2012, Getsinger et al. 2014). Within the United States, the U.S. Army Corps of Engineers is responsible for maintaining 3,219 km of inland and intracoastal waterways that require macrophyte management. However, when invasive aquatic plants that once dominated a water body are successfully controlled, significant changes to the ecosystem can occur (Bicudo et al. 2007, Kovalenko et al. 2010, Bugbee et al. 2020). Following management action, the ecosystem can shift (e.g., from macrophyte to phytoplankton dominated), resulting in the formation of harmful algal blooms (HABs) (Brooker and Edwards 1973a, Sabol 1987, Bicudo et al. 2007). HABs can pose their own set of risks to human and ecological health, requiring efforts to warn stakeholders and manage risks (ITRC 2020a). Concerns that macrophyte management will cause HABs has delayed and even halted treatments necessary to restore water resource uses (Ohio Department of Natural Resources, Florida Fish and Wildlife Conservation Commission, various public stakeholder meetings, personal communication). However, data syntheses regarding this phenomenon are lacking. The aim of this paper is to present and synthesize available evidence to address the current data gap and improve understanding of the specific risk factors and mechanisms that may contribute to or help mitigate this phenomenon.

Management of invasive aquatic macrophytes (e.g., *Eichhornia crassipes*, *Hydrilla verticillata*, *Myriophyllum spicatum*, *Potamogeton crispus*) is critical when there are significant impacts to human health and safety, ecosystems, and economics (Suedel et al. 2006, Gettys et al. 2009, Getsinger et al. 2014, Olden and Tamayo 2014, Liao et al. 2016, Keller et al. 2017, Zhang and Boyle 2019). Dense macrophyte mats slow water flow, creating ideal environments for mosquitos, posing direct risks to nearby communities because of mosquito-borne disease transmission (Getsinger et al. 2014, Turnipseed 2017). Drowning is also a concern for swimmers who become entangled in dense aquatic macrophyte mats (Getsinger et al. 2014). Ecologically, because of rapid growth rates, invasive aquatic plants can outcompete other aquatic plants and alter ecosystems causing decreases in biodiversity (Wersal and Madsen 2012, Vila and Hulme 2017). Economically, dense mats obstruct navigation (Wahl et al. 2020), alter water flows (Fox and Haller 1991), increase costs for hydropower and water treatment facilities (Fox and Haler 1991, Julien et al. 2001), and reduce residential and commercial property values (Liao et al. 2016, USGS 2026). Ultimately, the total cost from 1975 to 2020 to the global economy from invasive aquatic plants was estimated to be $32 billion (Macedo et al. 2024).

Similarly, HABs can also pose risks to human health and impact ecosystems and local economies. HABs are broadly defined as growths of algae and cyanobacteria that have the potential to pose risks to humans, ecological receptors, or

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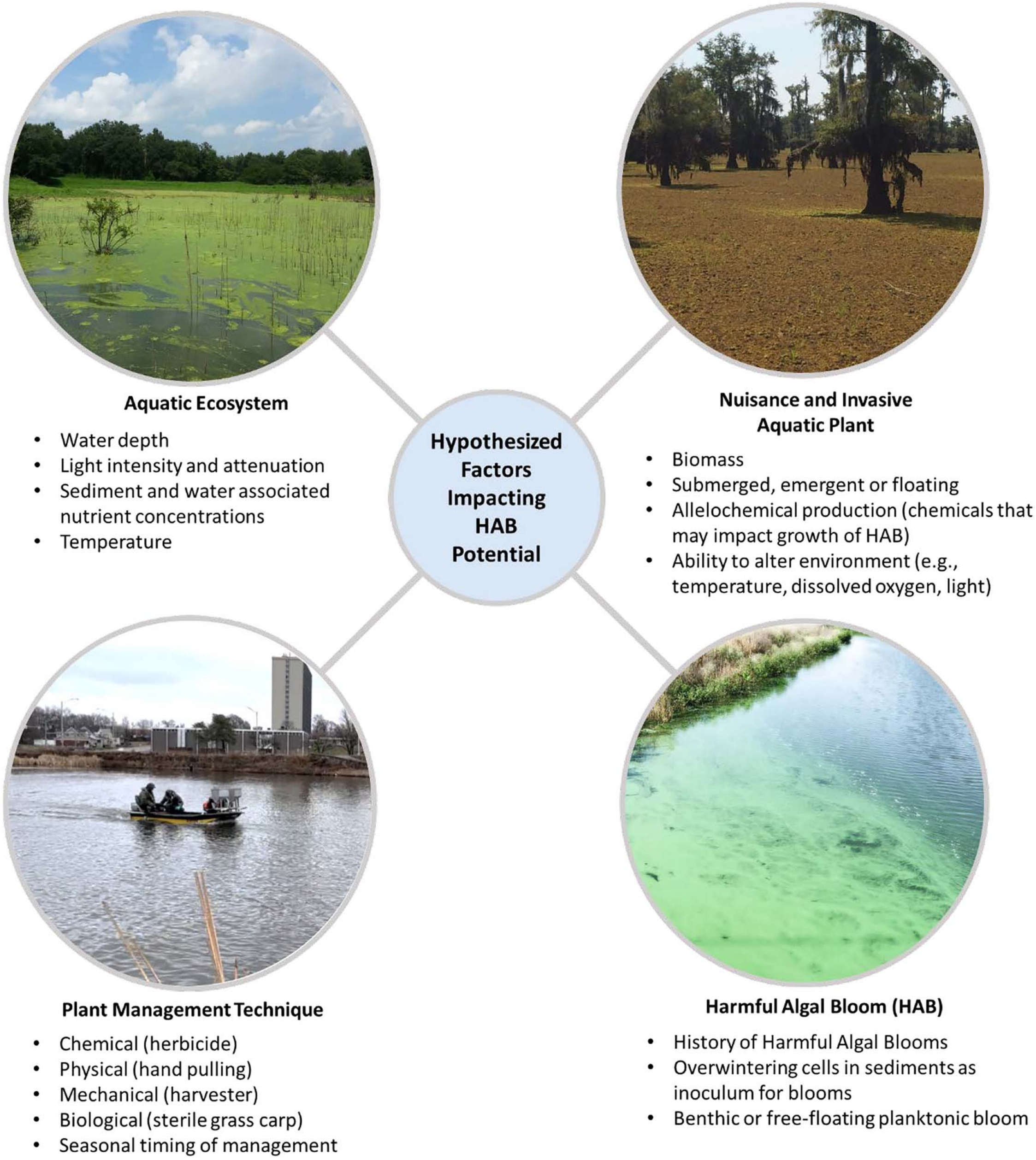

Figure 1. Interrelated factors that may impact the formation of a harmful algal bloom following macrophyte management.

both. Human health risks occur when the HAB produces toxins that enter potable water and food supplies or recreational areas (WHO 2020a,b,c,d). The U.S. Centers for Disease Control and Prevention (CDC) have documented human and animal illnesses inclusive of both freshwater and marine environments. In 2022 nearly 100 human and more than 100,000 animal illnesses were identified in 15 states (CDC 2024). HABs can also become problematic due to biomass production. Due to the inherent high biomass of a HAB, bloom metabolism can alter pH and dissolved oxygen concentrations causing ecological harm (Hudnell 2008). Ultimately, the perceived or actual linkage between macrophyte management and HAB formation would be a negative outcome of management action. Therefore, there is interest to be better able to predict, prevent, and manage HABs.

The linkage between macrophyte management and HABs is a complex and interrelated issue (Figure 1) that captures factors specific to the aquatic ecosystem, invasive aquatic plant, management technique deployed, and potential HAB. The stimulus in this case, management action, can vary in magnitude and duration of impact to the aquatic system depending on factors such as percent of the water body managed, prior level of effect caused by the targeted aquatic macrophyte, and amount of control achieved. Macrophyte management can sometimes act as a significant disturbance event to the aquatic system allowing a stable state shift toward phytoplankton (Scheffer 2004) including harmful algae and cyanobacteria (i.e., a HAB). Yet, for this to occur, conditions must be suitable to support the proliferation of a HAB. This includes temperature, light, and nutrient concentrations available at the location of existing HAB inoculum (Paerl and Otten 2013).

In this paper, data related to macrophyte management and the formation of HABs are explored with a scoping literature review. The first objective was to highlight this issue and to provide an overview of the available scientific literature related to this topic. The second objective was to explore potential strategies and techniques that could be used to lessen risks, offering a forward-facing perspective for how to harmonize macrophyte and HAB management. Our goal is that this foundational paper will stimulate further research interest and solution-focused decision making.

MATERIALS AND METHODS

Scoping review

A literature search was performed in December and January 2025 by a research librarian informed by the Preferred Reporting Items for Systematic reviews and Meta-analyses extension for Scoping Reviews Checklist (Tricco et al. 2018). Database searches included BioOne, MDPI, National Service Center for Environmental Publications, ProQuest, ScienceDirect, Springer Nature, Taylor & Francis, and Web of Science with unrestricted search years. Search terms were selected to prioritize manuscripts related to invasion biology and management. Permutations of "aquatic plant," "treatment," "harmful algal bloom," and synonyms were used for searches. Synonyms for "harmful algal bloom" included "algal bloom"; "treatment" included "control," "remediation," "management," and "containment"; "invasive aquatic plants" included "invasive," "noxious," "introduced," "alien," "exotic," "nonindigenous," "non-native," and "nuisance." The search strategy was reviewed by a subject-matter expert using the resulting literature identified from a subset of the databases included in the full review.

During screening of titles, abstracts and keywords, studies were included if they were published in English, focused on macrophyte management at microcosm, mesocosm, or field scale, and measured parameters relevant to HABs (e.g., chlorophyll-*a*, phycocyanin, cell density). Manuscripts detailing the results of interviews using social science approaches were also included to illustrate how communities perceive factors that cause HAB issues. Identified records were imported into EndNote for deduplication. Full texts were retrieved for review by four subject matter experts. The subject matter experts focused on the study type (e.g., microcosm, mesocosm, or field-scale experiment or synthesis of interviews), characteristics of the study site (e.g., water depth, surface area, historical HAB impacts, and trophic status), macrophyte issue (e.g., genera, percent coverage, duration of issue), management action, and parameters measured after macrophyte management (e.g, chlorophyll-*a*, phycocyanin, cell density) and if the authors discuss a putative mechanism for HAB formation. To synthesize information from this literature, we examined reported characteristics of the study site, macrophyte issue, and management action and measured HAB response across studies to identify areas of emerging consensus despite the limited number of records. We then identified recurring patterns or mechanistic explanations that were proposed by independent studies. Research questions presented in the "research questions derived from literature" section reflect these recurring patterns.

RESULTS AND DISCUSSION

Scoping review

The database search identified 83 records, with an additional three records identified through review and vetting of papers identified during searches. After removing five duplicates, 78 records were screened by title, abstract, and keywords. Of these, 70 were excluded as they did not investigate a correlation between a decrease in invasive macrophyte abundance and the occurrence or formation of harmful algal blooms. Eleven studies met the inclusion criteria and were included in the final review. Although the peer-reviewed literature likely underrepresents the true number of HAB-impacted sites after macrophyte management, relatively few field-scale experiments have empirically measured posttreatment increases in algal metrics. Specifically, increases in chlorophyll-*a*, a macroalga (i.e., Chara), and cyanobacteria abundance were reported in only two, one, and one experiment, respectively. There are likely several reasons for the limited number of manuscripts addressing this topic, including 1) lack of information sharing among macrophyte managers, HAB scientists, and water quality monitoring programs; 2) the absence of standardized monitoring protocols for HABs (e.g., what parameters to measure and over what duration); and 3) insufficient funding and support to monitor HABs aftermacrophyte management.

Field-scale experiments

Orange Lake, FL (Sabol 1987). Orange Lake, FL is a shallow (average depth 2.9 m) subtropical lake with a surface area of 5,260 ha (Table 1). A controlled field study was conducted to manage *H. verticillata* (hydrilla) with a standing crop of 99.8 g dry wt m^{-2} using two harvested treatment plots (0.58 ha each) and one unmanaged control plot (Sabol 1987). Within the two harvested plots, one location removed the plant material after harvesting, and at the other, the plant material was shredded and disposed of within the lake. Harvesting was conducted to a depth of 1.5 m. Pre- and postmanagement monitoring was conducted at six locations within each plot.

Water quality parameters measured posttreatment included dissolved oxygen, temperature, and chlorophyll-*a*. There was a negligible increase in chlorophyll-*a* with the highest difference being 15 μg L^{-1} (20 μg L^{-1} in the in-lake disposal plot compared to 5 μg L^{-1} in the unmanaged reference site) about 10 d after treatment. Chlorophyll-*a* is a nonspecific indicator as both beneficial and harmful algae and cyanobacteria contain this pigment, and, therefore, this increase does not confirm that a HAB occurred. Dissolved oxygen concentrations declined immediately following harvesting and in-lake disposal; however, these concentrations returned

Table 1. Summary of site characteristics, macrophyte management actions, and factors leading to harmful algal blooms from literature review.[1]

Field-scale experiments

Location	Characteristics of site: Depth (m)	Surface area (ha)	History of HAB	Management action	HAB occurrence	Key factor related to harmful algal bloom	Citation
Orange Lake, FL	2.9 (mean)	5,260	NR	Mechanical harvesting of *H. verticillata* to 1.5 m depth; three 0.58-ha plots. Plot 1 = removal of plant material Plot 2 = shredded and in-lake disposal Plot 3 = unmanaged control Partial-lake management.	No	No significant change in chlorophyll-*a* posttreatment.	Sabol (1987)
Gracas Reservoir, São Paulo, Brazil	4.5 (max)	536	Yes (E)	Mechanical harvesting. In 2 mo, 161 to 322 ha decrease in *E. crassipes* surface area coverage. Partial-lake (large-scale) management.	Yes	Higher relative abundance of cyanobacteria after harvesting. Changes to internal phosphorus cycling and decreased shading following water hyacinth harvesting.	Bicudo et al. (2007)
Man-made lagoon and laboratory study, Ohio	1 (mean)	630	NR	Chemical herbicide (5 mg L^{-1} a.i.) applied twice to treat *P. crispus*. Second treatment (19 L of liquid dipotassium salt of endothall) applied 5 d after first (45 kg of granular amine salt of endothall). "Whole-lake" treatment.	Unconfirmed. Increase in benthic chlorophyll-*a* (not specific to harmful algae and cyanobacteria) in second microcosm (laboratory). experiment.	Increase in benthic chlorophyll-*a*. Rapid release of phosphorus following herbicide-induced macrophyte mortality.	James (1984)
Experimental Pond in Ithaca, NY	1.2	0.04	Yes	Chemical herbicide (Diquat 1 mg L^{-1}) to treat *E. canadensis* prior to ice cover. "Whole-lake" treatment.	Yes	A spike in chlorophyll- *a* concentration in July following combined herbicide treatments in November and prior fertilizer amendments. Elevated nutrient concentrations from historic nutrient loading to sediments and degradation of plant tissue.	Peverly and Johnson (1979)
Reservoir, Barry, Wales, U.K.	0.8 to 0.25 (mean)	9	No	Chemical herbicide (1.0 mg L^{-1} paraquat) for treatment of sago pondweed. Whole-lake treatment.	Yes. The macroalga, Chara.	The macroalga, Chara, replaced the ecological niche of sago pondweed and Eurasian watermilfoil after herbicide treatment. Notably, no increase in planktonic algae was observed following treatment, and the typical seasonal increase after fall dieback of macrophytes did not occur.	Brooker et al. (1973)

Microcosm and mesocosm-scale experiments

Factor investigated	Main conclusion related to HAB	Citation
Allelochemical effects on algae	Allelochemicals impacted both green algae and cyanobacteria, but the green algae were more affected.	Zuo et al. (2015)
Presence of invasive aquatic plants on algal community	Presence of invasive plants increased the dominance of potential HAB-forming cyanobacteria. Measured a decrease in pH and dissolved oxygen, and increased oxidation-reduction potential when plants were present.	Shen et al. (2024)
Glyphosate treatments multiple magnitudes higher than label rates for aquatic herbicides	Phosphorus release from plant biomass and visible green color noted in glyphosate treatments. However, green color is not necessarily indicative of a HAB.	Fox et al. (2024)

Table 1. (Continued).

Interview synthesis and perspective papers							
	Characteristics of site						
Location	Depth (m)	Surface area (ha)	History of HAB	Macrophyte management	HAB occurrence	Hypothesized condition leading to HAB[1]	Citation
Kings Bay/Crystal River, FL	0.9 (min) to 3 (max)	243	No	Harvesting and herbicide treatments to control hydrilla	Yes	Selection of the benthic HAB *M. wollei* due to insensitivity to herbicide as well as increase in suspended sediment and turbidity from harvesting.	Evans et al. (2007)
North and central Florida Springs, FL	NR	NR	No	NA—a trophic shift occurred from native macrophytes to the benthic HAB *M. wollei*	Yes	Hypothesize the importance of multiple factors (some unrelated to macrophyte management) including changes in nutrients, grazer densities, spring flow velocity, light, and herbicide residues.	Heffernan et al. (2010)
Honeoyo Lake, NY	4.9 m (average)	720 ha	Yes (E)	Harvesting for the management of macrophytes in swimming and boating areas	Yes	Observe harvesting leading to decaying plant material on shoreline and potential resuspension of sediments correlated with HAB formation a few days later.	Armstrong et al. (2022)

[1]E = eutrophic; NA = not applicable; NR = not reported.

to premanagement conditions after 24 hr. The authors comment that a low, but statistically detectable, decrease in stratification after harvesting occurred. Potential hypotheses connecting HAB formation and management action are not presented by the authors in this study; however, they suggest that water quality changes may be reflective of small area harvesting operations like those used to maintain boating lanes (Table 1).

Gracas Reservoir, São Paulo, Brazil (Bicudo et al. 2007). Gracas Reservoir is a eutrophic tropical reservoir located in São Paulo, Brazil, with a history of HABs leading to fish kills (Bicudo et al. 2007) (Table 1). The reservoir has a surface area of 526 ha and a maximum depth of 4.5 m. High densities of mosquitoes linked to macrophytes as well as sloth deaths due to entanglement in floating macrophytes led to the management of *E. crassipes* (water hyacinth). Bicudo et al. (2007) reported *E. crassipes* surface area coverage increased from 10% in 1997 to 20% in1998. By 1999, surface area coverage increased to 40 to 70%, which resulted in the initiation of management operations via mechanical harvesting. The method of mechanical harvesting and biomass disposal (e.g., removal or in-lake disposal) was not reported. After 2 mo of harvesting, macrophyte coverage within the reservoir decreased to 10%. Sampling within this field study was temporally extensive but spatially limited. Sampling was conducted monthly for 8 yr: 3 yr pre-management and 5 yr postmanagement. Only one sample location (with five depths) was part of the study design. No data were reported for a unmanaged control location.

After *E. crassipes* management, water samples contained an algal assemblage with a higher relative abundance of cyanobacteria (confirmed via light microscopy) relative to premanagement sampling points. There were greater concentrations of total phosphorus (TP) and nitrogen (TN) following management, with higher TN and TP maxima. Greater temperature differences were measured at the water surface relative to mean depth after management and Secchi depths decreased which indicated higher turbidity. The authors hypothesized that removal of *E. crassipes* (water hyacinth) resulted in changes to internal phosphorus cycling within the system and decreased shading. This led to an abrupt trophic shift with greater intensity and persistence of HABs. Decomposition of the senesced HAB then extended periods of anoxia at the lakebed, further promoting phosphorus release from sediments and continuing the HAB bloom and senescence cycle.

Man-made lagoon and laboratory study, Ohio (James 1984). Fox and coauthors (1984) conducted a field study and two laboratory microcosm experiments investigating effects of endothall herbicide treatment of the pondweed *Potamogeton crispus* in terms of phosphorus leaching from macrophytes and consequent changes in autotrophic metabolism (Table 1). The field study took place in a man-made lagoon overtaken by *P. crispus* connected to West Twin Lake in Portage County, OH; the study area was approximately 630 ha with a water depth of about 1 m. The site was treated with endothall at a target application rate of 5 mg L^{-1} per active ingredient twice, with the first treatment on 3 May (45 kg of granular amine salt of endothall) and again on 8 May (19 L of liquid dipotassium salt of endothall). Changes in phosphorus, oxygen, and chlorophyll-*a* concentrations were measured for 14 d after herbicide treatment. The microcosm tests used 57 L glass aquaria 60 cm long by 30 cm wide by 30 cm high with sediment and water collected from the lagoon used in the field study. The microcosm tests measured changes in phosphorus, oxygen, and chlorophyll-*a* following treatment with 2 mg L^{-1} amine salt of endothall for 17 d (experiment 1) or 14 d (experiment 2). These microcosm exposures were assumed to be static as no water exchange was reported. The first experiment was a small-scale pilot study consisting of one untreated control and one treatment aquarium; the second bioassay consisted of six replicates for both the untreated control and treatment groups and measured metabolism for three autotrophic groups (macrophyte/epithyte, benthic, and planktonic).

Though the herbicide caused *P. crispus* mortality, epiphytic and benthic algae were resistant to the treatment. In the field and the first microcosm studies, there was a rapid release of phosphorus following herbicide-induced macrophyte mortality. Although no phosphorus pulse was observed in the second microcosm experiment, the increase in benthic chlorophyll-*a* indicated that the phosphorus may have been immediately taken up by algae in the sediment. The authors assume phosphorus was the limiting factor for algal production, but they acknowledge this was not confirmed in the study with targeted testing. Overall, the results indicated that phosphorus was rapidly leached from macrophytes killed by herbicide and may have absorbed to sediment, where it was assimilated by benthic algae. With algal productivity no longer limited by phosphorus, the authors suggest that the resulting growth of benthic algae following herbicide treatment may result in HABs. As such, the authors recommend that macrophyte management should take HABs into consideration. To prevent large phosphorus releases that may promote HABs, they suggest mechanical harvesting, biological control (e.g., with fish), or applying herbicide at intervals during early stages of the plant's growing season (e.g., maintenance management) as possible management options.

Experimental Ponds in Ithaca, NY (Peverly and Johnson 1979). Peverly and Johnson (1979) monitored nutrient levels and algal growth in outdoor experimental ponds for a year following application of the herbicide diquat (1 mg L^{-1}) for macrophyte treatment (Table 1). Ponds were 0.04 ha in bottom area with a uniform 1.2 m depth and 10 cm of topsoil at the bottom. Four ponds were used in the test: two with diquat addition and two without added herbicide; both treatments consisted of a pond that had N and P fertilizer added and a control pond without prior fertilizer application. The ponds with prior fertilizer application had been part of a previous study, with N and P added both 4 yr and 1 yr before the current study; massive algal blooms had occurred in the experimental ponds 4 yr prior, with only limited blooms subsequently. However, at the start of the current study, the ponds were chemically similar and were considered phosphorus limited. The plant community in the ponds consisted of submersed macrophyte *Elodea canadensis* at 90 to100% coverage, with similar densities (114 to 223 g m^{-3}) regardless of past fertilizer input. As the outdoor study was in Ithaca, NY, the ponds were subject to significant seasonal variation. Herbicide was applied in mid-November with ice forming over the pond the same day and covering the ponds until early March.

Within 24 hr of herbicide application, there was a sharp release of soluble inorganic phosphorus (MRP) due to cell autolysis. This release did not produce large algal blooms, and MRP returned to control levels in about 3 wk. However, in the summer months when water temperatures rose above 10 C (6 mo after herbicide application), there was a sharp spike in total soluble phosphorus in proportion to the amount of phosphorous in the macrophyte tissues prior to herbicide application, likely because of temperature increasing tissue mineralization rates. This phosphorus level was thus highest (exceeding 100 µg L^{-1} in July) in the treatment that had received both fertilizer and diquat applications (called the "F-D" treatment). A large spike in chlorophyll-*a* concentration followed for this F-D treatment only, suggesting that the total soluble phosphorus was an important variable in the growth of planktonic algae with the authors noting blooms (not identified as potentially harmful). Though potassium appeared a limiting factor for macrophyte growth, algae did not appear as dependent on this nutrient. Algae inhibited *Elodea* growth in the F-D treatment for 2 yr after herbicide application, presumably due to the heavy algal blooms shading the macrophytes; during the third summer, macrophytes were the dominant plant and the pond returned to conditions like its preherbicide treatment state and to the pond that received fertilizer but no diquat herbicide. The authors stress that a site's past nutrient inputs are important considerations when predicting impacts of herbicide treatment on algal blooms.

Reservoir, Barry, Wales, U.K. (Brooker and Edwards 1973a,b, 1974). Brooker and Edwards (1973a,b, 1974) conducted a comprehensive field assessment of herbicide treatments (i.e., paraquat) to manage problematic growths of sago pondweed (*Potamogeton pectinatus* L.) and Eurasian watermilfoil (*Myriophyllum spicatum* L.) that impeded recreational fishing (Table 1). The study was a multiyear monitoring effort to understand effects of paraquat on the ecology of the reservoir, in terms of herbicide efficacy, and changes in filamentous and planktonic algae, benthic macroinvertebrates, photosynthetic community metabolism, and water chemistry (e.g., nutrients, dissolved oxygen, pH). The study site was a shallow 9-ha reservoir with a mean depth ranging seasonally from 0.8 to 0.25 m located in Barry, Wales, United Kingdom. The littoral zone of the reservoir was dominated by a 2- to 5-m-wide strip of cattail (*Typha latifolia* L.), with a few areas of common reed (*Phragmites communis* Trin.). The reservoir had no significant input or discharge points, and presumably the primary water source was rainwater and local watershed drainage.

In the growing season prior to treatment, pondweed and watermilfoil had peak biomass densities of > 100 g/m^2, with nearly complete coverage of the reservoir surface area during the summer months. Based on preexisting monitoring conditions, algae were present prior to treatment including both filamentous planktonic species, but no problematic densities were reported.

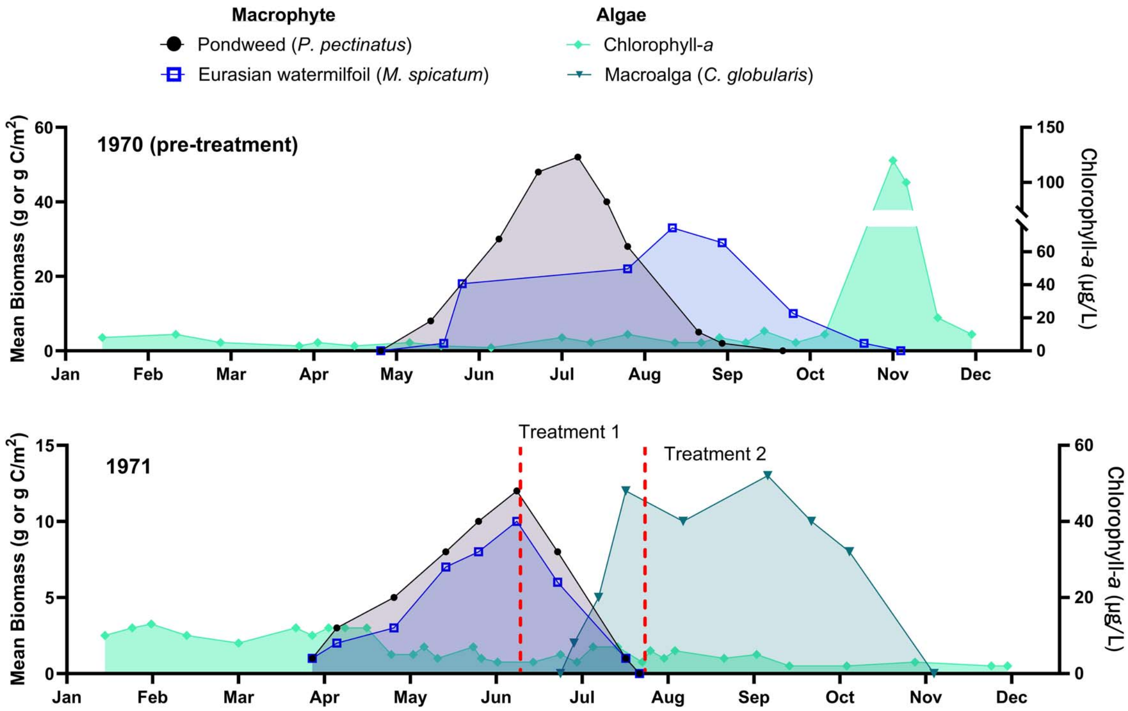

Figure 2. Changes in the mean biomass for plants and algae and changes in chlorophyll-*a* (right axis) for pretreatment year (top) and treatment year (bottom). Treatment 1 = paraquat at 1.0 mg $L^{-1}$and Treatment 2 = paraquat at 0.6 mg L^{-1}. Note: x-axis scales are not the same in the top and bottom graph. Modified from Brooker et al. (1973) using GraphPad Prism 10.5.0.

Following the 1.0 mg L^{-1} paraquat treatment in June, both pondweed and watermilfoil had died back and decayed within 26 d of treatment. Twenty days following this successful macrophyte treatment, the macroalga Chara (*Chara globularis* Thuill.) was observed, and within 26 d posttreatment it covered approximately 66% of the reservoir and was present in areas previously occupied by the aquatic macrophytes. The macroalga existed at such densities that a second application of paraquat (0.6 mg L^{-1}) was conducted targeting this species. This second application was not effective at treating Chara, and by 40 d the reservoir reached almost complete cover with a mean biomass of 25.5 g organic C m^{-2}. Filamentous species of algae were present in the reservoir prior to macrophyte treatment, including *Tribonema*, *Spirogyra*, *Enteromorpha*, and *Oedogonium*. Prior to treatment, *Tribonema* was abundant with a peak mean biomass of 19 g dry wt m^{-2}, with lower densities of *Entermorpha* and *Cladophora* present (not quantified). Within the first week of paraquat treatment, the filamentous algae appeared chlorotic, and after 8 d posttreatment, no filamentous algae were observed. After 16 d posttreatment, growths of *Zygnema* were observed in small regions around the reservoir. In July corresponding with the second paraquat treatment, *Enteromorpha* was present. *Cladophora* was also observed co-occurring within stands of *C. globularis* in the deeper reaches of the reservoir. In the next growing season, growths of filamentous algae were not abundant, and similar species were present as compared to prior to treatment.

Planktonic and epiphytic algae present in the reservoir prior to treatment included the green algae *Pediastrum* spp. (33,000 cells ml^{-1}) and *Scenedesmus* spp. (500 cells ml^{-1}) and the freshwater diatom *Nitzchia* (700 cells ml^{-1}). To track planktonic algae throughout the study, chlorophyll-*a* was measured as a proxy for planktonic cell abundance (Figure 2). Following macrophyte treatments, no significant increases in chlorophyll-*a* were seen during the remainder of the growing season, and the typical seasonal increases after the fall dieback of macrophytes did not occur (Figure 2).

In terms of changes in the reservoir water chemistry, oscillations of dissolved oxygen changed from 70 to 150% pretreatment to 70 to100% posttreatment, indicating lower photosynthetic activity following the dieback of macrophytes. The dieback of macrophytes also corresponded with changes in pH and alkalinity, correlating to changing macrophyte mediated respiratory and photosynthetic processes and the bicarbonate buffering capacity of the system. Prior to treatment, pH was higher in the macrophyte-dominated system associated with the consumption of CO_2 and the appearance of carbonate (influencing alkalinity). During the summers of the pretreatment and treatment years, ammonia levels in the reservoir were low, with most soluble combined nitrogen present as organic and nitrate forms in the pretreatment year, and mainly as organic nitrogen in the posttreatment year. In contrast, winter of the treatment year had a rise in ammonia concentrations to about 2.0 mg L^{-1}, making it the dominant nitrogen form. Phosphorus levels peaked during the summer in both years, reaching around 0.3 mg L^{-1}. This study reported no observable release of nutrients following macrophyte decay. However, the release of nutrients following normal seasonal dieback was present and corresponded with increased phytoplankton algal growths (Figure 1).

Microcosm and mesocosm-scale experiments

Allelochemicals (Zuo et al. 2015). Zuo et al. (2015) was a laboratory study investigating effects of macrophytes and allelochemicals on algal species (Table 1). Allelochemicals refer to secondary metabolites, compounds not directly involved in normal growth, development, or reproduction, produced by plants that positively or negatively affect the growth of nearby organisms (Van Aken 2011). The laboratory study was intended to simulate pollution conditions along with plant and algal species from Lake Chaohu in southern China. The tests took place in 20-L aquaria divided into halves with a baffle to prevent direct physical competition between the algae and macrophytes but allow chemicals to pass. Two species of cyanobacteria, *Anabaena flos-aquae* and *Microcystis aeruginosa*, and two species of green algae (Chlorophyta), *Chlorella pyrenoidosa* and *Scenedesmus obliquus*, were tested for the duration of the algae's life cycle (7 d for each of four growth stages). The bioassays tested how putative chemical interaction from macrophytes themselves or purified allelochemicals impacted competitive interactions between pairs of two algal species under three different regimes modeled after environmental pollutants—eutrophication (0.3 mg L^{-1} inorganic nitrogen, 0.3 mg L^{-1} nitrogen, and 0.005 mg L^{-1} total phosphorus), lead (0.9 µg L^{-1}), and PCBs (0.15 µg L^{-1} 3,4,4′-trichlorobiphenyl)—as well as an "unpolluted" control. No controls were reported for the algae cultures alone. For the macrophyte assays, each algal pairing was exposed to the following macrophyte treatments: 1) *Nymphoides peltatum* (floating plant) only; 2) *N. peltatum* and *Potamogeton crispus* (submerged plant); 3) *N. peltatum*, *P. crispus*, and *Ranunculus sceleratus* (emerged plant); and 4) *N. peltatum*, *P. crispus*, *R. sceleratus*, and *Alternanthera philoxeroides* (herbaceous wetland plant). Additionally, algal interaction assays were conducted using plant-derived allelochemicals rather than macrophytes themselves, with the following treatments: 1) phydroxybenzoic acid; 2) p-hydroxybenzoic acid and protocatechuic acid; 3) p-hydroxybenzoic acid, protocatechuic acid, and coumarin; and 4) p-hydroxybenzoic acid, protocatechuic acid, coumarin, and beta-sitosterol.

Putative chemical interaction from macrophytes and purified allelochemicals reduced growth of the cyanobacteria and green algae. The cyanobacterium *M. aeruginosa* was less impacted than the green alga *C. pyrenoidosa* when the pair was concomitantly exposed. Addition of allelochemicals had a greater effect on algae than macrophytes themselves did. These negative impacts on algae differed between species but increased with the addition of more allelochemicals or macrophyte species. The authors suggest that impacts of allelochemicals and algae are complex, being influenced by multiple factors including the algal species, growth phase, environmental and chemical conditions, and dosage.

Presence of invasive plants (Shen et al. 2024). Shen et al. (2024) was a microcosm study examining effects of invasive aquatic macrophytes on diversity of a phytoplankton and zooplankton community and on the growth of a native submerged plant species (Table 1). The outdoor microcosms were placed near (100 m away from) Yanque Lake, a freshwater lake in southern China, and used the natural lake water with its plankton assemblage. Each microcosm had 100 L of water and a water depth of 60 cm; the lake water had an intermediate nutrient level (0.010 to 0.035 mg L^{-1} total phosphorous) and was not considered eutrophic. Two species of invasive aquatic macrophytes were used in the study: the floating plants *Pistia stratiotes* and *Eichhornia crassipes*; to investigate effects of these plants on algal communities, the two macrophyte species were tested both individually and together in 50-day experiments.

Although the invasive aquatic plant species impacted water quality and changed the dominant species in plankton communities, they did not alter planktonic species diversity. The reduction in pH and increased oxidation-reduction potential in treatments with the invasive plants were believed to be a result of allelochemicals. The invasive plants also decreased dissolved oxygen in the water, which the authors conclude was because of the floating plants obstructing sunlight and thus reducing photosynthesis of phytoplankton and submerged plants, as well as impeding gas exchange at the water-air interface. Furthermore, presence of the invasive macrophyte species altered phytoplankton community dynamics. For example, the dominant phytoplankton species within a phylum differed between the invasive plant and control treatments. Invasive plants increased the dominance index for *Anabaena oscillaroides*, a HAB species, and other nuisance phytoplankton species. Additionally, co-occurrence network modelling suggested that the invasive plant species decreased stability of plankton communities and their resistance to environmental disturbances.

Herbicide (glyphosate) (Fox et al. 2024). Fox et al. (2024) was a laboratory study investigating effects of the commonly used herbicide active ingredient, glyphosate, on beneficial seagrasses (Table 1). Glyphosate acid concentrations were applied at exceedingly high concentrations: 1, 100, and 1,000 mg glyphosate acid L^{-1} (ppm). Glyphosate at 1 mg L^{-1} was reportedly $>$ 1,000 times higher than those measured in the Indian River Lagoon, FL, system. To provide an example to contextualize these high concentrations, glyphosate-based herbicides approved for aquatic use can only be applied to emergent aquatic plants at a maximum rate of 8.77 L ha−1 yr-1 (4.2 kg ha−1). Thus, a calculated resultant aqueous concentration, assuming no interception by vegetation, sorption to sediment, microbial degradation (i.e., worst case scenario), and a five-foot water depth, would be 0.28 mg glyphosate acid L^{-1}. Notably, at the concentrations used in this laboratory study (i.e., multiple orders of magnitude greater than example) the glyphosate molecule itself would have resulted in an increase in phosphorus concentration. The macrophyte species used in this study, was based upon those present in Indian River Lagoon, FL, an estuary that experienced a dramatic decrease in seagrass cover coinciding with an increase in phytoplankton biomass. The laboratory mesocosms consisted of 38-L aquaria with 8-L filtered seawater, a 10-cm layer of sand, and one of two seagrass species: *Ruppia maritima* and *Halodule wrightii*. The concentrations of dissolved nutrients were initially low, with orthophosphate at $<$ 0.04 µM and total dissolved phosphorus ranging from 0.18 to 0.47 µM. The glyphosate concentrations (ppm) and untreated controls were assessed for 22 d.

Treatment with glyphosate resulted in release of phosphorus into the system from decaying seagrass biomass as well as the phosphorus that is a component of the herbicide itself. Increased concentrations of dissolved phosphorus were measured at the first time point following treatment (10 min) and exceeded phosphorus additions from the glyphosate acid (18% phosphorus) alone, suggesting nutrient release from plant tissue had occurred. The 100 ppm glyphosate treatment was visibly green with significant epiphytic algae growth; in the 1 ppm treatment, the increased pH, stable dissolved oxygen, decreased total dissolved phosphates, and increased chlorophyll-*a* also suggested algal growth. These responses are indicative of algal growth; however, they are not specific to harmful algae/cyanobacteria and could include beneficial algae. Care should be used in applying these laboratory-based conclusions to environmental scenarios as glyphosate concentrations were multiple orders of magnitude greater than anticipated concentrations in water bodies from aquatic herbicide treatments.

Interview synthesis and perspective papers

Kings Bay/Crystal River, FL (Evans et al. 2007). Kings Bay in Crystal River, FL, is a spring-fed water bay (fed by at least 30 springs) forming the Crystal River that flows into the Gulf in central Florida (Table 1). The surface area is 243 ha, with water depths ranging from 0.9 to 3 m (Evans et al. 2007). This water body holds high ecological value providing critical habitat for the vulnerable species such as the West Indian manatee (*Trichechus manatus*) as well as great social and economic value. Evans et al. (2007) present an argument for rethinking management of nonnative species through interviews supplemented with peer-reviewed literature. Kings Bay has experienced a series of changes in vegetation dominance, beginning with the native grass *Vallisneria americana* followed by the spread of invasive macrophytes: *E. crassipes* (water hyacinth), then hydrilla and more recently the benthic HAB *Microseira wollei* (formerly *Lyngbya wollei*). Interview responses suggested a link between hydrilla management and the proliferation of *M. wollei*. These hypotheses included 1) selection for *M. wollei* due to insensitivity to herbicides used for hydrilla control and 2) development of better environmental conditions for *M. wollei* by harvesting hydrilla and subsequently increasing suspended sediment and turbidity. Although these hypotheses are briefly highlighted by the authors, they also note limited scientific data.

North and Central Florida Springs, FL (Heffernan et al. 2010). Heffernan et al. (2010) present a critical literature review and synthesis paper of putative factors that may influence the formation of algal blooms in Florida springs (Table 1). North and central Florida is dominated by springs with stable water chemistry and high-water clarity that historically supported the native macrophytes *Sagittaria kurziana* and *Vallisneria americana*. The authors do not report a specific invasive macrophyte issue or management action that targets a macrophyte; however, they hypothesize factors that may contribute to the shift from native plants to HABs, specifically the benthic cyanobacterium *Microseira wollei*. The authors highlight the fact that nutrient enrichment has been hypothesized as a key driver for HAB formation and that there are studies investigating nutrient enrichment of spring fed waters in Florida. Yet the link between nutrient enrichment and HAB formation in these waters is limited. Therefore, alternative hypotheses were explored, including changes in light, grazers, dissolved oxygen, spring discharge rates, and pesticide residues. The authors ultimately developed a hypothetical conceptual model of multiple factors that may impact the formation of HABs.

Honeoye Lake, NY (Armstrong et al. 2022). Honeoye Lake is a eutrophic shallow finger lake (average depth 4.9 m, areas 720 ha) in western New York state (Table 1). Armstrong et al. (2022) summarize resident opinions on the causes of HABs in Honeoye Lake. Most residents believe legacy phosphorus in sediment is the primary cause, while others believe nonpoint source pollution as the primary cause. A smaller portion of interviewees suggested a link between HABs and weed harvesting. Weed harvesting is used in shallow areas around the lake to maintain swimming and boating areas. However, some residents noted decaying plant material on the shoreline after harvesting and harvesting potentially also disturbing sediments, with the appearance of HABs a few days later.

RESEARCH QUESTIONS DERIVED FROM LITERATURE

Are shallow waterbodies more susceptible to HABs following macrophyte management?

Except for Honeoyo Lake (average depth 4.9 m), all water bodies in this literature review could be characterized as shallow with average water depths less than 3 m (Scheffer 2004). Although the sample size is relatively limited, shallow water bodies may be generally more susceptible to changes in alternative stable states, or a shift from a relatively clear macrophyte dominated system to a high turbidity system dominated by phytoplankton (Bachmann et al. 1999, Scheffer 2004). This may be due to a greater relative impact of macrophytes and sediments on lake ecology. At a whole-lake level, shallow lakes can support greater biomass of macrophytes as growth is not limited by light attenuation and depth. Further, mixing of the upper and lowest water layers within the warmer months allows relatively constant interactions with the sediment phase where biogeochemical processing of nutrients and quiescent HAB cells can co-occur (Scheffer 2004, Calomeni et al. 2022).

Are whole-lake treatments at higher risk for HAB formation following macrophyte management?

Whole-lake or other treatments leading to significant changes in macrophyte relative abundance may result in greater HAB risks than small-scale treatments. The following three examples represent management efforts encompassing a large portion of the surface area of their respective water bodies. Mechanical harvesting of *E. crassipes* (water hyacinth) in Gracas Reservoir resulted in a decrease of initial coverage ranging from 40 to 70% before harvesting to 10% 2 mo after harvesting. Herbicide treatments in the reservoir in Barry, Wales, resulted in nondetectable abundances of *M. spicatum* and *P. pectinatus* 26 d after treatment. Further, experimental pond treatments presented in Peverly and Johnson (1979) represent whole-lake conditions Following management, each of these water bodies reported increases in cyanobacteria relative abundance or chlorophyll-*a*. Alternatively, harvesting of 0.58 ha treatment plots within the much larger (5,260 ha) Orange Lake resulted in 24-hr changes in dissolved oxygen concentrations and negligible impacts to chlorophyll-*a*. In addition, management leading to greater macrophyte responses in short time frames may result in more significant shifts to water chemistry. For example, treatments of glyphosate multiple orders of magnitude higher than label rates may have resulted in immediate release of phosphorus from plant biomass in Fox et al. (2024).

Are suitable conditions for HAB formation needed?

For a HAB to occur following macrophyte management, suitable chemical, physical and biological conditions to support high densities of algae and cyanobacteria are also needed. In Peverly and Johnson (1979), diquat was applied in November in Ithaca, NY, immediately prior to ice cover of the experimental ponds. No chlorophyll-*a* increases were detected until the following summer, which the authors conclude were related to the November herbicide treatments and prior fertilization of the ponds. Although these treatments are outside the usual seasonal window for use of aquatic herbicides in the United States, typically from late spring through the summer, this paper illustrates the concept that there may be higher risk of HAB formation if the temperature and nutrient conditions for HAB formation are within a suitable range to support high densities. There is not a universal temperature or nutrient concentration that is known to trigger HAB formation as this is likely specific to the location, species, or ecotype (Litchman 2022). However, the presence of suitable conditions for HABs to occur may be obvious for a site, as in Bicudo et al. (2007), HABs were experienced prior to macrophyte management.

Are alterations in bioavailable nutrient concentrations and dynamics within the system a critical driver?

Four of five manuscripts that measured increases in potential HAB-related parameters (e.g., chlorophyll-*a* concentration, cyanobacteria abundance) following macrophyte management in the field hypothesized that changes in nutrient dynamics were a key factor. Increases in bioavailable nutrients are a key factor in the development and persistence of HABs in U.S. and global waterbodies (Heisler et al. 2008). Following plant management, nutrient concentrations may increase from 1) direct release from degraded plant biomass (Woodward et al. 2024) and 2) phosphorus release from sediments (Hupfer and Lewandowski 2008). However, nutrient release is context dependent. For example, Woodward et al. (2024) reported greater nutrient release from plant biomass with more effective herbicide exposures (i.e., Diquat), with peak release occurring prior to and during shoot discoloration of *Lagarosiphon major*, suggesting an exposure dependent relationship. Hupfer and Lewandowski (2008) highlight that oxygen-mediated phosphorus release from sediment occurs at sites where phosphorus is bound to iron oxyhydroxides. When dissolved oxygen concentrations decrease at the sediment-water interface due to microbial respiration during plant decomposition, phosphorus can be released to the water column, emphasizing the importance of site-specific conditions.

Management implications

Consistent with best practices for macrophyte management, maintaining invasive aquatic plant densities below their peak biomass may be beneficial. Early-season treatments or treatments during early stages of invasion can minimize disturbances to aquatic systems (Gettys et al. 2009, True-Meadows et al. 2016) and likely decrease risks of HABs. This approach may reduce nutrient release and other water quality changes that can contribute to HAB formation. Additionally, applying treatments during cooler water temperatures may result in nutrient release at a time when HAB growth is limited by temperature, thereby allowing more time for nutrient sequestration in sediments. If nutrient release as a contributor to the formation of HABs is a primary concern for stakeholders, the use of nutrient sequestration products may further decrease the bioavailability of released nutrients (ITRC 2020b).

It is important to acknowledge that nutrient release can originate from both internal and external sources unrelated to macrophyte management. Although such releases may coincide with plant management actions, they are not always causally linked. For instance, certain rainfall events can introduce nutrients independent of management (Reichwaldt and Ghadouani 2012). Moreover, during leaf turnover and as aquatic plants naturally senesce, they can release nutrients into the surrounding water, potentially stimulating blooms (Brooker and Edwards 1973a, Landers 2003).

In areas where actual or perceived HAB risk is high, aligning the management of aquatic plants and HABs may be necessary. Several adaptive management frameworks for HABs already exist (Calomeni et al. 2017, McQueen et al. 2024) and can be integrated with long-term macrophyte management strategies. These frameworks offer opportunities for coordinated actions targeting both macrophytes and HABs across different phases of adaptive management.

Under an adaptive management approach, managers could explore whether maintenance management (i.e., recurring management to suppress a plant at an acceptable level; Netherland and Schardt 2021) reduces HAB risk compared to large, annual treatments. HAB risk may be reduced because maintenance treatments target lower biomass and a smaller proportion of the lake, thereby decreasing the impact of management to the lake ecosystem. Stakeholders and managers might also trial herbicides with slower plant response rates (e.g., systemic herbicides), where appropriate, to moderate nutrient release rates. Finally, posttreatment monitoring using handheld meters or sondes to track phycocyanin concentrations could provide early indication of HAB development and support timely management.

DATA AND RESEARCH NEEDS

The formation of HABs following macrophyte management is a concern of some stakeholders and water resource managers (Evans et al. 2007, Evans et al. 2008, Heffernan et al. 2010, Armstrong et al. 2022). Yet limited empirical data are available on the issue. More research at the field and mesocosm/microcosm scales are needed to address the topics identified in this literature review. Future studies should be hypothesis driven and aim to better characterize the level of control of the macrophytes as well as responses of potentially problematic algae and cyanobacteria. For example, chlorophyll-*a* is contained within all photosynthetic algae and cyanobacteria and is therefore inclusive of both beneficial algae and harmful species. Therefore, future efforts would benefit with improved focus on algal identification and enumeration using traditional microscopic methods or metagenomic and molecular approaches (e.g., next-generation sequencing), improving the spatial and temporal scales of HAB formation using *in situ* monitoring of algal pigments (i.e., chlorophyll-*a* and phycocyanin) via remote sensing or in situ sensing approaches, and improving the monitoring the putative risk factors of HAB formation (e.g., light, temperature, nutrients). Several opportunities for future research exist to address remaining knowledge gaps, including the following:

- Regional correlative studies to determine characteristics of the water body (e.g., depth) and treatment (e.g., whole-lake, maintenance management) that predict HABs.
- Long-term HAB monitoring within a macrophyte managed waterbody.
- Characterization of factors (e.g., herbicide type, concentration, exposure duration, environmental conditions (capacity to sequester nutrients)) linked to nutrient release after macrophyte management.

CONCLUSIONS

Overall, the evidence from this review indicates that macrophyte management can, under certain circumstances, contribute to conditions favorable for HAB development through several possible mechanisms, including nutrient release, altered shading, and changes to habitat structure or sediment dynamics. However, responses of HABs following macrophyte treatments varied substantially among studies. These data indicate that various site-specific factors likely influence the rate and extent of HAB formation following treatments, including baseline nutrient loads, nutrient biogeochemical cycling, hydrodynamics, plant community composition, light and temperature changes, and management approaches (e.g., timing, intensity, formulation, rate). This underscores the need for integrated monitoring and adaptive management approaches to balance aquatic plant control with the mitigation of unintended HAB risks. This review provides an important first step and foundation for future research and to inform decision-making focused on practical solutions.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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