


Review

Controlling harmful algal blooms (HABs) in marine waters: Review of current status and future prospects

Donald M. Anderson^{a,1}, Mark L. Wells^{b,c,1}, Vera L. Trainer^{d,*,1} , Marc Suddleson^{e,1}, Kevin Claridge^f, Kathryn J. Coyne^g, Quay Dortch^h, Christopher J. Goblerⁱ, Cynthia A. Heil^f, Nobuharu Inaba^{j,k}, H. Dail Laughinghouse IV^l, Jorge I. Mardones^m, Natsuko Nakayamaⁿ, Taegyu Park^o, Melissa B. Peacock^p, Kaytee Pokrzywinski^q, Heather Raymond^r, Jennifer H. Toyoda^f, Dean Trethewey^s, Petra M. Visser^t, Yanfei Wang^{u,v}, Yongquan Yuan^{w,x}

^a Woods Hole Oceanographic Institution, Woods Hole MA 02543 USA

^b School of Marine Sciences, University of Maine, Orono, ME 04473, USA

^c State Key Laboratory of Marine Environmental Sciences, Xiamen University, Xiamen, Fujian 361005 China

^d University of Washington, Olympic Natural Resources Center, 1455 S Forks Ave, Forks, WA 98331 USA

^e Competitive Research Program, National Centers for Coastal Ocean Science, National Ocean Service, National Oceanic and Atmospheric Administration, 1305 East-West Hwy, Silver Spring, MD 20910 USA

^f Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, FL, 34236, USA

^g School of Marine Science and Policy, University of Delaware, 1440 College Dr., Lewes, DE 19958 USA

^h CSS Inc. under contract to Competitive Research Program, National Centers for Coastal Ocean Science, National Ocean Service, National Oceanic and Atmospheric Administration, 1305 East-West Hwy, Silver Spring, MD 20910 USA

ⁱ School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, NY 11790 USA

^j Civil Engineering Research Institute for Cold Region, Public Works Research Institute, Hiragishi 1-3-1-34, Toyohira-ku, Sapporo, Hokkaido 062-8602, Japan

^k Centre for Marine Science and Innovation (CMSI), School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052 Australia

^l Agronomy Department, Ft. Lauderdale Research and Education Center, University of Florida, 3205 College Avenue, Davie, FL 33314 USA

^m Centro de Investigación en Recursos Naturales y Sustentabilidad (CIRENYS), Universidad Bernardo O'Higgins, Santiago 8370993 Chile

ⁿ Fisheries Technology Institute, Japan Fisheries Research and Education Agency, 2-17-5 Maruishi, Hatsukaichi, Hiroshima 739-0452 Japan

^o National Institute of Fisheries Science (NIFS), Busan 46083 Korea

^p Northwest Indian College, 2522 Kwina Rd, Bellingham, WA 98226 USA

^q NOAA National Centers for Coastal Ocean Science, 101 Pivers Island Rd, Beaufort, NC 28516 USA

^r Office of Research and Graduate Education, College of Food, Agricultural, and Environmental Sciences, The Ohio State University, 2120 Fyffe Rd, Columbus, OH 43210 USA

^s Akvafuture Canada, 1040 Cedar St, Campbell River, British Columbia, Canada

^t Department of Freshwater and Marine Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94240, 1090 GE Amsterdam, the Netherlands

^u Shanghai Ocean University, Shanghai 201306 China

^v University of Delaware, 1044 College Drive, Lewes, DE 19958 USA

^w CAS Key Laboratory of Marine Ecology and Environmental Sciences, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071 China

^x Laboratory of Marine Ecology and Environmental Science, Qingdao National Laboratory for Marine Science and Technology, Qingdao 266237 China

ARTICLE INFO

Keywords:

HAB Control

Marine

Estuarine

Harmful algal bloom, HAB

ABSTRACT

The societal, economic, geographic, and environmental impacts from marine harmful algal blooms (HABs) have increased in many regions around the world. The growing array of impacts is large and varied, threatening human health, marine and freshwater wildlife, and ecosystems upon which many nations rely on for food, recreation, tourism, and a plethora of other goods and services. Although the HAB burden has grown substantially over the past few decades, marine and estuarine HAB control remains one of the least developed areas of HAB science. The disconnect between HAB control needs and solutions stems in part from public, stakeholder, and scientific uncertainties about the balance between benefits and potentially undesirable environmental

* Corresponding author.

E-mail address: verat@uw.edu (V.L. Trainer).

¹ Co-lead first authors; authors are in alphabetical order except for lead authors.

consequences. Other more practical challenges can include substantial regulation of in situ testing, scaling up laboratory-proven technologies to attack widespread blooms that can move in three dimensions in open marine waters, and an immature commercial market. Here we describe the status of control strategies targeting marine coastal and estuarine HABs, in particular those few approaches that have been tested in mesocosm or field applications. We identify the regulatory support, targeted science, investments, and public outreach that will be needed to accelerate the availability of applications for controlling HABs in marine waters worldwide.

1. Introduction

Harmful algal blooms (HABs) are a growing societal problem caused by the proliferation of algae that cause harm in diverse ways. Only a fraction of the many thousands of species of microscopic and macroscopic algae are considered HAB species, and the nature of their impacts vary widely. Many species, such as the dinoflagellate *Alexandrium catenella* and the diatom *Pseudo-nitzschia australis*, produce potent neurotoxins that can be concentrated in fish or shellfish (Anderson et al., 2021; Bates et al., 2018). Exposure to HAB toxins also can occur through inhalation when fragile cells, such as *Karenia brevis* or *Ostreopsis ovata*, release their toxins into marine waters and sea spray, causing respiratory issues in people (Ciminiello et al., 2014; Lim et al., 2023). Certain species in the diatom genus *Chaetoceros* possess barbed setae that can lodge in fish gill tissues and lead to fish mortalities (GlobalHAB, 2023). Other HAB species such as *Margalefidinium polykrikoides*, *Heterosigma akashiwo*, *Chattonella* spp. kill fish through mechanisms that remain poorly understood. Dense blooms of cyanobacteria and brown algae (e.g., *Aureococcus anophagefferens*) can shade submerged vegetation, impede the feeding of benthic organisms, impede recreational activities, and cause odor and oxygen-depletion problems (Gobler and Sunda, 2012). A variety of freshwater cyanobacteria genera also produce highly potent toxins that are a growing threat in estuarine and marine waters (Burford et al., 2019).

Over the last 30 years, a rich body of international research has enabled advance warning of some HAB threats and provided knowledge to support decision-making to avoid or minimize some HAB impacts. During this period, the freshwater HAB research community has moved forward to generate several commercially available methods for controlling HABs (e.g., Kibuye et al., 2021; Tullos et al., 2025) and supported the development of a robust freshwater algae control industry. In contrast, there has been far less progress in HAB control solutions for estuarine and marine systems (Anderson, 1997). At the same time, many regions have experienced increasing societal, economic, geographic, and environmental impacts from marine HABs (Hallegraeff et al., 2021) while societies continue to rely on marine and estuarine ecosystem benefits to sustain tourism, protect coastal property, and meet expanding global food demand. Further, mounting HAB-related losses have made aquaculture industry insurers more reluctant to provide coverage (Trainer et al., 2020). As a result, there is great pressure to accelerate the development of effective marine and estuarine HAB control.

Bloom control is controversial because of its invasive nature (Anderson, 1997). HAB species are often a minor component of a highly diverse, beneficial planktonic community supporting estuarine and marine ecosystems, and the challenge is how to control or suppress only those problematic species. Achieving an acceptable balance between benefits and perceived negative environmental consequences of control methods is an understandable concern. Adding to this challenge are the logistical hurdles of targeting control treatments within the dynamic, three-dimensional hydrographic environment of blooms that can span hundreds of kilometers.

Thirty years ago, many in the HAB science community believed that the challenges of control were too large and complex and that better understanding of these blooms and their impacts was needed, as were advances in HAB observing and forecasting capabilities (Anderson, 1997). However, there has been a growing demand among many stakeholders for HAB science to produce acceptable, effective, and

scalable HAB control approaches that can be transitioned to commercial partners. A staged, precautionary approach that advances only the most promising control strategies, through laboratory, mesocosm, and field studies, is showing that the benefits of control could outweigh potential undesirable ecosystem impacts (HAB RDDTT, 2008). This realization leads to the central questions of this paper:

1. What progress has been made over the last several decades in the field of marine and estuarine HAB control?
2. What bloom control efforts have been implemented over large scales in natural waters, and how successful (and transferrable and scalable) were those efforts?
3. What can we learn from the countries and regions implementing HAB control that might help advance the field even further?

The focus of this paper is on control strategies targeting marine and estuarine (hereafter, marine) HABs, in particular those approaches that have been tested on larger scales, from mesocosm tanks to direct field applications in marine waters. A review of the state of science for different control methods and case studies is presented to highlight successes and promising approaches. Also included is an overview of some regulatory requirements for HAB control in some regions, including those governing in situ testing and deployment, an evaluation of types of HAB events that are more amenable to control, considerations of relevant societal and scientific challenges, and identification of several government funding programs and a novel U.S. public-private accelerator program that advances HAB control. Although large-scale control treatments in marine waters are on-going in parts of Asia, they are rare in Europe and South America, and even less so in North America, where HAB scientists and engineers struggle with regulatory issues. We highlight here some of those regulatory issues in the U.S. to help inform those in other countries who wish to work towards bloom control but may face similar hurdles. We use this assessment to identify regulatory challenges, targeted science, and investments needed to advance the availability of marine HAB bloom control worldwide.

2. Prevention, control, and mitigation

Strategies to manage HABs typically fall under the headings of prevention, control, and mitigation (PCM), each having different goals and approaches (Boesch et al., 1997). Prevention strategies reflect *a priori* environmental management actions that reduce the incidence and extent of HABs. These schemes often are slow to have noticeable effects on bloom frequency and magnitude. For example, nutrient reduction is widely considered the most effective means of preventing some types of HABs, yet even when there is a solid link between anthropogenic nutrient loadings and specific HABs, effective remediation through improved watershed management or discharge policies can take years to decades to reduce HABs. Moreover, the majority of marine HABs are not related to cultural eutrophication in many nations (e.g., Anderson et al., 2008). Alternate ecosystem restoration efforts such as re-establishing bivalves, fish, and benthic macrophytes also can have bloom prevention benefits (Park et al., 2013; Imai et al., 2021), as can methods limiting the dispersal of non-native species (e.g. ballast water treatment; Gregg and Hallegraeff, 2007).

Mitigation strategies comprise approaches to limit or delay undesirable ecosystem, human health, or economic and social impacts

associated with HABs. The most effective mitigation strategies reduce HAB risks through detection, monitoring, forecasting, and event response. An additional benefit of sustained monitoring of cells and toxins, along with oceanographic and ecological parameters, is that it provides data to help understand HAB ecology - how HABs are impacted by changes in temperature, weather patterns, and other drivers. It also enables development and testing of new management strategies, including bloom control.

Control strategies on the other hand directly kill HAB cells or destroy their toxins, physically remove cells or toxins from aquatic systems, or limit cell growth and proliferation. These strategies are typically short-term (days) with fast response times (< 24 hrs) compared to bloom prevention and mitigation efforts. Control strategies must “thread the needle” to avoid unintended consequences to other ecosystem elements. Although challenging, HAB control strategies are becoming increasingly important for protecting human and ecosystem health given a growing world population, existing widespread HAB challenges, and forecasts that climate and global change may lead to greater prevalence of HABs in the coming years (Hallegraeff, 2010; Wells et al., 2015).

3. Feasibility of bloom control

HAB species are as diverse as the many habitats in which they occur, and HAB events may have minor to severe impacts. Due in part to this complexity, not all HABs are suitable candidates for control. The development, testing and implementation of HAB control strategies depend on four considerations: 1) the value or importance of the impacted resource, 2) the characteristics of the species, its regional scale, and bloom dynamics, 3) the feasibility and cost of implementation, and 4) societal support or resistance to action (Fig. 1).

The value of the impacted resource can vary dramatically, from small-scale artisanal fisheries to industrial-scale ocean aquaculture (e.g., salmon farms) and water-dependent infrastructure (e.g., power or desalination plants). Some impacts are more difficult to quantify, such as the extent to which tourism or recreation industries are affected by blooms, or the extent to which threatened or endangered species or critical habitat are episodically impacted.

Important species and bloom characteristics to consider when

implementing control methods include hydrographic location and spatial extent, cell densities and swimming behavior, and the nature of the harmful species (fragile, rigid, colonial, solitary) and its life cycle. Yet another consideration is the nature of the impact associated with that bloom (e.g., production of toxins versus large but non-toxic biomass).

The feasibility and costs of implementation depend on the geographic scale of the outbreak, the match between a specific control technology and the susceptibility of the HAB species being targeted, the potential adverse environmental impacts of the treatment, the expense and proximity of resources and infrastructure needed for full implementation, and the extent of regulatory compliance that is needed, which often can be the greatest feasibility challenge. An additional consideration is whether management strategies such as shellfish harvesting closures can mitigate impacts and protect valuable industries without the need for complex and potentially controversial control strategies.

Societal priorities and public perception of these three factors are critical aspects. That is, does the combined weight of these elements balance favorably against the perceived environmental consequences of treatment (Kidwell, 2015)? Public resistance to HAB control tends to stem from a fear of avoiding significant environmental harm, while supporters may prioritize managing the bloom to achieve a desired outcome (e.g., protecting fisheries, tourism, human health). This balance differs greatly among societies and often has determined where HAB control strategies have or have not been implemented. Where concerns over action are high, it is important that these (largely environmental) concerns be balanced against the environmental and socio-economic costs of no action (hereafter termed the no-treatment option).

4. Phases of bloom control research and implementation

There typically are four sequentially executed phases for developing a HAB control method: 1) evaluation of a preliminary product or proof of concept, 2) research and development on the product and application strategy, 3) demonstration and validation, and 4) full scale implementation for routine use (Table 1). These phases are sequential but also iterative. For example, products that have demonstrated efficacy and

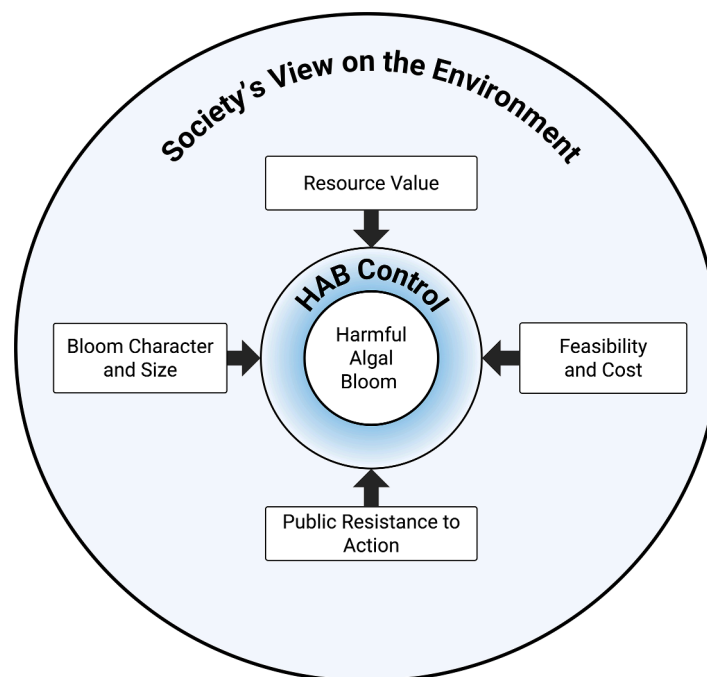


Fig. 1. Societal perspectives influencing decision-making on strategies and suitable candidates for HAB control implementation. Not all HABs are suitable for control but for those that are, methods need to be scaled according to the size of the HAB (shaded circle). Created in <https://BioRender.com>.

Table 1
Phases of HAB control technology development and implementation.

	1) Evaluation of Technology	2) Research and Development	3) Demonstration and Validation	4) Full-scale Implementation
Assessment Criteria	Efficacy optimization Specificity Toxicology Local biogeochemistry Toxin release	Matrix effects Efficacy Environmental impacts Environment biogeochemistry Storage stability Application timing Application duration & frequency	Federal approvals/regulations State/local permits Large-scale confined evaluations Scalability Cost Societal engagement Application licensing Criteria for success Standards of practice Contingency plans Commercialization potential	Operational permit Application license Product registration Local permitting Formalize standards of practice and periodically update Operational guidance Commercialization Law enactment Quality control
Special Considerations	Cost Scalability Resource availability Delivery mechanism Environmental impacts Permitting Technology comparison	Regulatory requirements Supply chain/resource availability Direct and indirect impacts to public health Application licensing Societal perceptions/impacts	Ease of use Transport and storage of large volumes of product Hazards/safety around obtaining & storing large amounts of product	Long-term field monitoring of potential side effects Near real-time HAB alert system to locate bloom Personnel and organization for field operation Training for field operation

safety will undergo re-evaluation after technological modifications to enhance efficacy or to optimize deployment strategies. Preliminary products or concepts generally need to meet specific requirements to advance to subsequent phases. These often include cost, environmental impacts, and efficacy against target species, among other factors.

4.1. Evaluation of new technology

New or improved technologies or products are tested at the lab scale in this phase (from test tubes to *ex situ* mesocosms), under controlled, isolated conditions so that response variables can be tested independently. Key considerations in this phase are product efficacy against target HAB species (based on variable application rates) and specificity (including species-specific considerations), contact-exposure time, impact on non-target organisms, potential release of intracellular toxins following treatment, the effects of natural water biogeochemistry (e.g., pH, salinity, temperature, dissolved organic carbon and other chemical compounds) on product performance, as well as how the product and process affects these parameters. Experiments are designed to support specific permitting data requirements for successive testing strategies.

4.2. Research and development

Products or technologies showing promise in preliminary evaluations move to the next stage of testing, which occurs in mesocosms or at smaller (< 1 acre) limited duration, confined field scales (sometimes termed pilot studies). These larger scales enable evaluation of more complex matrix effects, weather impacts, community-level non-target impacts, application timing and methods, product storage stability/viability, geographic and habitat differences, and means to increase overall effectiveness. These are all major challenges, and thus large and well-financed team efforts are often required. Limited-use permits are usually necessary prior to these field trials and may include safety protocols to modify or discontinue a trial in the event of unforeseen negative environmental impacts. Limited-use permits are often site-specific and require coordination with local, tribal, national, or international rules and regulations.

4.3. Demonstration and validation

In this transition phase the product or technology is tested for longer

durations in larger settings. Trial designs are informed by results from the Research and Development phase. Early societal engagement is critical in this phase to build trust with the community and foster an understanding of, need for, acceptance of, and willingness to see HAB control products tested locally. Regulatory evaluation and approval are centerpieces of this phase, and may require product testing permits or permit exceptions, as well as registration, application permits, or licensing depending on site-specific requirements. There is significant variability in regulatory processes among nations and sub-national jurisdictions. The regulatory approval process is often lengthy (months to years) and can have multiple criteria and timelines for implementation due to this variability. Engagement with all governing bodies is necessary to build support for large scale or longer duration trials.

Scalability and cost effectiveness are particularly important considerations during this phase to best inform on the potential for large-scale applications and broad commercialization. For example, some highly effective strategies may be cost-prohibitive to treat large areas but may be appropriate to protect highly valued resources at smaller scales. Alternatively, cost-effective and highly efficacious strategies for larger blooms may still face supply chain issues for raw materials or logistical constraints to large-scale dispersal that limit the possible scales for application. Additional considerations relate to the complexity and feasibility of product application, including availability of trained personnel, transport and deployment vehicles (aircraft, watercraft, trucks), protective equipment, spray drift, dispersal equipment, etc. Logistical considerations include availability of the product(s), long-term storage, transportation to treatment sites, dispersal methodologies, disposal of excess or spent product, etc. Managing the aerial or aquatic dispersal to maximize HAB exposure while limiting impacts to unaffected areas is a major consideration that may require engaging industry partners or professionals with relevant expertise, such as those with oil spill dispersant experience. Indeed, some product registrations that may be applicable to control methods require the use of licensed applicators to deploy the product. Lastly, the ease of access to the treatment sites needs to be considered, which may also require permits in restricted areas.

A feasibility study is typically conducted during the transition phase to establish the preliminary metrics for success. These include determining thresholds which include, but are not limited to, upper product limits for sensitive species or bloom phases, criteria to determine minimal effective concentrations, and benchmarks for termination or

modification of a trial if adverse environmental impacts are observed. An open line of communication is typically established with the local community, resource managers, and health officials to share metrics of success and potential concerns and to detail what to expect during a trial. Assistance can also be requested from interested parties to help monitor for potential adverse effects.

4.4. Implementation

A product can only move to the implementation phase once it has been proven to be effective and has all necessary product registration, regulatory approvals, and operational permitting. At this point products can be transitioned into routine use by governments or the private sector. Resource managers and product applicators need to follow local and national regulations, formalized standards of practice, and any related reporting requirements. Additional operational guidance may be needed, and should be periodically updated, to support appropriate and safe use of products to reflect technological advances.

5. Approaches to bloom control

Bloom control approaches are diverse but can be broadly grouped into biological, chemical and physical methods (Boesch et al., 1997; Table 2), although some bridge across these boundaries. No single approach is universally applicable, and each has unique short-term impacts relative to longer-term benefits. The balance among these must be compared against the consequences of the no-treatment option before implementation recommendations are possible.

We present here a brief review of each category, along with a few unique case studies of successful and promising applications to control marine HABs in several nations. These case studies highlight several approaches but do not represent all current bloom control efforts.

The case studies here span from experimental through pilot studies to full implementation strategies. In many (most) situations these studies have focused on the scientific demonstration of efficacy and ecological consequences but have not considered the ethical aspects. Given the broad variability in ethical standards among nations and regions, it is beyond the scope here to include these assessments in the following case studies. However, local ethical guidelines should be assessed within the strategies to gain public acceptance of bloom control approaches.

5.1. Biological bloom control

Biological control uses microorganisms, including pathogens, viruses, parasites, or their excreted products, to kill, inhibit, or remove HAB cells or toxins (see reviews: Anderson et al., 2017; Sellner and Rensel, 2018; Anabtawi et al., 2024; Balaji-Prasath et al., 2022; Coyne

et al., 2022; Imai et al., 2021; Pal et al., 2020). There can be overlap with some chemical control methods (e.g., use of algacidal compounds isolated from live organisms) but here we group these approaches under biological control.

Biological methods are increasingly recognized as environmentally sustainable options for controlling HABs (reviewed by Gallardo-Rodríguez et al., 2019). These methods can reduce biosafety concerns when native species (or their secreted or extracted compounds) are used. A benefit of biological approaches is that agents may target specific HAB groups or species, thereby reducing collateral effects on non-target organisms. An added advantage is that some bioagents may have the potential to both control HAB species and degrade released toxins (Coyne et al., 2022). An example is the algacidal bacterium, *Rhizobium* strain AQ_MP, that lyses *Microcystis aeruginosa* and contains functional genes and metabolic pathways that can degrade microcystin toxins in fresh-water environments (Li et al., 2021). The benefits of such approaches are likely to increase acceptance of biological control of HABs by the public and natural resource managers, which is crucial for the widespread application of these methods.

A common concern surrounding biological control is the potential that it may not solely target the problem organism but instead affect a broad range of species. Even if shown to be well focused in early field trials, there is concern that this specificity might shift after prolonged use, or when the background planktonic assemblages change, potentially leading to long-term and significant environmental consequences. Another concern is that environmental factors may affect the efficacy of bioagents. For example, Grasso et al. (2022) reviewed how temperature, nutrients, and irradiance can affect various facets of cyanophage ecology, including burst size, latent period, and infectivity, among others, which in turn impact the success of viruses in HAB control. Similarly, Coyne et al. (2022) discuss how temperature, grazing pressure, and bacterial densities influence the efficacy of algacidal bacteria in open-water trials.

Yet other issues are scalability and deliverability, as there are significant challenges with producing the volumes of organisms or their extracts necessary for economically and logistically feasible applications, even over moderate spatial scales. Most HABs occur sporadically in time and space so applications using live bio-treatment organisms would require a means to maintain enough healthy organisms to make usage-on-demand feasible. Extracts may be amenable to extended storage without significant loss of potency, but storage adds more testing steps and cost to the overall development process. Furthermore, most current research on biological control methods has primarily focused on their effects on algal species, with far fewer studies quantifying their impacts on higher trophic levels. More studies on non-target organisms at multiple trophic levels are required to ensure the biosafety and selectivity of bioagents for HAB control, e.g. Fernando et al., 2025;

Table 2
Overview of selected marine HAB control methods with current status of their use.

Control method	Current Scale of treatment	Nations	Status of methodology
Biological Control			
Seaweeds	Microcosms, mesocosms	Japan, USA	Experimental
Virus	5 km ²	Japan	Routine in one prefecture
Algacidal bacteria	Mesocosms	USA	Experimental
Chemical Control			
Hydrogen peroxide	0.12 km ²	Netherlands	One successful application, but none since
Copper	40 km ²	USA	Two field applications successfully removed <i>Karenia brevis</i> , but not tried again due to collateral lethality and cost
Physical Control			
Plant-based chemicals	4000 m ²	USA	Early experimental field testing at select sites
Deep-water upwelling	10,000 m ²	Canada, USA, Scotland, Norway, Chile, Tasmania/Australia	Operational at fish farms in Canada, USA, Scotland, Norway, Chile, Tasmania/ Australia
Clay flocculation	100 km ²	China, South Korea, Malaysia, Vietnam, Turkey	Routine operational use in China and Korea; still under evaluation in other countries

Simons et al., 2021, 2025).

In the following sections, three biocontrol case studies are highlighted - one using a virus, one an algaecidal bacterium, and a third using a cultivable and allelopathic seaweed. In terms of other biocontrol options, no large-scale treatments have been attempted using parasites, but that approach should not be ruled out as studies suggest that parasites may play a role in the termination of some natural HAB outbreaks. Current research primarily focuses on parasitic dinoflagellates, such as *Amoebophrya* spp. (Bai et al., 2007; Long et al., 2021; Velo-Suárez et al., 2013; Park et al., 2004) and *Parvilucifera* spp. (Alacid et al., 2020; Park et al., 2004), which infect other dinoflagellates and contribute to the termination of their blooms. These parasites are less specific than viruses, with some being capable of infecting over 50 HAB species across various genera (Alacid et al., 2020; Bai et al., 2007; Park et al., 2004; Velo-Suárez et al., 2013). Parasitic fungi such as chytrids from the phylum Chytridiomycota infect both marine and freshwater HABs, including cyanobacteria, dinoflagellates, and diatoms (Gleason et al., 2015). Chytrids have shown potential in controlling freshwater cyanobacterial blooms (e.g., Gerphagnon et al., 2013; McKindles et al., 2023) and marine HAB species, including *Pseudo-nitzschia* (Hanic et al., 2009; Gleason et al., 2015). However, their effects on other marine HAB species are less studied (Lepelletier et al., 2014). Non-parasitic fungi have been applied for HAB control in freshwater ecosystems. Anabtawi et al. (2024) provide a detailed review of this and other strategies in freshwater environments.

Likewise, another type of biocontrol involves bacterial communities associated with seagrasses and macroalgae. Substrates like seagrass and macroalgal beds attract natural algaecidal bacteria that kill or inhibit the growth of various HAB species (Imai et al., 2006b, 2021; Inaba et al., 2017, 2018, 2020; Onishi et al., 2020; Mehrotra et al., 2021; Mayali and Azam, 2004; Meyer et al., 2017). Types of seagrasses and macroalgae reported as sources range across multiple taxonomic groups, including two seagrass species (*Zostera marina* and *Z. japonica*), four green algae (*Cladophora ohkuboana*, *Ulva australis*, *U. lactuca*, and *Ulva* sp.), five red algae (*Chondrus ocellatus*, *Corallina pilulifera*, *Gelidium elegans*, *Gelidium* sp., and *Gloiopeltis furcata*), and three brown algae (*Saccharina japonica*, *Sargassum duplicatum*, and *S. thunbergii*), with the detected bacterial densities ranging between 10^4 and 10^8 CFU (or MPN) g⁻¹ wet weight (reviewed by Inaba, 2024). Bloom suppression can be substantial, e.g., the growth of a *Chattonella marina* var. *antiqua* culture was terminated when filtered seawater containing natural antagonistic bacteria from a *Z. marina* bed was added (Inaba et al., 2019).

The taxonomic groups of the antagonistic bacteria isolated from seagrass and macroalgal beds are mostly from two phyla, *Bacteroidetes* and *Proteobacteria*. Although the specific algaecidal mechanism is not known, both groups appear to be related to bacteria known for decomposition of polysaccharides (Inaba, 2024), constituents of the cell surfaces of dinoflagellate and raphidophyte species (Yokote and Honjo, 1985; Wang et al., 2020).

In addition to hosting antagonistic bacterial communities, macroalgae and seagrass also are known to produce allelopathic substances to suppress the growth of HAB species (Tang and Gobler, 2011; Tang et al., 2014; Sylvers and Gobler, 2021; Díaz-Alonso et al., 2024). These findings suggest that protection and restoration of macrophyte beds may enhance nearshore coastal resilience against HABs.

5.2. Case studies of biological control of HABs

5.2.1. Case study: use cultivatable seaweeds to mitigate blooms of *Alexandrium catenella*

Background: Annual global seaweed aquaculture production exceeds 32 million metric tons and is worth >13 billion USD per annum with Asian nations dominating this global market (FAO, 2020; Ferdouse et al., 2018). While North America is not currently a major contributor to global seaweed aquaculture production, there is vast potential for growth, particularly in the cultivation of phaeophyte *Saccharina*

latissima, also known as sugar kelp (Kim et al., 2015; Augyte et al., 2017, 2019). Seaweeds can be a primary component of integrated multitrophic aquaculture (IMTA) systems (Chopin et al., 2001; Neori et al., 2004; Park et al., 2018), as many cultivated seaweeds have a high assimilative capacity for nitrogen and phosphorus (Ahn et al., 1998; Kim et al., 2015; Marinho et al., 2015), allowing for effective nutrient control. There is also emerging evidence that aquaculture of macroalgae has the potential to mitigate coastal acidification via rapid CO₂ assimilation (Wahl et al., 2018; Young and Gobler, 2018; Fernández et al., 2019; but see Hurd et al., 2024). The nutrient control and potential pH elevation from open-water seaweed aquaculture both have potential for mitigating HABs. The incidence of HABs may decrease as nutrient management strategies are established to reduce eutrophication (Heisler et al., 2008; Imai et al., 2006a; Paerl et al., 2018) and it has also been shown that many microalgae, including harmful dinoflagellates, may experience reduced growth rates in higher pH waters (Hansen, 2002). Additionally, there are many studies documenting the allelopathic activity of several seaweeds and seaweed extracts towards HABs (Tang and Gobler, 2011; Tang et al., 2014; Gharbia et al., 2017).

Implementation: For this case study (Sylvers and Gobler, 2021) a series of experiments were performed that scaled in complexity and realism, ranging from simple culture experiments to mesocosm experiments that simulated IMTA with bivalves and seaweeds exposed to *Alexandrium*. Culture experiments were performed with multiple strains from the Northeast U.S. and Canada. Mesocosm experiments were performed using cultures and bloom water. Seaweeds assessed included *Ulva* spp., *Chondrus crispus*, and *Saccharina latissima* (a.k.a. sugar kelp), all of which have been used in an aquaculture setting in the U.S. and/or elsewhere. While *Ulva* spp. and *C. crispus* were collected from the wild across New York, USA, estuaries, *S. latissima* was obtained from the Great Gun oyster farm in Moriches Bay, NY, USA. Prior to deployment on the oyster farm, the sugar kelp was cultivated in a laboratory with reproductive tissues collected from Montauk, NY, and spores released from this tissue set on seed string that was subsequently deployed onto ropes on the oyster farm after six weeks of laboratory cultivation. *Alexandrium* strains and wild bloom populations were co-cultured with and without each seaweed over one-week periods and changes in cell densities, nutrients, pH, and photosynthetic efficiency were monitored. Mesocosm experiments with 300 L of *Alexandrium* bloom water were similarly performed (Fig. 2). Finally, mesocosm experiments with *Alexandrium* cultures, seaweeds and blue mussels (*Mytilus edulis*) were performed to assess how seaweed exposure might mitigate saxitoxin accumulation during a HAB. In all cases, seaweeds were administered at the range of densities (grams per liter) found on the Great Gun oyster farm, ensuring environmental realism. While smaller scale culture experiments utilized pieces of seaweeds excised from larger blades (*S. latissima*, *Ulva* spp.) or branches (*C. crispus*), larger volume mesocosm experiments used intact blades and stipes of *S. latissima* and *Ulva* spp.

Application Evaluation: Co-culture growth assays of *A. catenella* exposed to environmentally realistic concentrations of each macroalgae showed that all species except low levels of *C. crispus* caused cell lysis and significant reductions in *A. catenella* densities relative to control treatments of 17–74 % in 2–3 days and 42–96 % in ~one week ($p < 0.05$ for all assays). Bottle incubations of field-collected, bloom populations of *A. catenella* experienced significant reductions in cell densities of up to 95 % when exposed to aquaculture concentrations of all three macroalgae ($p < 0.005$ for all). The stocking of aquacultured *S. latissima* within mesocosms containing a bloom population of *A. catenella* (initial density: 3.2×10^4 cells l⁻¹) reduced the population of *A. catenella* by 73 % over 48 h ($p < 0.005$) while *Ulva* addition caused a 54 % reduction in *A. catenella* over 96 h ($p < 0.01$). In a toxin accumulation experiment, *S. latissima* significantly lessened ($p < 0.05$) saxitoxin (STX) accumulation in blue mussels (*Mytilus edulis*), keeping levels (71.80 ± 1.98 µg STX 100g⁻¹) below U.S. closure limits (80 µg STX 100g⁻¹) compared to the untreated control (93.47 ± 8.11 µg STX 100g⁻¹). Among the three seaweeds, *S. latissima* was the most effective at inhibiting *A. catenella*

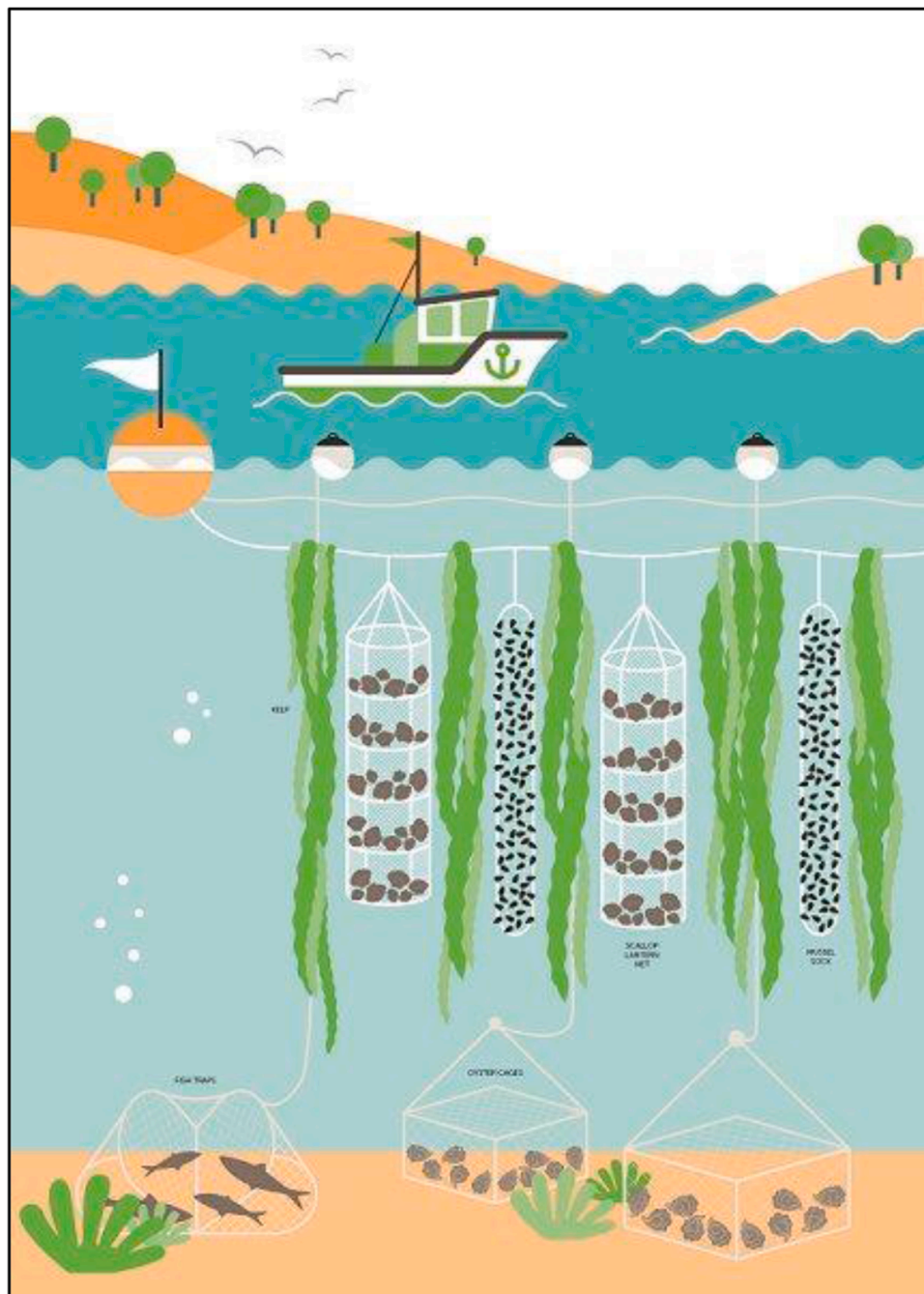


Fig. 2. Three-dimensional ocean farming of seaweeds deployed vertically with bivalves and/or fish in an aquaculture setting; image from Sustainia with permission.

followed by *Ulva* spp. In contrast, *C. crispus* was less effective. Careful monitoring and manipulation of nutrients, pH, and bacteria during experiments indicate that the seaweeds' primary anti-*A. catenella* activity was the release of allelopathic chemicals. Nutrient competition, pH elevation, and macroalgae-attached bacteria may have played a contributory role in some experiments and in an ecosystem setting all factors would contribute to mitigating HABs. Collectively, these results suggest that the integration of seaweeds with bivalve aquaculture establishment should be considered as a non-invasive, environmentally friendly, and potentially profit-generating measure to mitigate *A. catenella*-caused damage to the shellfish aquaculture industry.

Large Scale Treatments: To date, the large-scale deployment of seaweeds to mitigate HABs has not been purposely evaluated. In New York, 4000 m² kelp deployments have been established in regions that

experience *Alexandrium* blooms (e.g., Violet Cove oyster farm, Moriches Bay, NY, USA; C. Gobler, pers. obs.). In southeast Alaska, the Seagrove Kelp Company has cultivated 0.5 km² of *S. latissima*. The seaweed farming region near Rongcheng city in east China's Shandong Province is purported to cover 100 km² of the Yellow Sea (Cheng et al., 2022). Such large-scale deployments of seaweeds hold the promise to provide 'natural experiments' to evaluate the efficacy of seaweeds in mitigating HABs in an ecosystem setting.

Environmental Impacts: Unlike most HAB control approaches, seaweeds are naturally occurring components of coastal ecosystems. The environmental impacts of seaweed farming are largely positive. Seaweeds such as kelp provide habitat and a predation refuge for marine animals (Norderhaug et al., 2005; Teagle et al., 2017; Smale et al., 2013) while concurrently sequestering significant amounts of carbon (Chung

et al., 2013; Laurens et al., 2020; Hurd et al., 2022) and mitigating eutrophication and deoxygenation (Gao et al., 2022). Extensive kelp deployments can be important for nutrient control and can serve as the basis for symbioses with marine organisms (Duggins, 1980; Teagle et al., 2017). Seaweeds are also a food source for some marine organisms (Norderhaug et al., 2005; Vanderklift et al., 2008) and are known to moderate temperature fluctuations and reduce seabed erosion (Løvås and Tørum, 2001; Rothäusler et al., 2011). Studies have shown kelp aquaculture can regionally mitigate ocean acidification and subsequently increase the growth rates of bivalves (Young et al., 2022) and may even serve as a supplemental food source for some bivalves. When deployed at scale, negative environmental impacts of seaweed farming could include occlusion of light reaching submerged aquatic vegetation and creation of a navigation hazard for vessel traffic in coastal zones.

Successes and challenges: While the success of the case study described here is fully consistent with peer-reviewed studies of other HABs being mitigated by seaweeds (Tang et al., 2011, 2014; Sylvers and Gobler, 2023, 2025), presently the largest challenge for the seaweed control of HABs is understanding and executing it at ecosystem scale. In an ecosystem setting, all control mechanisms including allelopathy, nutrient control, pH elevation, and algacidal bacteria will be active in mitigating HABs. The spatial sphere of influence of these factors around seaweed aquaculture locations, however, is currently unknown. Most aquaculture farms that deploy seaweed and bivalves use a three-dimensional (3D) farming approach whereby seaweeds are deployed vertically along the horizontal deployment of bivalves, with seaweeds often in physical contact with bivalve aquaculture gear (Fig. 3). In some cases, seaweeds are deployed within aquaculture bags containing bivalves, assuring physical contact. Still, in an open water aquaculture setting, allelochemicals, algacidal bacteria, high pH / low nutrient waters created by seaweeds will be continually exchanging with

ambient seawater, diluting the impacts of seaweeds. Ultimately, the effectiveness of seaweed aquaculture for mitigating HABs will be determined by this dilution, suggesting that success will be maximal for larger scale seaweed deployments that have minimal tidal/seawater exchange, and therefore that small-scale deployments in regions with strong water movement will be less likely to impact regional HABs.

Regulatory, social, and application issues; scalability and breadth of applicability: Seaweed farming is common practice in many coastal zones across the globe including the U.S. As such, it is somewhat unique among HAB control approaches in that it is already being used globally at significant scale (e.g. >100 km² in China) and, therefore, the regulatory structure for permitting such activities already exists and there is already broad social acceptance for seaweed farming. Moreover, seaweed farming is a revenue-generating practice and is often adapted into bivalve farms by vertically deploying seaweeds across regions where bivalve aquaculture already exists, meaning bivalve farms need not compromise the spatial extent of their existing bivalve crops when incorporating seaweed aquaculture. And beyond bivalve farms, seaweeds have also been shown to mitigate the ichthyotoxicity of HABs caused by *Margalefidinium polykrikoides* (Sylvers and Gobler, 2023) demonstrating that seaweed aquaculture could also be used to mitigate HABs on fish farms. Among the HAB control options available, it would seem seaweed aquaculture may be considered the least invasive and easiest to implement due to the ability to generate revenue and the ubiquity of its current use globally.

5.2.2. *Heterocapsa circularisquama* virus in Japan

Background: Viruses have the potential to be effective agents for controlling HABs in both marine and freshwater systems (reviewed by Grasso et al., 2022; Ibrahim et al., 2022; Pal et al., 2020). Viral treatment relies on species-specific interactions leading to viral lytic or lysogenic

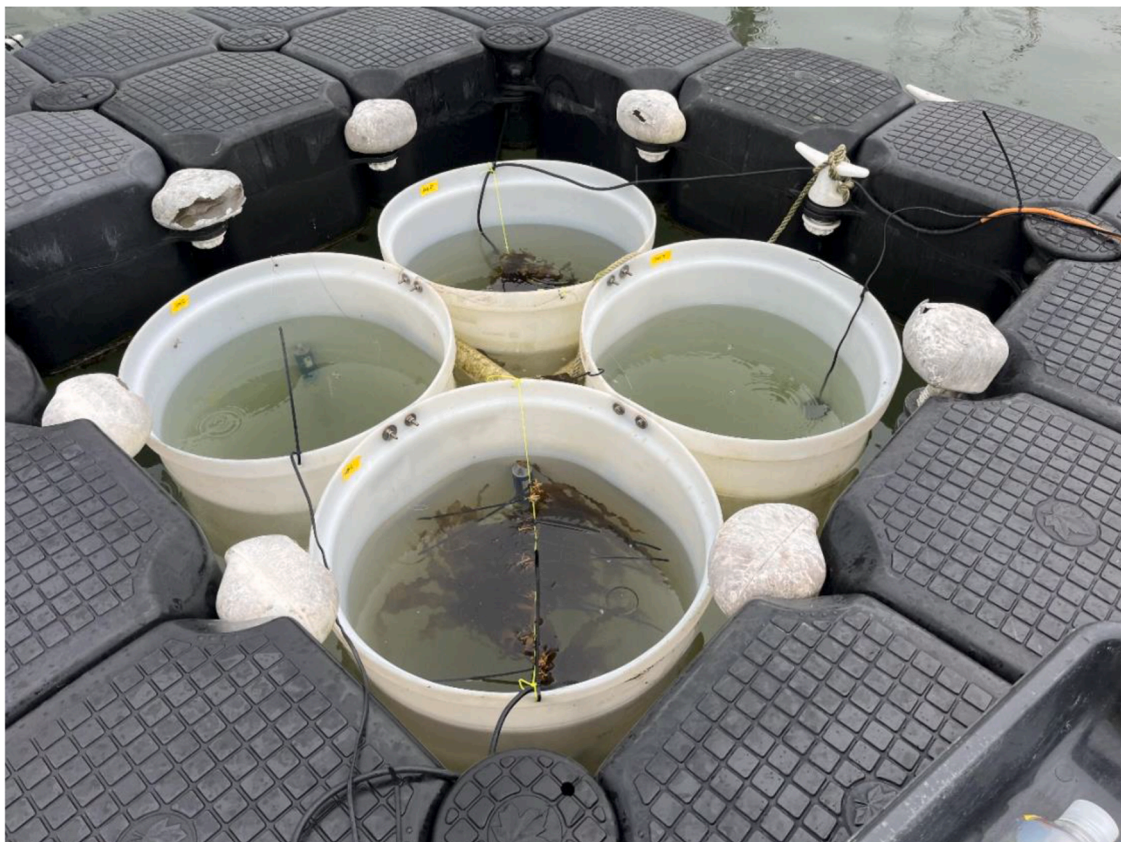


Fig. 3. Deployment of *A. catenella* bloom water in 300-liter mesocosms with and without kelp at the Stony Brook – Southampton Marine Science Center, Southampton, NY. Exposure to kelp significantly reduced *A. catenella* after 48 h. Image from Laine Sylvers.

life cycles (reviewed by Anabtawi et al., 2024; Grasso et al., 2022). Most studies on viral control of HABs have focused on cyanophages, which specifically target cyanobacteria (e.g., Grasso et al., 2022; e.g., Lin et al., 2020; Rong et al., 2022; Zhang et al., 2020a). Cyanophages display varying levels of host specificity, from infecting a single strain within a species to multiple genera. For example, cyanophage Ma-LMM01 specifically infects a toxic strain of *Microcystis aeruginosa* (Yoshida et al., 2006), while cyanophage A-CP1, isolated by Deng and Hayes (2008), can infect multiple species of *Microcystis*, *Anabaena*, and *Planktothrix*.

Fewer studies have explored the use of viruses to control marine eukaryotic HABs. Notable examples include the viruses HaV (Nagasaki and Yamaguchi, 1997) and HaNIV (Lawrence et al., 2001), which infect the raphidophyte *Heterosigma akashiwo*, and the virus HcRNAV, which lyses the dinoflagellate *Heterocapsa circularisquama* (Mizumoto et al., 2007; Nakayama and Hamaguchi, 2022; Nakayama et al., 2020) - see below. These marine eukaryotic HAB-infecting viruses are highly species-specific. For instance, the virus HaV, isolated from Japan's coastal waters, infects and lyses *H. akashiwo* without affecting other raphidophytes or phytoplankton in other classes (Nagasaki and Yamaguchi, 1997). Additionally, two types of HcRNAV (UA and CY) have been described based on their intra-species host specificity and the amino acid sequence of the major capsid protein, highlighting the complexity of the HAB host-virus system (Nakayama et al., 2013).

Case Study: Lake Kamo, Japan is a saltwater lake on Sado Island, Niigata Prefecture, with a shore length of 17 km, an area of 5 km², and a maximum depth of 9.7 m. The Lake was originally a freshwater lake fed by four rivers. Approximately 120 years ago, a channel was excavated to connect it to the open sea to make it a saltwater lake. The channel is small, with a width of 28 m, a length of 200 m, and an average depth of 1.7 m, leading to poor seawater exchange. Operations of cultured oysters in Lake Kamo suffered the first serious bloom of the marine dinoflagellate *Heterocapsa circularisquama* in the fall of 2009, resulting in economic losses estimated at over 2 million USD. This dinoflagellate specifically kills bivalves, including cultured Pacific oysters and pearl oysters. To address this problem, a biological control method was developed using the *H. circularisquama* RNA virus (HcRNAV).

Routine monitoring demonstrated that HcRNAV proliferates during the declining phase of *H. circularisquama* blooms, followed by virus accumulation in the sediment (Tomaru et al., 2007; Nakayama and Hamaguchi, 2016). The virus is generally host-specific and has high replication rates, and therefore has limited effects on co-occurring organisms, allowing high viral titers to be used. One significant benefit is that the method uses natural sediment containing HcRNAV, instead of HcRNAV alone, as adding natural sediment to surface waters is more acceptable to the public than the introduction of cultured viruses. Sediments are also abundant and can be easily collected whereas culture facilities to produce pure virus can be expensive and time-consuming.

Implementation: From 2019–2023, this method was implemented three times in Lake Kamo in collaboration with local officials and fishermen but has not yet been used in other areas where *H. circularisquama* occurs. The safety and effectiveness of the sediment containing HcRNAV was first demonstrated under laboratory and field conditions, revealing the amount of sediment required to kill *H. circularisquama*, the environmental impact of sediment dispersal, and the effects of the HcRNAV in the sediment on other aquatic organisms (Nakayama et al., 2020). These data were required for the approval and cooperation of fishermen and the city, local, and prefectural governments. From the start of this research in 2011, it took almost 8 years to receive permission for the practical use of sediment-containing virus as a HAB control method in 2019, as detailed below.

Application Evaluation: The permitting process began with a small-scale microcosm experiment (closed-bottle test) conducted in 2011 to verify the effect of virus-containing sediment on a natural *H. circularisquama* population. When *H. circularisquama* increased to about 8000 cells mL⁻¹ in Lake Kamo, bottles were filled with bloom water. Then, virus-containing sediment (frozen in 2009, then thawed

before use) was added to the treatment bottles and autoclaved sediment was added to the control bottles. The effect of the added sediment was assessed after 5 days of exposure. To incubate the bottles in as natural a state as possible, they were immersed in the lake at a depth 50 cm from the surface (Nakayama et al., 2013).

Field demonstrations were essential to move this biological method to larger-scale use, but such experiments had never been conducted in Japan. The regulatory and social permissions for a mesocosm field trial took 5 years after the first successful bottle test (Table 3). Permission was needed from the Fisheries Agency (under the Ministry of Agriculture, Forestry and Fisheries of Japan), the Niigata Prefectural government, the Niigata city office, the fishing association, and local fishermen. Among these, Prefectural government permission was most critical. Prolonged consultations with local fishermen led them to eventually request approval of the trials. As a result, the prefectural government recognized the potential effectiveness and environmental acceptability of this method and responded positively to the request. This decision, a first for Japan, led to the de facto approval by the Fisheries Agency and Sado City Hall, which enabled the 2016 field trials to begin in Lake Kamo (to be followed later by a larger-scale application in 2019).

Two floating cage mesocosm experiments were used for the first field trials. The mesocosms were made with canvas sheets used for aquaculture and each was filled with 15,000 L of ambient lake water containing ca. 3800 cells mL⁻¹ of *H. circularisquama*. Control and treatment sediments were added to the respective mesocosms as was done for the earlier bottle experiments. There was a 99 % decrease in *H. circularisquama* cell density in the treatment relative to the control mesocosm (from ca. 3000 to ca. 40 cells mL⁻¹) within five days (Nakayama et al., 2020).

Large-scale treatment: The field treatment in Lake Kamo in 2019 (Fig. 4a) was preceded by collection of sediment containing HcRNAV (Fig. 4b) from the Lake in 2018, after the termination of a *H. circularisquama* bloom. In July 2019, a *H. circularisquama* bloom was detected in its early stages (760 cells mL⁻¹). The prefectural government immediately approved the application of sediment. First, the bloom water and the sediment containing HcRNAV were mixed in a small container and incubated for 3–4 h to increase HcRNAV abundance before dispersal. Because this approach effectively creates water that is highly enriched with HcRNAV, only a very small amount of sediment was needed to treat the entire lake. Specifically, ~ 5 kg of bottom sediment was used in this way, with the resulting enriched water used to treat 5 km² (Fig. 5). The spraying was carried out every month from July to September in 2019, effectively limiting *H. circularisquama* cell proliferation to low densities. It was decided that additional treatments would be done if a *H. circularisquama* outbreak returned, but the bloom declined to low densities after the application in 2020, and treatment has not been necessary since 2021. In recent years, however, *H. circularisquama* blooms have been occurring at other locations in Japan, so local governments are preparing to spread sediment containing HcRNAV in these areas. The success of the treatment at Lake Kamo has led to an acceptance of this method in Japan.

Environmental Impacts: Two steps were taken to minimize the potential environmental impacts of dispersing water and sediments

Table 3

Timeline for approval of virus use as a method of HAB control in Japan.

2009	<i>Heterocapsa circularisquama</i> bloom outbreak occurred. Efficacy and protocols of virus control were studied in the lab.
2011	A closed-bottle test was conducted in Lake Kamo. Field test permits were negotiated with the Niigata prefectural government and local authorities.
2014	Niigata prefectural government approved field testing of the method.
2016	An open field trial using floating mesocosms was conducted in Lake Kamo. Practical application permits were negotiated with the prefectural government.
2019	In a full field implementation of the method, all of Lake Komo was successfully treated with HcRNAV. The prefectural government provided the permit.

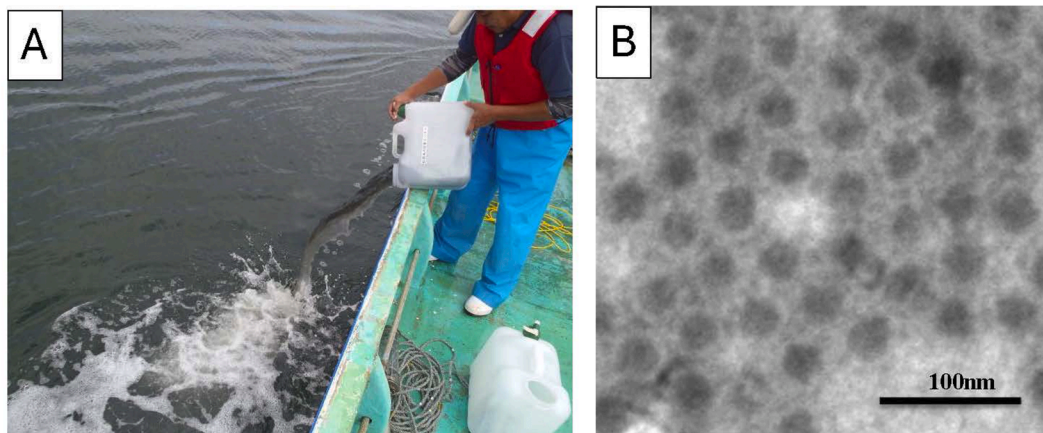


Fig. 4. (a) Spreading sediment containing HcRNAV and (b) negative staining image of HcRNAV by transmission electron microscopy.

containing HcRNAV on marine life such as shellfish and plankton. The first was to minimize the impact of sediment-linked nutrients and turbidity by using a two-stage process. As noted above, small amounts of sediment containing HcRNAV were incubated with seawater containing *H. circularisquama* in a ~50 L tank to increase viral abundance, after which the solution was sprayed onsite (Nakayama et al., 2020). This method reduced the amount of sediment to be spread while enriching the abundance of HcRNAV in the application. A 2016 field demonstration revealed the effectiveness of this two-stage application (Nakayama et al., 2020). Second, the sediment was frozen to ensure that the cysts of harmful or toxic species were non-viable, which was confirmed by testing (unpublished data). Furthermore, the sediment was tested against bivalves and the findings show that sediment dispersal did not affect their survival (N. Nakayama, unpubl. data). The combination of these steps confirmed that the spreading of sediments containing HcRNAV would have negligible effects on the environment and other aquatic organisms.

Successes and challenges: The public generally views the word “virus” as a synonym for a pathogen, so it is difficult to obtain social approval for the practice of spraying viruses in the natural environment. Of benefit here was the planned use of natural materials from the local sediments (i.e., not from other regions). Regular project outreach was conducted at a variety of biannual meetings with local officials, including workshops that explained efforts to improve the local marine environment in addition to the control of *H. circularisquama* blooms. In parallel, outreach was conducted at biannual local community meetings to explain this method and to present research results. The current challenge is to replicate the treatment success demonstrated in Lake Kamo at other coastal locations in Japan that are impacted by *H. circularisquama* blooms. As a cautionary note, care will be needed with routine testing to ensure that the host range of natural viral batches isolated for treatment do not expand through viral recombination or horizontal gene transfer.

Regulatory issues: The Japanese government had no official regulations concerning the spreading of organisms in the environment and was thus reluctant to permit these unprecedented activities. In Niigata Prefecture, where Lake Kamo is located, fishermen and the local community gradually came to understand this method and sought approval from the local government. The local prefectural government granted a permit to conduct a mesocosm test four years after communications began, and a total of nine years was needed to receive a permit for an open-water application of the virus-containing sediment in the Lake.

Social Issues: Researchers were proactive in explaining to fishermen and local communities how HABs were contributing to poor oyster growth in Lake Kamo. This effort helped to develop a relationship of trust between the researchers and local communities. In Japan, even if most people agree, no major change will occur unless a local leader or

government official approves. For example, permits were also requested from another prefectural government for a different region, but approval has yet to be granted due to the negative social perceptions about spreading viruses. If a *H. circularisquama* bloom occurs in a different area, it will be easier to obtain permission from the local government if sediment (containing HcRNAV) from that specific area is used for bloom treatment. Therefore, outreach activities will be conducted in each area where treatment is needed, and the manual describing the detailed technique will be shared.

Scalability and breadth of applicability: A review by Grasso et al. (2022) argues that scalability is the most significant challenge to the use of viruses as bloom control agents. This may be true for many applications, but in the case of HcRNAV, the presence of virus in bottom sediments and the ability to amplify those abundances in a seawater slurry immediately before dispersal, as described above, have eliminated this concern. Given the small amount of sediment (5 kg) needed to treat a 5 km² lake, the HcRNAV bloom control method is well suited for treatment of large areas when necessary. Treatment of a 100 km² area might only require 100 kg of sediment, which would be quite easy and inexpensive to collect, amplify, and disperse. In terms of the applicability of the method to other HAB species, viruses coinciding with blooms of *Karenia mikimotoi* and *Heterosigma akashiwo* (Nagasaki and Yamaguchi, 1997; Lawrence et al., 2001) have been isolated but have not yet been used in targeted control efforts. The characteristics of these viruses and their relationships to their hosts are currently being investigated. Note also that high levels of virus specificity as well as differing environmental conditions (Grasso et al., 2022) might result in an effective biocontrol agent from one coastal region not being effective in another.

Application issues: Viruses accumulate at the sediment surface, so manpower, special equipment, and a vessel are needed to collect sediments prior to freezing and HAB treatment.

A manual is currently being prepared, describing the series of operations, including collection of sediment containing HcRNAV, sediment preservation, and sediment spreading. This will be published on the Japan Fisheries Research and Education Agency website and local officials will be trained to implement this method using the manual as a guide.

5.2.3. *Shewanella* sp. IRI-160 in the United States

Background: The interaction between phytoplankton and bacteria in aquatic ecosystems is diverse and complex (Fei et al., 2025; Amin et al., 2015; reviewed by Coyne et al., 2022; Durham et al., 2017; Seymour et al., 2017). While some bacteria generate beneficial effects for phytoplankton (e.g., Burgunter-Delamare et al., 2020; Cruz-López and Maske, 2016; Cruz-López et al., 2018; Yarimizu et al., 2018), many exhibit algacidal activity by inhibiting algal growth or lysing algal cells (e.g., Dungca-Santos et al., 2019; Hare et al., 2005; Shi et al., 2023;

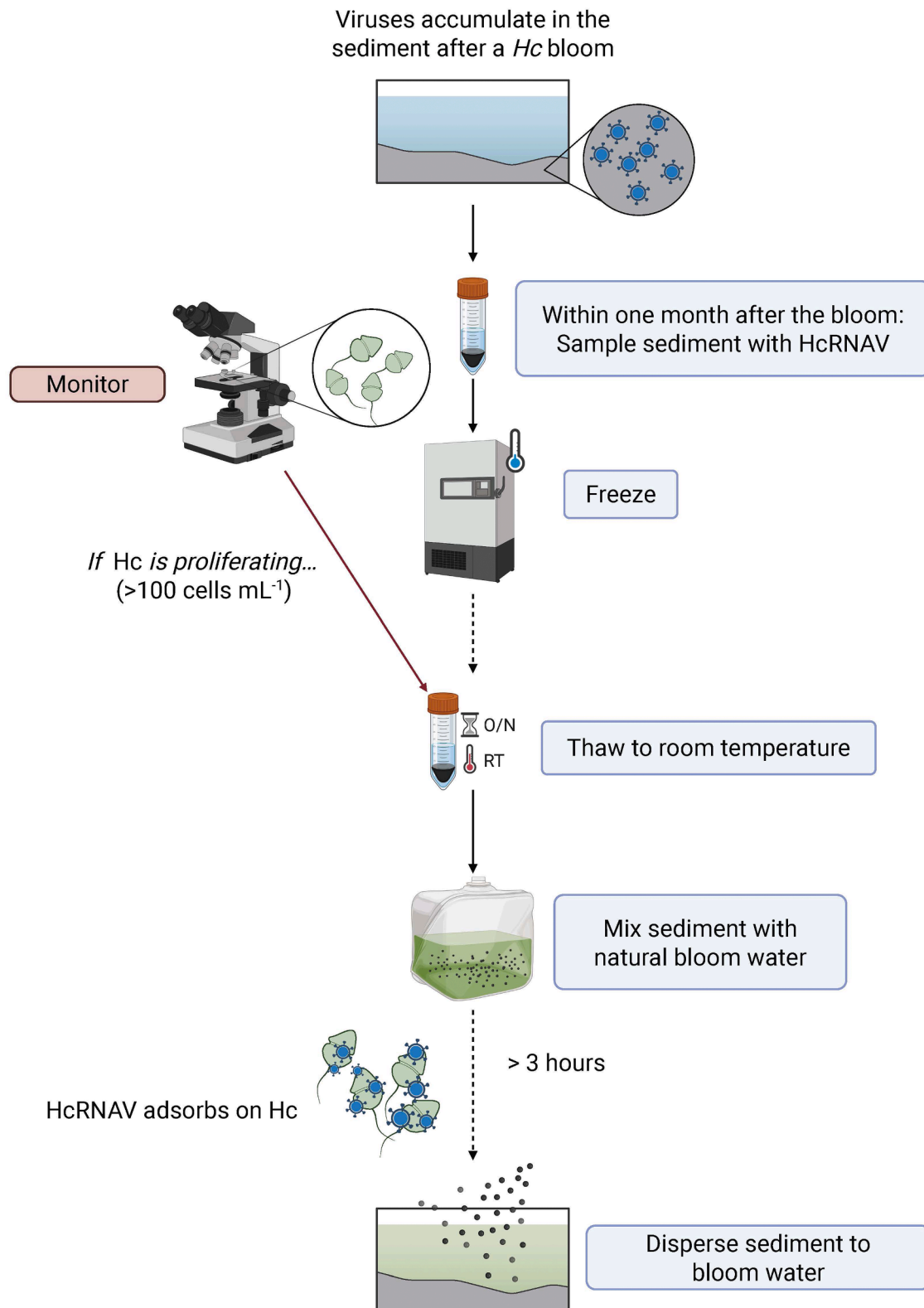


Fig. 5. Method for concentrating and storing naturally-occurring *H. circularisquama* RNA virus (HcRNAV) from sediment following a bloom, then dispersing it into the natural environment to control subsequent blooms. Created in <https://BioRender.com>.

Zhang et al., 2020b). These algaecidal activities occur through two primary modes: direct attachment and attack on algal cells (Coyne et al., 2022; e.g., Imai and Kimura, 2008; Roth et al., 2008; Shi et al., 2023) or, more commonly, the secretion of active compounds causing cell death (e.g., Chen et al., 2022; Pokrzywinski et al., 2012; Shi et al., 2022; Zhang

et al., 2020b; Coyne et al., 2022; Wang, 2021; Fernando et al., 2025). For instance, *Tenacibaculum* sp. GD3 exhibits strong algaecidal activity against *Karenia mikimotoi* by direct contact, while utilizing algal metabolites for growth (Shi et al., 2023). Conversely, *Shewanella* sp. strains IRI-160 (Pokrzywinski et al., 2012), Y1 (Chen et al., 2022), and Lzh-2 (Li

et al., 2014a) secrete algacidal compounds, with strains IRI-160 and Y1 targeting dinoflagellates and Lzh-2 inhibiting cyanobacteria, highlighting the specificity and complexity of these interactions - see below. Recent research has focused on developing strategies for algacidal bacterial application, which include direct dispersal of bacteria or their compounds, immobilized algacidal bacteria for targeted dispersal (e.g., Wang et al., 2025, 2020; Mao et al., 2022; Ruangrit et al., 2025), multi-functional systems (e.g., co-immobilized algacidal bacteria and microalgae, co-immobilized bacteria with different functions, and bio-engineered bacteria with multiple functions). The variability among habitats and the diversity of HAB species means no single approach is suitable for all cases.

Case study: *Shewanella* sp. IRI-160 is an algacidal bacterium isolated from the Delaware Inland Bays, USA, with algacidal activity that has high specificity for dinoflagellates (Hare et al., 2005; Pokrzywinski et al., 2012). This bacterium secretes water-soluble bioactive compounds (referred to as IRI-160AA) and does not require direct attachment for effect (Pokrzywinski et al., 2012). Toxicological studies demonstrated there were no negative effects of this algacide on non-target organisms, including non-dinoflagellate phytoplankton, zooplankton, invertebrates, or juvenile finfish tested at levels required for dinoflagellate control, and only transient effects on activity of crab zoeae (*Callinectes sapidus*) (Pokrzywinski et al., 2012; Simons et al., 2021, 2025; Tilney et al., 2014a). Over a decade of study has been conducted to understand the mode of action of this product on model dinoflagellate species. The algacide directly targets the dinoflagellate nucleus by destabilizing chromosomes resulting in the translocation of nuclei and subsequent cell cycle arrest (Pokrzywinski et al., 2017a,b). The algicide also secondarily impacts photobiology by damaging chloroplasts and causing their displacement within the cells (Tilney et al., 2014b; Pokrzywinski et al., 2017a; Grasso 2018). Collectively, these initial cellular reactions induce stress responses and related programmed pathways resulting in cell death (Pokrzywinski et al., 2017b). Confirmation of these processes at the molecular level has been obtained through transcriptomic (Wang, 2021; Wang and Coyne, 2023) and metabolomic studies (Wang, 2021; Wang and Coyne, 2022). Recent work has focused on elucidating the active compounds in IRI-160AA, which include ammonium and polyamines (e.g., putrescine), that work synergistically against dinoflagellates resulting in reduced growth or mortality (Johnson, 2023; Terner et al., 2018; Wang, 2021; Wang and Coyne, 2024).

Implementation: Field trials of *Shewanella* sp. IRI-160 are in the preliminary stages and are awaiting the necessary regulatory approval.

Application Evaluation: While effective, the direct dispersal of large quantities of bacteria or their algacidal compounds may cause biosafety concerns (Coyne et al., 2022). To address this issue, alternative approaches were explored to limit the need for high-dose and frequent re-applications by concentrating and immobilizing algacidal bacteria or their algacides for controlled release. Algacidal bacteria have been demonstrated to be effective at controlling algal growth after immobilization in porous matrices (Coyne et al., 2022). Therefore, current work on *Shewanella* sp. IRI-160 application is investigating novel deployment methods (including immobilization in alginate hydrogels), for both the *Shewanella* sp. IRI-160 bacteria and their algacidal compounds in field applications. Several matrices have demonstrated high retention of *Shewanella* sp. IRI-160, including alginate hydrogel (Wang and Coyne, 2020). Alginate is a natural polymer produced by bacteria and brown algae, and is non-toxic, highly biodegradable, and low-cost (reviewed by Lapointe and Barbeau, 2020), characteristics that make it a good carrier matrix for applications of *Shewanella* sp. IRI-160 and its algacidal compounds (Wang and Coyne, 2020; Wang et al., 2025). Collectively, alginate beads prepared with *Shewanella* sp. IRI-160 or IRI-160AA are termed DinoSHIELD (Fig. 6). DinoSHIELD may be strategically deployed in areas that are experiencing, or at risk for, HABs, and then removed when no longer needed.

Large-scale treatment: DinoSHIELD is currently in the Demonstration

and Validation phase (see Section 4.3) where researchers are working to optimize DinoSHIELD efficacy, stability, and scalability in preparation for larger-scale field demonstrations. The goal of this work is to demonstrate that DinoSHIELD can be used to control blooms caused by the toxic dinoflagellate *K. brevis* along the Florida Gulf Coast. Before moving into field trials, to ensure the safety of DinoSHIELDS in natural environments, a study was conducted at the mouth of the Broadkill River, Lewes, DE, USA, treating over 2900 L of site water (Wang et al., 2025; Fig. 7). This study assessed DinoSHIELDS embedded with live *Shewanella* sp. IRI-160 under non-bloom conditions, showing negligible effects on non-target microbial communities. A series of field demonstrations are now planned along the U.S. Gulf Coast of Florida that will use both turbidity and bubble curtains to confine the trial in the native environment. The goal of the field studies is to optimize the delivery of the algacide from DinoSHIELDS containing either the immobilized *Shewanella* sp. IRI-160 or cell-free algacidal product and demonstrate the utility of this technology for continuous red-tide management in Florida and other states that experience blooms of *K. brevis*.

Successes and Challenges: The in-situ mesocosm findings (Wang et al., 2025) indicated that DinoSHIELD minimally affected water quality parameters such as pH, salinity, and dissolved oxygen at levels shown to be effective against *K. brevis* in lab settings. *Shewanella* sp. IRI-160 release from DinoSHIELDS was limited, and the overall bacterial density did not increase in the treated mesocosms. DinoSHIELDS did not affect the overall photosynthetic biomass of the algal community but did increase species diversity and richness. These findings support the potential of DinoSHIELDS as an environmentally neutral method for managing dinoflagellate blooms.

There remain two primary challenges for implementation of DinoSHIELD products for HAB control. The first are the complex regulatory issues for obtaining permits for full field testing, for which societal acceptance is vital. The second relates to scalability issues for both producing sufficient product on relevant time scales and application of these products at temporal and spatial scales that enable effective bloom control.

Regulatory issues: The permitting process for DinoSHIELD, including the initial field tests, has been particularly challenging (see above) because it involves federal, state and county regulations which vary considerably. Two examples highlight the diversity of permitting needs. Federal requirements are needed for any U.S.-based application. At the local level, in Delaware, where the initial mesocosm trials were conducted, the regulatory process is relatively straightforward. A single permit from the Delaware Department of Natural Resources and Environmental Control (DNREC) (<https://dnrec.delaware.gov/>) is sufficient for applying DinoSHIELD in all natural waters of Delaware for several years. However, this permit does not allow use of dissolved agents isolated from *Shewanella* sp. IRI-160 (IRI-160AA). Additional permits will be needed because deploying the product from mesh bags throughout the water column could cause potential navigational hazards.

Social issues: A notable challenge with any biological control method is managing public perception and societal acceptance. A major component of the DinoSHIELD development process is to inform and engage representative stakeholders on the use of DinoSHIELD, as well as assess the risks and benefits of this technology. Several strategies are being used to communicate research findings and garner support and feedback early and often. These include technical bulletins, informational videos, surveys, and technical workshops involving critical stakeholders, including state, regional, and local water resource managers, representatives from the aquaculture community, technical experts, and the public. This also provides an opportunity for the community to give feedback on the technology and request further information or to voice lingering concerns that they may have before implementation.

After years of engaging with stakeholders, there has been a growing acceptance of DinoSHIELD and other biological control methods. This shift is particularly evident when stakeholders are informed about the

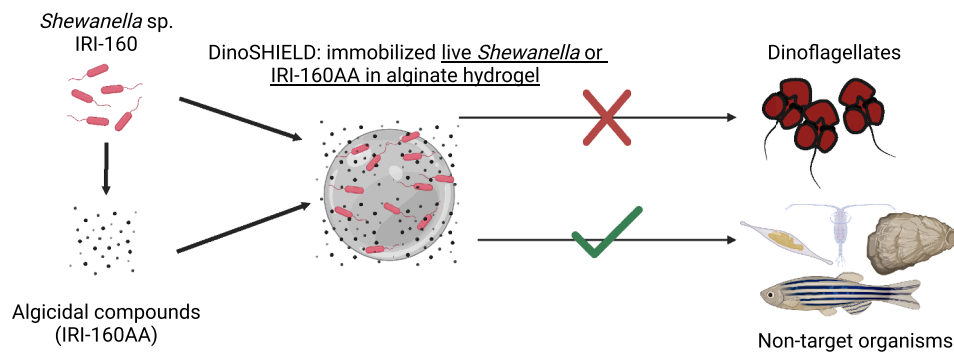


Fig. 6. DinoSHIELD is a biocontrol technology that embeds either the algaecidal bacterium *Shewanella* sp. IRI-160 or its secreted algaecidal compounds (collectively referred to as IRI-160AA) in non-toxic, biodegradable alginate hydrogel. The algicide specifically targets dinoflagellates (red X) without causing negative effects on non-target aquatic organisms (green check mark). The porous alginate matrix enables a passive continuous slow release of IRI-160AA into the surrounding water, maintaining algaecidal activity over time while limiting the need for frequent high dose applications. The DinoSHIELD formulation is currently undergoing testing to confirm no effect on higher trophic levels; due to its simple formulation and non-toxic hydrogel it isn't believed to have major non-target impacts. Created in <https://BioRender.com>. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

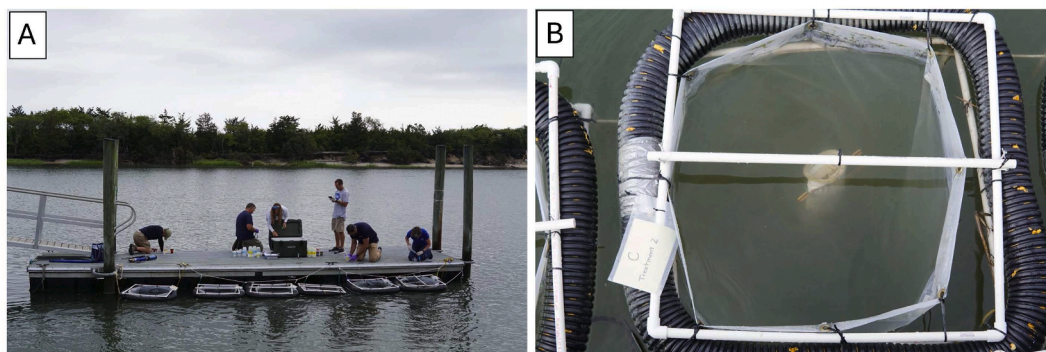


Fig. 7. DinoSHIELD in action in the field. A. *In situ* mesocosm study in Delaware, USA showing deployed DinoSHIELDS in B. suspended bags conducted under non-blooming conditions to assess potential impacts to non-target species in the microbial community (Wang et al., 2025).

native characteristics of the bacterium and their safety to non-target organisms. Garnering this stakeholder and public support will be critical components to successfully transitioning this control strategy to implementation and routine use.

Scalability and breadth of applicability: Scalability poses a significant challenge for DinoSHIELD. Expanding field applications of DinoSHIELD will require an effective supply chain for the substantial amounts of reagents necessary for both hydrogel fabrication and bacterial culturing. This scale-up also demands a considerable workforce and extended time frames for production. To improve the scalability of DinoSHIELD products, the research team is optimizing bacterial growth and algaecide production, aiming to identify more cost-effective production protocols. The team also is working to maximize algaecide delivery rates by testing different concentrations of bacteria or extracted algaecide to reduce the hydrogel quantities needed to achieve effective treatment. Additionally, the team is determining the stability of DinoSHIELD under various storage and transportation conditions to establish thresholds for production lead times and product shelf life.

Several related challenges have been identified including efficient management of funds for sufficient reagent purchase (especially challenging for the U.S. federal government), creating reliable supply chains, and maintaining large quantities of bacteria or algaecide while ensuring matrix stability of the DinoSHIELD products. Current thinking is that this control method is most applicable to HABs in relatively protected systems like canals or embayments. Large-scale treatments in the more dynamic open marine environment would currently be challenging for this methodology.

5.3. Chemical bloom control

Chemical bloom control refers to methods that rely on the release of dissolved organic or inorganic algaecides that kill, inhibit, or remove algal species or their toxins. In many cases the distinction from other control methods is clear—a direct impact of a substance on cell metabolism—while in other instances, the relationship is more complex. For example, the addition of clays and dissolved polymers (see below) act by chemically inducing cell flocculation, but “control” depends on physical transport processes to remove these flocs from surface waters. Another example is ozone nanobubbles, yet to have documented use in marine environments. Nanobubbles are generated to physically disrupt and kill cyanobacterial cells and degrade their toxins (Chaffin et al., 2024). Generally speaking, chemical control strategies tend to have rapid response times, less specificity for target organisms, and a range of environmental impacts that are unique to each approach.

Perhaps the best example of chemical control for HABs is the use of copper sulfate and other algaecides to regulate phytoplankton blooms in reservoirs and other freshwaters. While higher levels of copper can cause decreases in primary production and biodiversity, and increases in nutrient stress, deoxygenation, and impacts at higher trophic levels (Watson, 2024), there are few data available on the effects of copper-containing algaecides in controlling marine HABs beyond two 1950s large-scale field studies that tested the efficacy of copper sulfate for controlling offshore *K. brevis* blooms in the U.S. (Case Study 5.2.3). This situation is primarily due to the heightened chemical regulatory environment and increased public awareness of the importance of protecting marine ecosystems.

This regulatory setting, while crucial for safeguarding of coastal

waters, is at the same time problematic because in most cases it prevents the small-scale field trials essential for evaluating the safety and effectiveness of control strategies. While there is some overlap with biological and physical control strategies, these regulations are most restrictive to the study of chemical methods of HAB control. Perhaps the most well-developed regulatory structures among countries and regions are in the U.S. and Europe, which we review before presenting three case studies of chemical control strategies. Building an understanding of the variation in national regulatory schemes that govern the evaluation and adoption of marine control HAB strategies will help promote international collaboration and a more globalized marketplace for solutions.

5.3.1. Regulatory issues in the U.S. and Europe

In the U.S., new chemical algaecides have strict review, manufacturing, and labeling requirements under the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA) that set maximum application rates and identify use restrictions. The review process is long (years) and costly for manufacturers and has limited the availability of new products but has protected the environment from unintended negative effects from new and untested chemicals. A new “pesticide” (the term in the U.S. that describes any chemicals used to control HABs) cannot be used or marketed for algae control on waters of the U.S. without being registered (licensed) by the U.S. Environmental Protection Agency (EPA). Before EPA can register a pesticide under FIFRA, the applicant must show it will not cause unreasonable adverse effects on the environment. This means there cannot be: 1) any unreasonable risk to man or the environment, considering the economic, social, and environmental costs and benefits of its use; or 2) a human dietary risk from residues that result from a use of a pesticide in or on any food.

The U.S. Federal Food, Drug and Cosmetic Act (FFDCA) authorizes EPA to set tolerances, or maximum residue limits, for pesticide residues on foods. In setting tolerances, EPA must make a finding that the tolerance is “safe,” defined as meaning that there is a “reasonable certainty that no harm will result from aggregate exposure to the pesticide residue.” To make the safety finding, EPA considers: 1) the toxicity of the pesticide and its break-down products; and 2) aggregate exposure to the pesticide in foods and from other sources of exposure. Since HAB control treatments will be tested or eventually implemented in marine waters that contain fish, shellfish, and other animals that are considered food, FFDCA represents another set of regulatory constraints or hurdles to developing a chemical HAB control strategy. Not only must developers demonstrate that their product does not negatively impact benthic animals, for example, but they must also show that there are no dangerous residuals from their product in fish or other potential human foods living at the treatment site. In practical terms, the foregoing means that those developing HAB control methods for U.S. marine systems that are based on chemicals, or chemically modified substrates (see below) need to carefully consider the regulatory pathway for testing approval and eventual product registration under FIFRA and FFDCA. A result is that some choose chemical constituents from the “exempted” minimum risk pesticide lists rather than trying to evaluate novel and potentially more effective compounds.

The European Union also regulates the application of chemicals in natural waters, and approval must follow the procedure outlined in the Biocidal Products Regulation (EU) No 528/2012 (Regulation E.U. (2012)). In this regulation, algaecides are classified as biocidal products, specifically under Product-type 2 (PT2). To gain approval, the active substance must first be evaluated and approved at the EU level by the European Chemicals Agency (ECHA), based on evidence of efficacy and safety for human health and the environment. Once the active substance is approved, the algaecide product itself must be authorized—either through a national authorization in a single member state or a Union authorization for EU-wide use. Products intended for use in aquatic environments must undergo a detailed environmental risk assessment, particularly to evaluate impacts on water quality and non-target organisms.

5.3.2. Case study - chemical control using hydrogen peroxide in the Netherlands

Background: Hydrogen peroxide (H_2O_2) is a naturally occurring reactive oxygen species (ROS) known to induce oxidative stress in cells, leading to physical damage and a reduction in photosynthetic yield (Mittler, 2002). A key advantage of H_2O_2 over many other chemicals is its rapid breakdown into water and oxygen within hours to days, depending on aquatic conditions, form and formulation of the product.

Liquid and granular H_2O_2 -based algaecides are commonly used in the U.S. to control cyanobacterial HABs (cyanoHABs) in freshwater systems (e.g., Kinley-Baird et al., 2021; Pokrzywinski et al., 2022; Lefler et al., 2022,2024), with recent studies looking at their effectiveness in marine species (e.g., Hu et al., 2022) and/or modifications in H_2O_2 based algaecide labels. Controlling the activity of harmful eukaryotic algae such as dinoflagellates requires higher concentrations of H_2O_2 due to both instability of peroxides in marine waters (Hu et al., 2022) and lower sensitivity of eukaryotic algae (Weenink et al., 2022). Effective concentrations thus have the potential to harm other algae and zooplankton. Despite this drawback, H_2O_2 can be an optimal choice for treating isolated HABs in confined areas. H_2O_2 has been investigated for treating dinoflagellates in the ballast water of ships (Ichikawa et al., 1992; Bolch and Hallegraeff, 1993; Gregg et al., 2009). Its effectiveness has also been tested on the brown tide HAB species *Aureococcus anophagefferens* (Randhawa et al., 2012) and red tide HAB species *K. brevis* (Hu et al., 2022). The effective dosage of H_2O_2 varies significantly among different species. For example, *A. anophagefferens* is highly sensitive to H_2O_2 , and a bloom of this species could be eradicated by a final concentration of 1–2 mg l⁻¹ of H_2O_2 (Randhawa et al., 2012). Hu et al. (2022) found that concentrations between 4.89–7.08 mg l⁻¹ of H_2O_2 killed *K. brevis* in 24 h. In contrast, Ichikawa et al. (1992) found that concentrations up to 30 mg l⁻¹ were needed to render the cysts of *Alexandrium catenella* non-viable. Cysts of *Gymnodinium catenatum* from ballast water were highly insensitive and required concentrations up to 5000 mg l⁻¹ to eliminate them (Bolch and Hallegraeff, 1993).

Implementation: A notable example of using H_2O_2 to mitigate harmful dinoflagellates in the field is the treatment of an *Alexandrium* bloom in the Netherlands (Burson et al., 2014). A very dense bloom of *Alexandrium ostenfeldii*, exceeding 1 million cells l⁻¹, occurred in the brackish Ouwerkerkse Kreek in The Netherlands. The bloom produced both saxitoxins and spirolides, and was implicated in the death of a dog with high saxitoxin stomach content. Since the Ouwerkerkse Kreek regularly discharges its water into the nearby Oosterschelde estuary, prompt action was necessary to avoid contaminating extensive shellfish beds there. Treating the water with a concentration of 50 mg l⁻¹ of H_2O_2 effectively eradicated the bloom, marking the first successful field application of H_2O_2 to eliminate a dinoflagellate bloom.

Application Evaluation: The treatment to eradicate *A. ostenfeldii* in the Ouwerkerkse Kreek followed a three-step approach. First, the required H_2O_2 dosage was determined through laboratory experiments with *A. ostenfeldii*. A concentration of 50 mg l⁻¹ H_2O_2 was needed to effectively kill the dinoflagellate. Second, the method was then tested in a small, isolated canal adjacent to the Ouwerkerkse Kreek to evaluate its effectiveness in a controlled, natural environment. Finally, after being successful in the canal, the treatment was scaled up to the entire creek system with a surface area of 0.12 km², an average depth of 5 m, and a maximum depth of 8 m. The creek was partitioned into a southern section of 317,000 m³ and a northern section of 107,000 m³ through construction of a temporary sand-filled dam along the bridge which crosses the creek. Another temporary sand-filled dam isolated the creek from the agricultural canals and ditches at the northern end. A 15,000 L tank with a 50 % (v/v) H_2O_2 concentration was placed on a raft in the water. The H_2O_2 was prefiltered with water from the creek in an intermediary tank to arrive at a 1 % (v/v) H_2O_2 concentration which was injected in the water using a specially designed injection system called a “water harrow” (Matthijs et al., 2012). The target concentration of 50 mg l⁻¹ H_2O_2 was achieved after 8 h of injection in the entire creek.

Following this, the H_2O_2 injection was halted, and the concentration gradually declined to natural background levels within 50 h.

The photosynthetic yield of the *Alexandrium ostenfeldii* population in the creek decreased to <5 % of its initial value within 8 h after the H_2O_2 treatment (Burson et al., 2014). This decline was similar to the response in the laboratory and canal tests. The number of *A. ostenfeldii* cells and cysts declined from about 1.1 million cells l^{-1} before the treatment to <2000 cells l^{-1} (> 99.8 % removal) after 48 h, while green algae and euglenophytes became dominant. Concentrations of 13-desmethyl spirulide C and saxitoxin were reduced below local regulatory levels of 15 mg l^{-1} after 96 h. The numbers of zooplankton decreased from over 40,000 individuals l^{-1} at the start to <15 individuals l^{-1} after 50 h. The zooplankton community consisted mainly of rotifers and copepod nauplii.

Scalability: There have been no steps to date to expand H_2O_2 treatments to larger scales for bloom control in the Netherlands. However, as mentioned earlier, both liquid and granular H_2O_2 -based algaecides are a common management tool to control cyanohABs in fresh waters around the USA. In this context, small ponds and lakes (< 1 km^2) are regularly treated with H_2O_2 algaecides for HAB control. Whole lake treatments up to 4.6 km^2 have also occurred, and larger lakes, >6 km^2 , are also commonly treated, but in these cases, the treatment occurs mostly in the littoral areas (e.g., beaches where there is accumulation of HABs due to winds) to restore recreational activities or prevent contamination in drinking water intakes (for cyanohABs). Thus, large scale treatment using H_2O_2 -based algaecides is feasible, pending the ability to move sufficient product to the location and having enough boats, helicopters or planes in place for dispersal.

Successes and Challenges: The results indicate that H_2O_2 treatment is an effective emergency management option for mitigating toxic *Alexandrium* blooms, particularly when immediate action is necessary. To date, there has been no reported follow-up or adoption of this method in other countries for *Alexandrium*, though some H_2O_2 -based algaecides are now labeled for use in marine waters in the USA and in usage. In the Netherlands, while it remains a viable option for future use, high-density blooms requiring such intervention have not reoccurred since 2012.

While H_2O_2 can effectively control toxic dinoflagellate species, its broader ecological effects raise concerns about unintended lethality towards non-toxic dinoflagellates (Mardones et al., 2023). One major risk is the potential for oxidative stress-induced lipid peroxidation in microalgal blooms, which can trigger the formation of aldehydes that may further exacerbate toxicity, such as in mortalities of farmed fish (Dorantes-Aranda et al., 2015). The ecological implications of reactive oxygen species (ROS)-mediated toxicity remain insufficiently understood, highlighting the need for further research to elucidate the underlying mechanisms. Given these uncertainties, the application of H_2O_2 for HAB control should be approached with caution near aquaculture sites. To mitigate potential risks, environmental impact assessments (i.e., real-time in situ cytotoxicity assays) should be conducted before large-scale application, considering species-specific responses and possible secondary toxic effects.

Regulatory issues. In the Netherlands, adding H_2O_2 to natural systems requires a license from the Dutch Board for the Authorisation of Plant Protection Products and Biocides (Ctgb). The urgency for treatment was high due to a threat to human health at a nearby campsite, the death of a dog, and the risk of contaminating mussel beds in the Oosterschelde estuary if the brackish water containing toxic dinoflagellates was discharged from Ouwerkerkse Kreek. Due to this emergency, the license for H_2O_2 application was expedited.

Social Issues: The public was informed about the background findings and plans for treatment with H_2O_2 through local community meetings, and the community was supportive of the planned bloom control under the extreme circumstances caused by this bloom.

5.3.3. Case study - chemical control using copper in the United States

Background. Blooms of the red tide-forming organism *K. brevis* can readily cause massive mortality of fish and other marine organisms, as well as produce aerosols in the surf environment that impact humans (Landsberg et al., 2009; Pierce and Henry, 2008). Based largely on HAB control successes using copper compounds in freshwater systems, early work in the 1950s and 1960s examined the use of copper and other chemical algaecides for use in marine systems. Two lab studies were conducted in the early 1960's to find chemicals that could kill or inhibit *K. brevis* with low-level doses. >4306 compounds were screened (Marvin and Proctor, 1964a) with the goal to achieve 100 % lethality after 24 h at doses between 0.01 and 1.0 ppm. Marvin and Proctor (1964b) found only five compounds that could achieve these goals, and of these, copper sulfate was determined to be the most promising.

Application Evaluation: More recently, the efficacy of three copper-based, EPA-registered algaecides were tested in the lab for potential use as emergency HAB treatments for *K. brevis* control: copper citrate and copper gluconate, copper ethanolamine complex, and copper sulfate pentahydrate (Hu et al., 2022). The authors found that their lowest tested concentration, ~0.3 mg Cu l^{-1} , killed *K. brevis* within 24 h but did not test its effects on non-target species. More work is needed on the broader ecological treatment effects, the longer-term fate and persistence of the copper substrates, and the effects of site characteristics (particularly water chemistry) on the efficacy of copper-based HAB control.

Large Scale Treatment: There have been no recent studies using large scale treatments of copper-based algaecides in marine waters. However, two large-scale field trials conducted in the 1950s tested the efficacy of copper sulfate for HAB control, the first along the west Florida coast (Rounsefell and Evans, 1958) and the second in a man-made lagoon near Galveston, TX USA (Marvin et al., 1961). The first field trial in 1957 used CuSO_4 pentahydrate ($5\text{H}_2\text{O}$) to mitigate an outbreak of *K. brevis* on the Florida Gulf Coast in open waters 4.5 km offshore and ~50 km along-shore near St. Petersburg (Rounsefell and Evans, 1958). The treated area covered ~40 km^2 . The initial bloom density was ~10 million cells l^{-1} . Using an estimated copper concentration of 0.18 mg Cu l^{-1} , a total of 95 t of CuSO_4 was dispersed in the bloom by dragging burlap sacks containing CuSO_4 behind ships, and over broader areas, using crop-dusting aircraft. *K. brevis* concentrations became undetectable in most areas immediately following the treatments and reports of respiratory irritations decreased, signifying the rapid success of the treatment. In contrast, a similar copper treatment did not kill *K. brevis* in Galveston Bay, TX, despite applying copper twice (Marvin et al., 1961). The difference in response was likely due to the large amount of suspended matter and organic chelators (e.g., humic matter) in the shallow bay water, which would have reduced concentrations of copper in its freely available state (Sengco, 2009). Therefore, the use of copper was not recommended as a viable control mechanism for *K. brevis* blooms in enclosed bays, despite being successful against *K. brevis* (Sengco, 2009).

Successes and Challenges: Following these early applications of CuSO_4 , bloom concentrations in the Florida Gulf Coast trial increased again after <2 weeks in two of the five monitoring areas. It is not clear if this re-appearance was due to currents advecting new bloom-containing waters into these areas, or if it was attributable to resurgent growth of cells that remained after copper treatment. Estimates for the treatment (in the 1960s) were considered too costly for routine applications over large areas (though are cheaper than many current efforts), particularly given that it provided only temporary relief from the bloom and aerosols. The collateral damage to the ecosystem would be of concern due to the broad toxicity of copper sulfate; however, the presence of large blooms mitigates the toxicity of copper so this can vary substantially (Bishop et al., 2018).

Regulatory and social issues: The mixed results of the early field

trials led to the method never being recommended for widespread use in marine systems. Some believe that this failure stifled progress in chemical HAB control in the U.S. for many years (Sengco, 2009). Social issues were generally a small consideration at the time, beyond the simple assessment of treatment effectiveness and costs. The increasing awareness of environmental issues in the following decades was an additional impediment. Only recently have there been efforts to re-examine the potential use of copper-based compounds as a “backup” for marine HAB control. It is noteworthy that similar environmental concerns are much less prevalent for copper-based HAB control in many freshwater systems used for drinking water or recreational activities. For these applications, the permitted concentrations in the U.S. have been shown to be below levels that would have minimal impacts on non-target organisms.

5.3.4. Case study - chemical control using plant-based chemicals in the United States

Background: As discussed in Section 5.2.1, the U.S. FIFRA regulations specify a list of “minimum risk” pesticides that require minimal regulatory oversight. The majority of these are plant-derived. Many plants produce secondary metabolites, such as polyphenolics, N-containing compounds, fatty acids/esters, and terpenoids (Zhu et al., 2021), which act as chemical defenses against herbivory, pathogens, or can negatively influence the growth, survival, or reproduction of nearby plants and microorganisms. Perceived advantages of plant-derived chemicals include biodegradability, history of use in humans and agricultural animals which informs occupational and wildlife safety, and less aggressive off-target effects. Examples include lysine and malonic acid, which were shown to be successful against a *Microcystis aeruginosa* bloom in experimental enclosures (Kaya et al., 2005), and the plant-derived flavone, 5,4'-dihydroxyflavone, which has been shown to inhibit *M. aeruginosa* and *Phaeocystis globosa* (Xu et al., 2022). Several herbs and spices also have been tested against algae blooms, including curcumin, the bioactive phytochemical produced by turmeric, was shown to reduce *K. brevis* cell and toxin concentrations in flask and mesocosm experiments (Hall et al., 2024; Devillier et al., 2025).

Application evaluation: An example of a minimum risk, plant-based, chemical formula for HAB control is Xtreme-RT, a commercially-available anti-microbial and anti-viral product for food-use and non-food use surfaces. All ingredients within Xtreme-RT are listed as exempt active or inert ingredients (40CFR152.25; 40CFR180.950). Xtreme-RT has been tested in lab-scale culture experiments against the Florida red tide dinoflagellate, *K. brevis*, and was found to reduce cell concentrations, presumably by inducing cell lysis.

Approach: Laboratory and mesocosm-scale studies were performed with Xtreme-RT and cultured *K. brevis* to evaluate the effects on cells and brevetoxins and to determine the effective concentration. In 1.5 L beaker experiments with *K. brevis* cultures diluted with filtered seawater to $\sim 1.0 \times 10^6$ cells l^{-1} , additions of Xtreme-RT at 10 μl l^{-1} and 50 μl l^{-1} concentrations reduced cells within 4 h by 88.8 % and 100 %, respectively. Scaling up to 1400 L mesocosms with an initial concentration of ~ 1.2 million cells l^{-1} of *K. brevis*, dosing at 25 μl l^{-1} reduced cells by 87.6 % within 4 h and by 99.6 % within 24 h. No direct effect on toxin reduction was shown in either test.

A near-shore bloom in 2025 presented the opportunity to test Xtreme-RT deployment in the field. Site selection for field deployment and testing was accomplished through a modified survey sampling of likely bloom areas in coastal waters within a three-day window immediately prior to application. A residential canal adjacent to the Venice, Florida, USA inlet was chosen for testing due to the elevated *K. brevis* concentrations present ($>4 \times 10^6$ cells l^{-1}), the canal size and configuration with a single access area, and nearby available boat access. Target dosage (25 μl l^{-1}) of Xtreme-RT was calculated for the estimated volume of the one-acre area of the canal. The depth of the canal at high tide is roughly 2 m, and so 48.9 gallons of product were required to achieve a 25 μl l^{-1} level in the canal.

Product delivery was achieved by a small barge equipped with a multi-nozzle sprayer on an adjustable arm which can deploy product across a 10-ft wide area and down to 6 feet below the water surface. During delivery, 50 gallons of Xtreme-RT was applied to the canal in a lap formation, dispersed approximately one foot below the surface. Xtreme-RT is heavier than water and will sink, making surface application feasible. The use of subsurface spraying was intended to disperse the product to the final target concentration quickly, without the need of high surface concentrations.

Water was sampled at two depths (~ 0.5 and 1 m) within the canal at four sites, both immediately prior to product application, and then 1 and 2 h after. Initial *K. brevis* cell concentrations were highest near the closed end of the canal (Site 1; Fig. 8) and lower towards the mouth of the canal (Site 4; Fig. 8). Initial cell concentrations averaged 1.7×10^6 cells l^{-1} at the four sites. *K. brevis* cell concentrations decreased on average 31.4 % 1 h after treatment and 51.4 % two hours after treatment. The percentage of abnormal spherical shaped *K. brevis* cells, an indicator of stress (Owen, 2015; Novoveská and Robertson, 2019), increased from 2.2 % initially, to 22.4 % across all sites after 2 h, indicating that further cell reduction may have occurred after testing. As in previous lab tests, effects on toxins were minimal. Total analyzed brevetoxin concentrations were reduced by 20 % and 19 % at sites 1 and 2, respectively, while site 3 showed no change in brevetoxins and site 4 had an increase of 8 % toxin concentration (Fig. 8).

Successes and Challenges: This field study was the first test of a plant-derived formula on a *K. brevis* bloom in situ. Removal efficacy had not previously been tested in such a short time frame or on a high-density natural bloom. Results demonstrated that a plant-based liquid can be quickly deployed by boat, and that multiple vessels can be used to conduct synchronized sampling and dispersal. Dispersal of 50 gal of Xtreme-RT applied at a rate of 3-gal min^{-1} was achieved in under 20 min over a one-acre area (4047 m^2).

Removal of *K. brevis* averaged 51.4 % across all sampling sites and depths. Efforts are underway to enhance efficacy since the population of *K. brevis* could readily rebound to the initial population density just a few days after the initial dispersal, requiring further treatment. Higher concentrations of 50 μg l^{-1} removed nearly 100 % of cells in flask studies, but cost and potential non-target toxicity concerns encouraged the use of lower concentrations in this field study.

Toxins were not reduced during the field trial. Studies have shown brevetoxins transform in water due to bacterial, chemical, and photolytic degradation (Shetty et al., 2010; Abraham et al., 2006; Baden et al., 2005; Hardman et al., 2004). Thus, removal of cells is expected to lead to toxin removal over time and expedite the restoration of the impacted area.

Although the effect of treatment with Xtreme-RT on the broader ecosystem was not measured in this preliminary study, there were no apparent negative impacts on the abundance of the diatom *Skeletonema costatum*, the next most abundant phytoplankton species at the start of the experiment. Future studies would benefit from comprehensive ecosystem monitoring to evaluate effects on marine animals, submerged vegetation, and aerosolized toxins.

The cost of Xtreme-RT to treat an acre with 50 gallons was 3000 USD, which scales to approximately 741,000 USD per km^2 . Clearly, additional work is needed to determine how economies of scale can reduce costs and how these balance against impacts. Furthermore, a challenge, especially for biodegradable formulas, is to confirm chemical concentrations during in situ testing.

5.3.4.1. Regulatory and social issues. Regulatory issues for pesticides in the U.S. are minimized using “minimum risk” ingredients, but the level of social acceptance is not yet known for these types of chemicals dispersed into coastal waters with sensitive resources present (e.g., coral reefs, manatees, seagrasses). Though FIFRA registration is not required for Xtreme-RT, determination of the concentration, frequency, and

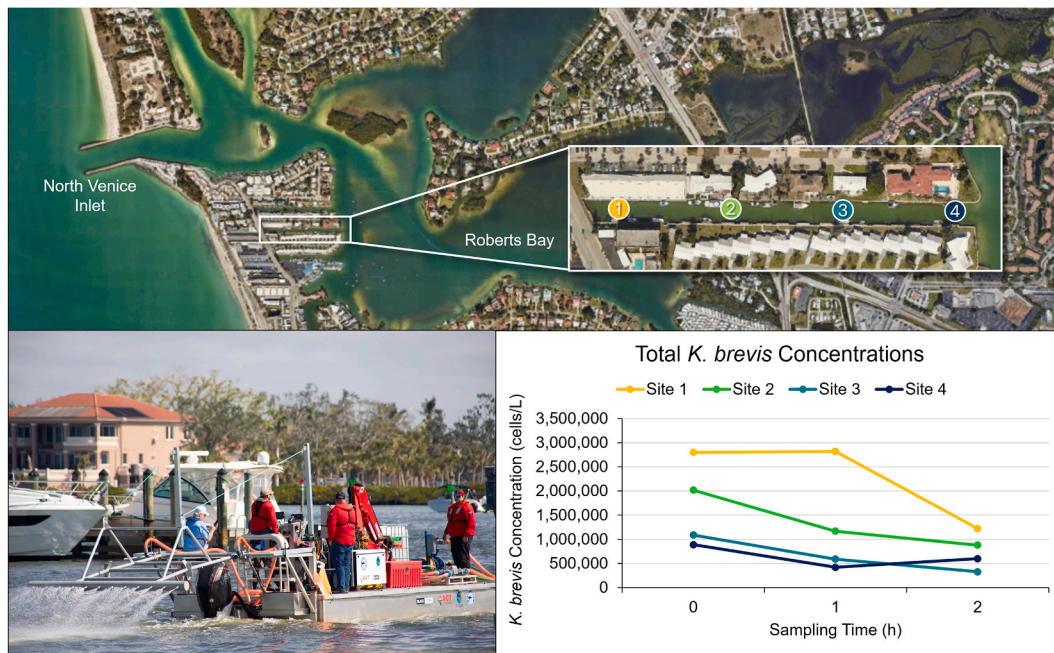


Fig. 8. *Karenia brevis* control field trial near Venice, Florida USA. Location of canal and test sites (top). Barge equipped with mobile sprayer arm (left). Total *K. brevis* cell concentrations before and after treatment, average of 2 depths per site (right).

optimal sites for potential large-scale control activities must be informed by additional investigations into off-target toxicities, residues, changes in water quality, and long-term ecosystem effects.

5.3.4.2. Scalability and breadth of applicability. Xtreme-RT already has a commercial market and thus the inventory, production, and distribution capability for the product is large enough to treat a 100 km² area. Tests show the product degrades or dilutes within 24–48 h. Biodegradation is attractive for preventing residue accumulation, but it remains unknown if multiple treatments would be required to sustain bloom suppression, particularly if an organism migrates through the water column. A liquid plant-based bloom control tool could be applied by land- or boat-mounted sprayers in canals and near-shore areas and in theory, aerial spraying could cover large bays.

5.4. Physical bloom control

Physical control methods for blooms span methods that physically harvest, settle and bury algal cells, as well as methods that limit or block the spatial extent or impact area using booms or other barriers. Mechanical means of managing algal blooms include dredging of sediments, sonication, aeration, oxygenation, deep-water upwelling, and clay dispersal.

Physical removal of sediment through dredging can effectively eliminate HAB resting stages, including akinetes, diatom resting cells, and cyst beds. Sediment disturbance or deposition of sand or other material (e.g., offshore sediments; Brown et al., 2019) can bury these cells below the oxygenated surface layer, inhibiting germination (Kidwell et al., 2015; Anderson, 2017; Brown et al., 2019; Sellner and Rensel, 2018). Tilling or plowing of bottom sediments also may help control HABs by resuspending non-harmful, fast-growing algae species (e.g. diatoms) along with nutrients, helping to rapidly form blooms of non-harmful species that competitively outnumber HAB species (Imai et al., 2021; Ohara et al., 2023; McClimans et al., 2010).

Ultrasonic technologies have been investigated as a management option for freshwater cyanobacterial HABs but not yet for marine HAB control. The method is based on longitudinal ultrasonic waves forming cavitation bubbles that potentially lyse or inactivate cells when they

collapse (Suslick and Flannigan, 2008; Wu and Nyborg, 2008). However, the effects are not restricted to HAB species and there are conflicting results in its application (Li et al., 2014b; Park et al., 2017; Lüring and Tolman, 2014a,b; Lüring et al., 2014; Klemenčič and Klemenčič, 2021; Bohrerova et al., 2023; Purcell et al., 2013). Bubble curtains (or direct aeration) have been used to form physically protective rings around fish enclosures during marine HAB events, which can significantly improve survival over that in non-treated cages (Sellner and Rensel, 2018; Gallardo-Rodriguez et al., 2019). Although exploratory work continues using all these approaches, the two most widely used physical control methods are deep-water upwelling and clay dispersal.

Other than potentially restricting nutrient inputs (Lapointe et al., 2021), there are no documented approaches for controlling harmful macroalgal blooms (e.g., *Sargassum*, *Ulva*). Control of these events include a variety of physical approaches, including collection at sea, physical barriers to contain blooms, and manual or mechanized removal of macroalgal biomass from beaches and sensitive habitats.

5.4.1. Case study - deep-water upwelling at Canadian fish farms

Background: Deep-water upwelling or airlift aeration is one of the most widely used and efficient methods to protect fish aquaculture net cages from HABs (Sellner and Rensel, 2018), though this method might be characterized as a mitigation strategy rather than bloom control or suppression. The goal of airlift upwelling is to replace surface water occupied by high concentrations of HAB cells with deep water where few cells are present. The bottom water functions as a dilution mechanism but also creates lateral advection at the surface that can transport HAB cells away from the fish cage. Results are improved using perimeter skirts. Fish-killing HABs act by damaging fish gills through either exposure to toxins or other harmful compounds, or to mechanical damage from diatom spines. While reduced feeding of the fish (less respiratory demand) helps to mitigate these impacts, deep-water upwelling also can help by increasing the dissolved oxygen saturation, particularly when the airflow is combined with oxygen.

Fish farms in British Columbia, Canada, are large, typically producing 2500–5000 tons of salmon and are sites where HABs can have major economic impacts (Trainer et al., 2020). The primary HAB threat in

British Columbia is *Heterosigma akashiwo*, a raphidophyte, though a few other HAB species also are of concern (e.g., species of the genera *Chaetoceros* and *Pseudo-nitzschia*).

Implementation: Deep-water upwelling systems currently are utilized across all aquaculture farms in British Columbia, with growing interest and adoption by other countries as they face increasing occurrences of annual plankton blooms and associated fish mortalities. The decision process for activating upwelling relies on high quality phytoplankton monitoring of the surrounding waters, with a focus on problematic species. Companies rely primarily on manual microscopy techniques, and some have adopted automated microscopy (e.g., the FlowCam or the Imaging FlowCytobot), or both (D. Trethewey, pers. comm.), with qualitative and quantitative sampling being done during each tidal cycle during the elevated risk months. Characterizing both the spatial and vertical distributions of HAB species with discrete sampling and net tows (for low-density HABs) is important as it informs whether the depth of water drawn for upwelling will decrease or exacerbate the HAB impacts. It is also critical that the farmers capture and enumerate all HAB species, as each has a different threshold for triggering the bloom control protocol.

For implementation, a compressed air hose is lowered below and in the middle of the fish cages to allow the drawing of deep water upwards into the cages. In British Columbia, many fish farm sites are in areas with strong current velocities, and the net cages are large enough to receive the upwelled water without excessive lateral dispersion. If the cages are placed in a side-by-side configuration parallel to the current (Fig. 9), adjacent cages can share the upwelled water, reducing the need for additional pumping systems.

Application Evaluation: The use of deep-water upwelling has been optimized by fish-farm personnel through a long interval of trial and error. What follows is the best practice approach that has evolved at Grieg Seafoods in British Columbia.

Dispersing compressed air at depth with a surface pumping system requires substantial energy. Finding the right balance between air pressure and volume of transport is a constant challenge to farmers, with the effectiveness of these systems being constrained by their capacity. For instance, a system generating 90 PSI can push air down to a maximum depth of 14 m, which may not be deep enough for water to be HAB-free. Modern systems often feature multiple compressors—up to six, providing a total of 72 cubic meters per minute—and can reach

depths of ~25 m. These systems use a network of aeration disks, combined with precise control over the direction of airflow, to target areas with high plankton concentrations within the cages. Integration of oxygen into the aeration system also helps farms maximize dissolved oxygen concentrations, a particularly important feature to reduce the stress on cultured fish when upwelled deep waters have low oxygen concentrations.

Large Scale Treatments: Farms typically use a combination of leased compressors and purchased (capitalized) assets. The financial investment for a comprehensive aeration system on such farms generally falls within the range of 200,000 to 400,000 Canadian dollars. This cost primarily depends on the number of fish pens that need coverage, and the complexity of the distribution channels required to ensure effective air or oxygen delivery throughout the system. At maximum operational capacity, each compressor consumes approximately 400 L of fuel per day. It's common for farms to operate between two to five compressors simultaneously, depending on the scale of the operation and the immediate environmental challenges faced, such as the intensity of the HAB. If air compressors or suitable air blowers are already available, capital costs for airlift aeration will be restricted to air lines and diffusers. In regions where HABs are typically seasonal events (spring to early fall), fish farmers may utilize rental compressors to further reduce capital costs (Fig. 9).

Site selection and the use of proper equipment are critical concerns. Depending on water clarity, some shallower sites may contain algal populations throughout the water column, rendering the method ineffective. If bottom waters or sediments are rich in H_2S , mixing of this gas into surface waters could cause mortalities of the densely packed fish. Another concern is high nutrient (N, P, Si) concentrations in the upwelled waters will promote algal production, potentially exacerbating HAB conditions.

Successes and challenges. Currently, deep-water upwelling systems are utilized with successful results across all aquaculture farms in British Columbia, and there is growing interest and adoption by other countries as they face increasing occurrences of HABs and associated fish mortalities. One of the challenges is obtaining timely data on phytoplankton species abundance and composition. In the past, salmon farmers had to submit water samples for phytoplankton analysis, which took several days. This has been overcome by employing their own algae experts who have built image libraries of local species of algae. These in turn have



Fig. 9. Deep water upwelling system used during a *Heterosigma akashiwo* bloom at a British Columbia, Canada, fish farm on the west side of Vancouver Island. Photo credit: CPI Equipment, Inc.

facilitated the use of automation and machine learning in surveillance. In 2019, Grieg Seafoods had fewer mortalities from HABs than they would have experienced without the combined deep-water upwelling and automated monitoring. They also avoided starving the fish unnecessarily when algae were not toxic. The number of hunger days in 2018 were reduced by 41 % on their facilities in the Esperanza area, where harmful algae can be a challenge.

Although deep-water upwelling generally has good results for British Columbia fish farms (Sellner and Rensel 2018), it was not effective against a bloom of the raphidophyte, *Pseudochattonella*, in Chilean salmon farms during a major outbreak in 2016 (Clement et al., 2016). This may be because fish farms were too shallow, such that the upwelling brought HAB cells to the surface, rather than the desired cell-free water. However, deep water upwelling and monitoring has become the preferred approach of global fish aquaculture companies with the approach now operational on fish farms in Canada, USA, Scotland, Norway, Chile, and Tasmania/Australia (Table 2). It's unclear whether the impetus stems from an actual increase in HAB detection on farms, an insurance industry requirement due to perceived risks, or some combination of such factors.

It is noteworthy that fish farms that experience HABs infrequently often report higher mortality rates. This paradoxical outcome can largely be attributed to a lack of experience among staff members, who may be less prepared to effectively respond to HAB events. Conversely, sites that conduct daily monitoring of HABs are typically more aware of potential threats and are quicker to implement bloom control strategies. The insurance industry, recognizing the economic benefits of such proactive approaches, is increasingly advocating for the effective implementation of deep-water upwelling systems to manage these risks more effectively.

Regulatory issues. There are no regulatory issues with deep-water upwelling in Canada, mainly because aquaculture falls outside of the equipment/construction government agency oversight. In British Columbia, aquaculture companies often follow local laws regarding electrical and construction standards. For plankton control systems, this is mainly affected under boiler regulations which pertain to compressed air requirements. A certified welder must put the manifold together, and any vessel holding >15 PSI of air storage must undergo annual inspections.

5.4.2. Clay control of HABs

Background: Clays are surface active substrates that rapidly adsorb dissolved organic phases in seawater, including the mucopolysaccharides on the surfaces of phytoplankton. Spraying a slurry of clay minerals onto surface waters leads to the formation of clay/cell flocs that sink rapidly to the bottom sediments (reviewed in Yu et al., 2017). In recent years the method has been optimized through the use of the more reactive clays and through additions of polymers, oxidants, or other materials to the clay that can: 1) alter the surface charge of the clay particles to improve their electrostatic reactivity with HAB cells; 2) create long polymer chains to bridge among flocs, thereby trapping cells through net or sweep capture as the aggregates settle through the water column; and 3) sequester or destroy HAB toxins in the water column that are released by cells captured and ruptured during flocculation.

A particular benefit of clay flocculation is that the flocs continue to collect cells as they sink, so clay treatments added at the surface can be effective through the mixed layer of the water column, an advantage over most other HAB control technologies. There is also considerable experience with the successful use of this approach at large scales (>100 km²) in marine waters of Korea and China for over 30 years (see below). An attractive feature of this method is that it uses inexpensive and environmentally benign minerals that often are a common constituent of marine sediments. Another benefit is that the extent of removal of different species from the phytoplankton assemblage varies with cell size, cell concentrations, and cell wall constituents and morphology (Qiu et al., 2017; Siclari, 2019). So, while it has been shown to be effective for

many HAB species, its application still leaves a significant planktonic "seed" community for ecosystem recovery.

One concern with the method is that although the clay mineral matrix is chemically inert, any toxic materials (e.g., metals, toxins) sorbed to clay surfaces may be ultimately released in the water column or pore waters. However, studies have shown no negative effects on benthos from multiple clay applications in Korea (Park et al., 2013) or in China (Song et al., 2021), though the field treatments for these studies have involved algal species that do not produce true neurotoxins. Recent laboratory studies have shown no mortalities of crabs, urchins, or clams exposed to sedimented clays containing brevetoxins (Devillier et al., 2023; 2024). Another concern is that continued application of clays may negatively affect benthic environments, though this is not an issue in relatively well-flushed marine waters (Park et al., 2013). For other areas, the quantity of clay needed for HAB removal can be remarkably low (4–10 g/m² or 4–10 tons/km²; Yu et al., 2017), so negative impacts are unlikely (Song et al., 2021).

5.4.2.1. Case study - use of clay to control HABs in South Korea. The marine aquaculture industry in South Korea has a market value of 2.7 billion USD (Statistics Korea: kostat.go.kr/anse/). These fish and shellfish farms are distributed widely along the 2000 km-long southern coast of Korea, primarily located at about 15–30 m depths, 200 to 500 m offshore. The use of clay flocculation for HAB control is considered to be one of the most advanced strategies based on the number of algal species and habitats that have been studied, the number of studies on ecosystem and environmental impacts, and the multiple uses of this technology over relatively large areas (>100 km²; Park et al., 2013). The bulk of this work has been done in Korea and China, both actively using clay flocculation, but with significant differences in the types of clay used and the way the clay is deployed. While other HAB control methods have been examined in Korea [marine bacteria (Kim et al., 2008), microscreen filtration and ozone (Kang et al., 2001), ultraviolet radiation (Jung, 2000), parasitic dinoflagellates (Park et al., 2004, 2013), and microzooplankton predators of bloom species (e.g., Jeong et al., 2003, 2008)], only clay control methods have been used extensively in Korean waters (Na et al., 1996; Choi et al., 1998; Kim, 2000; Sun et al., 2004).

Implementation: Historically, the first massive *Margalefidinium polykrikoides* blooms (maximum 30,000 cells mL⁻¹) occurred in 1995, resulting in 60 million USD loss of farmed fish (about 10 % loss of all cultured fish products that year). This massive economic loss to the aquaculture industry and the resulting public pressure resulted in the decision by the Korean government to apply clay to control *M. polykrikoides* blooms and to protect aquafarms in 1996. This decision was based on studies in the late 1980s in which a field trial using natural clay was conducted to control *M. polykrikoides* blooms near fish farms in Japan (Shirota, 1989). In Korea, this natural clay was a yellow loess that was readily available locally from nearby rivers.

Since its first application in 1996, natural clay dispersal has become the prime control technique of Korea's HAB management scheme for fish farms (Notification no. 2024-760 of Ministry of Ocean and Fisheries 2024; Park et al., 2013). Since that implementation, *M. polykrikoides* blooms have occurred almost annually (1000 to 50,000 cells mL⁻¹), but with considerably lower fish-kill losses of 1–20 million USD each year (Fig. 10).

Application Evaluation: Rigorous lab testing of the potential effects of natural clay on shellfish and fish started after its emergency use in the field in 1996. High concentrations of natural clay and with continuous resuspension had initial negative effects on shellfish health, but health returned to normal within 2 d after the clay treatment (Seo et al., 2008; National Institute of Fisheries Science (NIFS) HAB report, 2013). No negative effects were found on fish at 10 g l⁻¹ of clay (NIFS HAB report, 2013), concentrations generally well above that of clay dispersed in the sea for HAB control ($\leq 10 \text{ g l}^{-1} = \sim 100\text{--}400 \text{ g m}^{-2}$ clay dispersed).

The yellow loess used in all these lab studies and field applications is

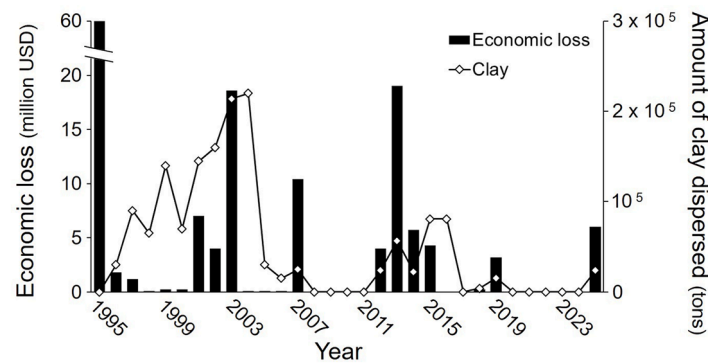


Fig. 10. Fish kill loss by *M. polykrikoides* blooms and amounts of natural clay dispersed in Korean marine waters for HAB control. Key milestones: 1995 - first bloom occurrence (maximum 30,000 cells mL⁻¹, bloom period 55 days), 1996 - first generation (1 G) clay dispenser, 1999 - second generation (2 G) clay dispenser, 2001 - start of electrolyzed clay dispersal (3 G), 2003 - the largest red tide outbreak (maximum 48,000 cells mL⁻¹, bloom period 62 days), 2013 - earliest bloom (July 17) occurrence (maximum 34,800 cells mL⁻¹, bloom period 48 days), 2016 - start of modified clay dispersal, 2020 to 2024 - no fisheries damage caused by red tide (low density blooms occurred at 300 to 8500 cells mL⁻¹).

a natural material that is only moderately effective in removing HAB cells. Studies showed that using electrolysis to alter clay surface charges greatly improved cell removal (Park et al., 2013), and further study examined the use of chemical modifiers to enhance HAB removal efficiencies. The following four clay types have received approval for use in South Korean marine waters:

1. Unprocessed clay: Seawater is pumped and mixed with natural clay in a chamber to produce a slurry of clay aggregates that is sprayed over the sea using a first generation (1 G) clay (slurry) dispenser. This method is simple to apply and can be used by small fishing boats or fish farm rafts.
2. Fine clay: Breaking the natural clay into finer aggregates before dispersal improves the efficiency of HAB removal by ~10 %, though application costs increase 60-fold. A second generation (2 G) clay dispenser was developed that uses three blades rotating at high speed in a mixing chamber, which crumbles the clay and mixes it with seawater before spraying the slurry directly into the sea from boats. This method generates a larger portion of clay aggregates < 50 µm, roughly equivalent to the ~40 µm size of *M. polykrikoides*, which increases cell-clay aggregation rates and HAB removal efficiencies by 10 % to 60 %.
3. Electrolyzed clay: The short-term dispersal of large amounts of clay has the potential to negatively impact benthic organisms (e.g., clams) by disturbing feeding patterns, suffocation, or burial (Shumway et al., 2003; Archambault et al., 2004). A third generation (3 G) clay dispenser (electrolytic clay dispenser, ECD) was therefore developed that minimizes the quantity of clay used and enhances the HAB removal efficiency. With ECD, the seawater is hydrolyzed via an electrical current to produce sodium hypochlorite (NaOCl) and then clay is added to the hydrolyzed seawater to produce a seawater/clay slurry. NaOCl is widely used as a cost-effective way to inhibit seawater biofouling of ship and electric power plant cooling systems (e.g., Christian et al., 1995). The concentration of NaOCl is controlled by adjusting the electrical input, and NaOCl is converted back to NaCl under sunlight (Jeong et al., 2002). The potential harmful effect of electrolyzed clay was tested against various marine organisms. Electrolyzed clay can kill red tide dinoflagellates at 300–500 ppb of NaOCl on the clay, but other organisms including finfish, diatoms, brine shrimp, and macroalgae (LD₅₀ at 1200–12,000 ppb) were much more tolerant to NaOCl (Jeong et al., 2002).
4. Modified clay: To identify better control substances to use with clay, 160 commercially available materials used for other purposes (e.g., water or soil treatments) were investigated by the Korean Ministry of Oceans and Fisheries. Of these, four were found to be safe and effective, and are approved and applied in Korean waters: a) clay

powder with palm oil; b) clay plus shells of shellfish; c) mudstone; and d) clay with sophorolipid (glycolipid liquid from the yeast, *Candida bombicola*). The timeframe for approval of modified clay was 3 to 10 years from their initial evaluation, primarily due to the funding needs at each step of the process.

Ecosystem impacts due to clay dispersion, particularly the benthos, have been assessed since 1998. The National Institute of Fisheries Science has monitored environmental changes in areas where yellow clay has been frequently dispersed during *M. polykrikoides* blooms, with an emphasis on the benthos. No significant impact on the biomass or species composition of the benthos, such as annelida, mollusca, decapoda, or Arthropoda have been observed in the areas of clay dispersion and control (Park et al., 2013). Due to the effectiveness and practicality of clay, clay dispersal has become a central element of Korea's management scheme. In fact, many fish and benthic organisms in the treatment area seem to thrive on the clay substrate (Park et al., 2013). For the last 15 years, effects of clay dispersal on the benthos have been monitored in clay dispersal areas. Before and after clay dispersal, no significant changes were found in the number and diversity of benthic organisms. No fish or shellfish kills were observed following treatments with high concentration (10 g l⁻¹) of natural clay in laboratory and mesocosm experiments (NIFS, 2013).

Large Scale Treatment: Modified clays currently are used for HAB control primarily at commercially valuable shellfish farms (e.g. abalone) even though the costs are up to 10 times higher than for natural clay. The higher costs are offset in part by using smaller amounts of modified clay for similar levels of HAB removal, which is a benefit because it minimizes potential negative impacts on the quality of shellfish products. For example, dispersal of 200 tons of natural clay km⁻² yields ~ 70 % HAB removal, while only 100 tons of modified clay km⁻² is needed for a similar level of removal. Local governments can choose control methods from 1, 2, or 3 G clay dispensers (described above) or modified clay, which depends on budget, the commercial value of the aquafarm, farmed fish or shellfish, geographical location, and HAB density (Fig. 11). Electrolyzed clay is used when blooms are large (>100 km²) and significant fish kills are expected.

The decision to initiate clay dispersal is guided by the South Korea Ministry of Ocean and Fisheries online alert system, which reports local government data on the concentrations of *M. polykrikoides* near fish farms. Clay dispersal is initiated when concentrations exceed 100,000 cells l⁻¹ over a wide area. The clay already has been moved from storage (usually in June) before the typical bloom season onto a barge centrally located offshore for easy distribution to the participating boats. Several hundred boats owned by local fishermen and local governments are directed by the Ministry of Ocean and Fisheries to the locations where

they should spray the clay. Clay is sprayed while facing away from the farms, targeting the areas where the *M. polykrikoides* bloom is occurring. In the case of large-scale blooms, clay dispersion may continue for up to four months. Spraying is repeated daily until *M. polykrikoides* cell abundance is below the threshold levels established by the Ministry of Ocean and Fisheries. These data are collected by: 1) marine police using helicopters to give real-time locations; 2) local government monitoring of coastal water; and 3) research vessel monitoring. Data are entered into a central database using cell phones by all groups to allow real-time decision-making by the government. Each local government makes the decision to continue or stop spraying, then reports this decision to Ministry headquarters. Every year in June, a practice event is held so that all participants in the actual spraying event are prepared. A detailed 300-page manual has been written describing the step-by-step operations to guide the practice sessions and the entire spraying process, including the decision-making by various government entities.

Regulatory Issues: The evaluation process for new control materials in Korea follows a standard four-step protocol for approval of any water-treatment chemical: 1) assess and document the potential natural toxicity; 2) evaluate the control method in the laboratory; 3) evaluate the method at sea; and 4) undergo committee review for approval. The first step is a document review that includes affordability, usability, eco-friendliness, and accessibility. An important aspect is that the material cannot include toxic components by environmental water quality standards. The second step is laboratory tests, including efficacy of *M. polykrikoides* removal and survival rate of phytoplankton, zooplankton, shellfish, and fish in bioassays. The third step involves a mesocosm experiment in the sea including evaluation of water quality, survival rate, and cell removal efficiency. This step is a primary road-block for moving forward, primarily due to cost. Candidate methods must have a high likelihood of success to reach the mesocosm stage. The last step of the evaluation is field deployments along the southern coastline of Korea. Separate funding is required for each of these steps, so the process takes several years before approval is granted.

Once the evaluation studies are completed, the findings are reviewed for approval by a 15-member committee composed of experts from universities as well as local and national government. Following approval, the local and national governments pay all the preparations needed for implementation in the field (Table 4). There is no cost for government employees used for the clay dispersal (up to 120 people per day).

Societal Issues: There is strong government and society support for the use of clay dispersion as a HAB control method along the south coast of Korea. Moreover, there is active societal participation in its implementation. This enthusiasm likely stems primarily from the demonstration of limited environmental impacts from clay dispersion after many years of use, along with the broad economic consequences that untreated HABs generate.

Scalability and Breadth of Applicability: The clay products tested and implemented already have a demonstrated broad scalability in marine waters. The use of clays for HAB organisms other than *M. polykrikoides* needs testing, as its effectiveness will be influenced by algal surface to clay interactions, and relative particle sizes, with aggregation potential increasing as particle sizes become more equal. Likewise, since the

yellow loess used for HAB control is not very effective in removing ichthyotoxins (Seger et al., 2017), other clay choices should be considered.

5.4.2.2. Case study - use of clay to control HABs in China. China has been working with clays to control HABs for more than three decades. The clay used most frequently in China is a purified kaolinite clay that has been combined with the inorganic polymer polyaluminum chloride (PAC). This step reverses the inherent net negative surface charge of the clay to positive, thereby increasing the electrostatic attraction of the clays to net negatively charged HAB cell surfaces (Yu et al. 1994a). The result is that HAB cell:clay aggregation rates increase, due both to improved particle:particle electrostatic attraction (coalescence) as well as the formation of large, more diffuse aggregate networks linked together with the long PAC chains. The network of PAC-linked flocs that settle through the water column “sweep capture” HAB cells, augmenting electrostatic cell removal. The resultant higher single-cell capture rates and higher particle sinking rates creates more effective bloom control with this modified clay relative to non-modified clays (Fig. 12). In addition, a residual effect of MC sorption of HAB cells is the inhibition of cell division, further restricting HAB development (Zhu et al., 2018).

Note that the Chinese researchers who developed this technology call their product Modified Clay (hereafter MC). There are, however, multiple clay formulations from other research teams that incorporate oxidants, polymers, algacides, or other materials, so we refer to these with the generic term “modified clays”.

Implementation: Studies of the efficacy of MC as a HAB control approach have been conducted in both large mesocosm tanks and in open waters. The first field studies using MC were conducted in 2005 to suppress cyanobacterial blooms in a 4 km² freshwater lake in Nanjing, China. The Nanjing Environmental agency monitored the bloom and environmental changes during MC treatment and concluded that MC was effective in controlling the cyanoHAB while being environmentally benign (Mei et al., 2010). Following that successful application, MC was gradually accepted by the Chinese government, the public, and marine stakeholders, which enabled its large-scale use for marine HAB suppression on multiple occasions in Chinese coastal waters from 2005 to 2011 (Yu et al., 2017; Qiu et al., 2017; Jiang et al., 2023; Zhu et al., 2024).

Application Evaluation: The efficacy of MC for HAB control has been tested in the laboratory with many HAB species, including *Heterosigma akashiwo*, *Procentrum minimum*, *Procentrum donghaiense*, *Nitzschia closterium*, *Alexandrium tamarense*, *Skeletonema costatum*, *Chattonella marina*, *Phaeocystis globosa*, *Aureococcus anophagefferens*, *Scrippsiella trochoidea*, *Isochrysis galbana*, *Karenia mikimotoi*, *K. brevis*, *Chlorella vulgaris*, *Litopenaeus vannamei*, *Nannochloropsis* sp., *Alexandrium catenella*, *Amphidinium carterae*, and microscopic propagules of *Ulva prolifera* (Yu et al., 1994b,c; 1995; 1999; Song et al., 2003; Cao et al., 2004; Cao and Yu, 2003; Wang et al., 2014a; Liu, 2016; Liu et al., 2016a, 2016b; Jiang et al., 2021; Qiu et al., 2017, 2020; Jiang et al., 2021, 2023; Dong et al., 2021; Liu et al., 2022; Wang et al., 2023a,b; Yu et al., 2023; Li et al., 2023; Zang et al., 2024). Removal efficiencies during these lab tests typically can reach ≥ 80 - 90 % at doses ranging from 0.1 - 0.5 g l⁻¹.

The effects of MC also have been tested on a wide range of non-target



Fig. 11. Various methods of clay dispersion for HAB removal in Korea. (A) 2 G clay dispenser; (B) 3 G clay dispenser; (C) Spraying modified clay.

Table 4
Cost of clay dispersal for HAB control in Korea (USD). Modified from Park et al. (2013).

Details	Price of clay	Clay stored (10 ⁴ tons of clay)	Cost of clay transport (1 dump truck, 1 excavator) ¹	Cost of 1 clay dispenser and 1 ship	Cleaning costs of ship (1 sprinkler truck) ²
Cost	20 USD per ton	820 USD per year	1250 per day	1900 USD per day	1500 USD per day
To control 200 km ² of HAB area	20 tons per day	820 USD per year	4–5 vehicles per day	20–40 ships per day	5–10 trucks per day
Total cost per day (200 km ² of HAB area)	400 USD	820 USD per year	5000–6300 USD	38,000–76,000 USD	7500–15,000 USD

¹ Clay is transported by dump truck from storage facilities near the coast to bloom-affected areas. Then excavators are used to transfer the clay onto vessels, including ships and barges, used for HAB control.
² After the dispersion process is completed, sprinkler trucks are used to clean the control vessels.

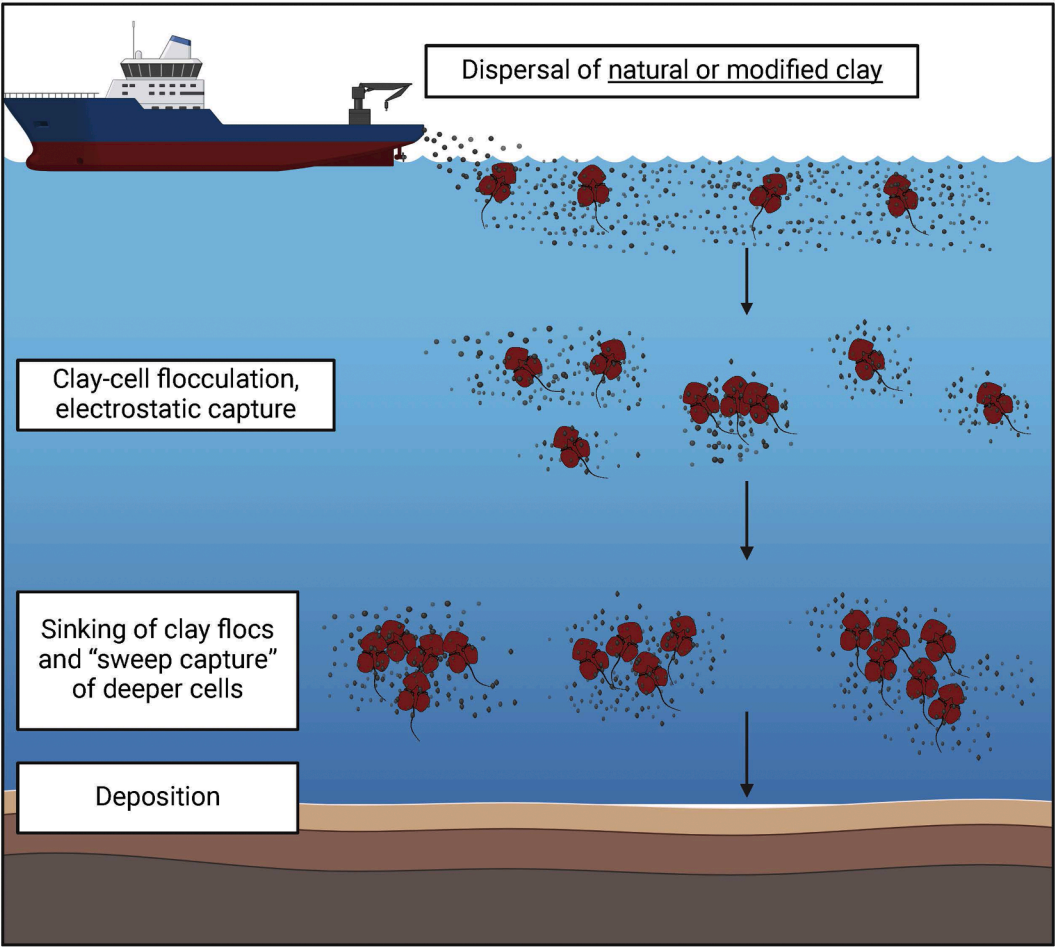


Fig. 12. Method for HAB control using MC. At the surface, the clay/PAC mixture is sprayed as a slurry over the water surface, where flocs form between positively charged clay particles and negatively charged HAB cells. As these flocs settle, polymer chains linking floc particles act as a net and sweep capture additional HAB cells lower in the water column. The flocculated materials are then deposited on the sediment surface. Created at <https://BioRender.com>.

planktonic, pelagic, and benthic organisms. These studies include fish species (turbot embryos, Zhang et al., 2019a; Atlantic salmon, Zhang et al., 2019b; marine medaka *Oryzias melastigma*, Zhang et al., 2022), a number of shrimp species (the opossum shrimp *Neomysis awatschensis*, Wu and Yu, 2007; juvenile kuruma shrimp *Penaeus japonicus*, Song et al., 2003; Cao et al., 2004; Wu et al., 2006; the white leg shrimp *Litopenaeus vanamei*, Song et al., 2021), bivalve species (the Pacific oyster *Crassostrea gigas*, Gao et al., 2007a; the yesso scallops *Patinopecten yessoensis* and *Mizuhopecten yessoensis*, Wang et al., 2014a; Meng et al., 2022; the hard clam *M. mercenaria*, Wang et al., 2019), abalone (*Haliotis discus hannai* juveniles, Zhang et al., 2020c), and sea cucumber (*Apostichopus japonicus*, Wang et al., 2014b). In all cases, no significant negative impacts

have been observed at MC loadings used for effective HAB removal in laboratory cultures and tanks (typically 0.1–0.3 g l⁻¹; reviewed in Song et al., 2021). The low environmental risk from MC is expected given that the modifying agent PAC is used as a flocculant in water purification treatments for drinking water and wastewater treatment.
An attractive feature of MC is that the surface modification can be optimized for different HAB species. In recent years the method has been optimized through the use of more reactive clays, and through additions of polymers, oxidants, or other materials to the clay that can alter the surface charge of the clay particles to improve electrostatic reactivity with HAB cells (Li et al., 2023; Liu et al., 2023), create long polymer chains to bridge among flocs, thereby trapping cells through net or

sweep capture as the aggregates settle through the water column (Yu et al., 2023; Jiang et al., 2023, 2025), and sequester or destroy HAB toxins in the water column that are released by cells captured and ruptured during flocculation (Song et al., 2023).

A new formulation of MC was developed to regulate excessive proliferation of picoplankton (e.g., *Nannochloropsis* sp.) that can negatively influence shrimp culture in Chinese aquaculture ponds. Rather than PAC, clays were modified with other organic polymers, e.g. polydimethyldiallylammonium chloride (PDA), a polymer of longer chain length than PAC, to enhance the capture efficiency of the smaller cells. In addition to successful removal of excessive picoplankton, this version of MC also removed organic matter and pathogenic microorganisms, such as ciliates, bacteria, and viruses (Chi et al., 2022; Chi et al., 2024; Ding et al., 2022, 2021; Zhu et al., 2023). Over 300 acres of culture ponds have benefitted from this MC usage since 2020.

MC has the added potential benefit of influencing water quality in ways that can reduce the intensity of HABs. PAC and alum (a closely related aluminum compound) are used in lake restoration to immobilize dissolved nutrients and transport them to bottom sediments (e.g., Kasprzak et al., 2018). MC is particularly effective for removing dissolved phosphate (up to 98 % at high MC loading; Deng and Shi, 2015) and dissolved silicate (40–60 %) in diatom cultures (Lu et al., 2015). In contrast, there is minimal absorption of nitrate or ammonia (Song et al., 2021). MC also has been shown to slow the release of nutrients from sinking cell:MC aggregates, thereby reducing the influence of legacy nutrients (Lu et al., 2015). Reductions in chemical oxygen demand have also been reported with the use of MC (Gao et al., 2007b; Yu et al., 2017).

Large Scale Treatment: During early-stage applications, specially modified fishing boats were used to disperse MC by pumping from tanks containing a clay/seawater slurry. Later, multiple platforms and equipment were developed for different types of applications and scales.

A dedicated clay dispersal craft was designed for applications in shallow waters. For nearshore, localized treatments such as around aquaculture ponds, a series of portable, self-feeding sprayers were developed and are available through manufacturers affiliated with the Institute of Oceanology, Chinese Academy of Sciences (IOCAS). Larger-scale applications, such as an ongoing program for nuclear power plant treatment, necessitated the development of a ship-mounted sprayer module capable of holding six tons of MC that can be automatically mixed with seawater and applied with a 55 m wide spray. At loading rates of 4–10 g MC m⁻² (=4–10 tons km⁻²), this bloom control strategy is relatively inexpensive for use over large areas, as is currently the case in China.

One highly publicized effort was to clear a *Chattonella* bloom at the sailing venue of the 2008 Olympics in Qingdao, China (Yu et al., 2017). Thirty fishing boats were used to spray 360 tons of MC over an area of 86 km² (4 tons/km²) in 30 h, successfully clearing the water for the event (Fig. 13). Another major field treatment occurred in 2015 when a massive *Phaeocystis globosa* bloom threatened to clog intakes for the critical cooling water of a nuclear power plant in Fangchenggang City, Southern China (Yu et al., 2017). The MC product and sprayers were mobilized to the site, an implementation plan was developed, staff were trained, and a three-month campaign implemented from Dec. 2015 to Feb. 2016. Repeated treatments were applied to the 2 km² cooling water intake channel and pond, as well as a 6 km² buffer area adjacent to the inlet channel (Fig. 14). These efforts were successful at keeping bloom concentrations low which enabled the nuclear plant to continue uninterrupted operations.

Successes and Challenges: MC dispersal is now widely accepted for HAB control in China. Over 20 large-scale MC treatments have been conducted nationwide to date, the largest covering 86 km² in 2008. To meet the many different HAB and water quality challenges nationwide, >10 formulations of MC have been developed and manufactured, some focused on the control of HAB species, and others on environmental



Fig. 13. Large scale HAB suppression using marine clay in open (oceanic) waters in China.

improvement, water quality, and aquaculture.

The surface modifications of clay offer an avenue for control not just of HAB species but also the toxins they release on lysis or death. Many of these lipophilic toxins still cause harm to higher trophic levels (e.g., fish kills). While some clays have been shown to remove up to 58 % of dissolved brevetoxin (Pierce et al., 2011), the current versions of MC are much less effective for brevetoxin (~0 - 30 %; D. M. Anderson et al., unpub. data). MC also showed no significant effects on dissolved paralytic shellfish toxins (PSTs; Song et al., 2021). Efforts are underway to develop MC with immobilized oxidants that can target toxins. For example, MC modified with potassium peroxymonosulfate (PMPS-MC) effectively removed *Alexandrium pacificum* cells and rapidly reduced intracellular and extracellular PSTs toxicity at a concentration of 0.1 g MC l⁻¹ (Song et al., 2023).

In this context, it is worth noting that some ichthyotoxins (e.g., from *Margalefidinium*, *Karenia*, *Karlodinium*, *Prymnesium*) can be effectively removed by clays at lower concentrations (down to 0.1 g l⁻¹) than are needed for cell flocculation (e.g., Seger and Hallegraeff, 2022). With this as the focus, reduced quantities of clay might be used to prevent fish mortalities at a lower expense and scale of effort than that associated with efforts to remove significant numbers of intact cells.

Costs. MC is available commercially in China, and costs vary among different formulations. The recommended loading rate for open water application using a general type of MC is 4–10 tons km⁻² (Yu et al., 2017). At the higher end of the loading range and assuming a dense picoplankton bloom with high cell concentrations in an enclosed area, 20 tons km⁻² might be needed. Regardless of the formulation used, the total cost for MC products in most scenarios would be ~10,000 USD per km², not including the cost of vessels to disperse the clay, or the labor involved. For applications in countries other than China, licensing agreements would be needed so that MC could be produced nearer to the treatment site at a lower cost.

Regulatory Issues: The approval of MC for HAB control proceeded from lab tests to field applications, during which the public and local authorities provided step by step comments and approvals. Initially, there was no precedent for field control of large-scale blooms in China, making it challenging for local authorities to approve potential technologies for field application. However, successes of field applications using clay flocculation to suppress HABs in Korea helped to facilitate the approvals. As there were no laws guiding the evaluation of the effects of HAB control and potential impacts during the application, local authorities asked the organization that developed the technology to provide relevant literature and a third-party evaluation to prove the effects

and ecological safety. Independent experts were asked to evaluate the potential approaches for field tests, and a third-party entity monitored the field tests and provided those data to the experts for final judgement. Further, an additional independent evaluation of the findings was conducted to ensure their validity. The repeated applications and findings then were summarized in the National Standard of Red Tide Control and Emergency Plans of Red Tide Control documents, which provide a baseline guide for the authorities and the public to use for future applications.

Societal Issues: MC now is accepted by multiple stakeholders, including local and national government authorities, infrastructures (e.g., power plants), aquaculture companies, and the public. MC has been listed in the National Standards issued by the Ministry of Nature Resources (Technical guidelines for treatment with red tide disaster, GB/T 40,743–2014) as well as being incorporated into the emergency plans for red tide control in many coastal provinces/cities of China. A Standard Operating Protocol for applying MC in the field has been developed (Technical specification for red tide control with modified clay, DB37/T 4753–2024). This success has led to MC being commercialized in China. Stakeholders can obtain the products in the market to use independently according to the instructions, and third party, site-specific evaluations are recommended before and after field application.

Scalability and Breadth of Applicability: As with clay dispersal in South Korea, the scalability and breadth of applicability have already been well demonstrated. Success of the method is leading to its expanded use in Chinese coastal waters and multiple other countries. For example, in a tilapia aquaculture area in Temenggor Lake, Malaysia, 2025, MC was sprayed around and into the cages for cyanobacterial suppression. In Turkey in 2025, İZDENİZ, the Izmir Marine Enterprise Inc, carried out a 10 km² operation with MC in Izmir Bay to control *Polykrikos hartmannii* which caused serious fish mortalities. Beyond these two cases, MC has also been applied in the field in the Barramundi aquaculture sites in Vietnam, in the Johor Strait of Singapore, and has been introduced into several other countries on a trial basis, including Chile, Peru, Thailand, and Scotland.

5.4.2.3. Case study - use of clay to control HABs in the United States. Clay flocculation to control HABs has been explored experimentally for over two decades in the U.S., but this control strategy remains less advanced compared to China and Korea, largely due to more stringent regulatory requirements. After considerable early work on a range of clay types (e.g., Sengco et al., 2001; Lewis et al., 2003; Sengco and Anderson 2004), U.S. researchers moved away from this line of research due to strong

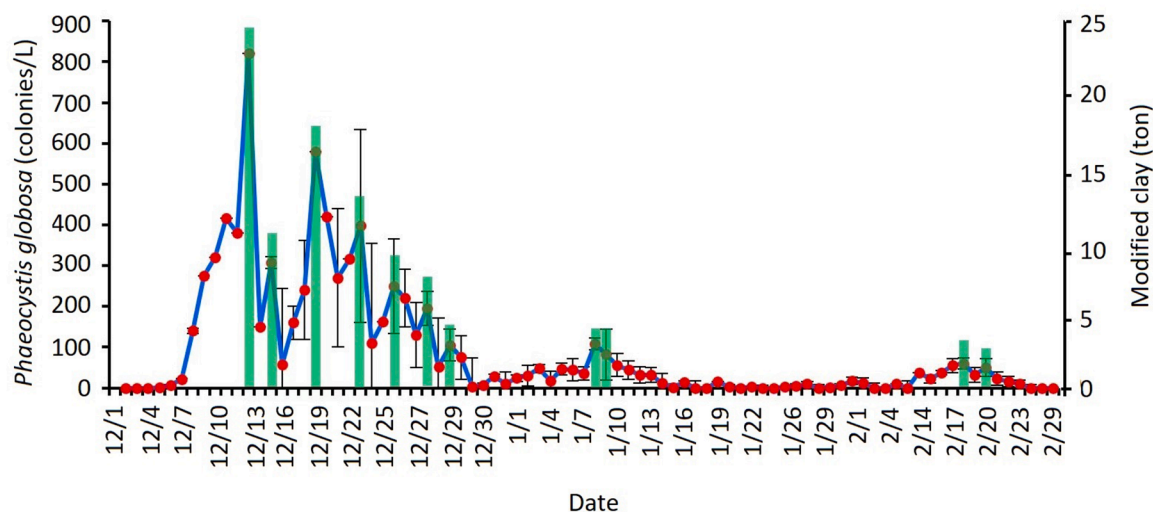


Fig. 14. HAB control in the cooling water pond of Fangchenggang Nuclear Power Plant from 2015 to 2016. Red circles denote the concentration of *Phaeocystis globosa* colonies; green bars show the MC amount released into the pond. Modified from Yu et al., 2017.

opposition from some segments of the public. A major problem was that the most effective clay used by U.S. researchers at the time (termed phosphatic clay; Sengco and Anderson, 2004) was a byproduct of phosphate mining in Florida, and this material (and phosphate mining in general) was associated with many deeply held environmental concerns relating to organic contaminants and radioactivity in the clay. The public was deeply concerned about the potential use of this material in natural waters, despite its extraordinary efficiency in removing *K. brevis* cells (Sengo and Anderson, 2004).

Work on clay flocculation essentially restarted in 2018 following a major Florida red tide of *K. brevis* that lasted more than a year (Weisberg et al., 2019), prompting many in the state to push for effective bloom control strategies. The decision was made to work with new clays, including the Chinese MC combined with PAC described above (Section 5.4.2.2). Since *K. brevis* was not a species that Chinese colleagues had studied to that point, and the effects of MC treatment on potent neurotoxins produced by *K. brevis* had also not yet been studied by the Chinese, the work began with small flask and tank studies, with and without benthic animals (e.g., Devillier et al., 2023). Experiments then shifted to small (80 L) and large (1400 L) mesocosm tanks containing clams, urchins, and crabs (Devilleir et al., 2024), again with MC as the main clay to be evaluated, but with other clay formulations tested as well.

Application Evaluation: Although considerable work had already been completed on the use of MC for HAB control (reviewed by Yu et al., 2017) a major knowledge gap was the effects of potential release of lipophilic neurotoxins when treating *K. brevis*. In this case, the treated water as well as flocculated cells and clay debris could negatively impact planktonic and benthic communities. In that instance, special constituents added to the clay might destroy or sequester toxins (e.g., oxidants, activated charcoal) greatly limiting these impacts.

Recent studies (Devilleir et al., 2023; 2024) used MC in aquarium tanks containing *K. brevis* as well as blue crab (*Callinectes sapidus*), and in 1400 L mesocosms containing *K. brevis*, blue crab, urchins (*Lytechinus variegatus*), and hard clams (*Mercenaria campechiensis*). The MC treatments effectively controlled *K. brevis* cells, with >95 % cell removal in several hours at clay loadings as low as 0.2 g l⁻¹ with no significant negative impacts on the exposed animals compared to controls (*K. brevis* only and clay only; Andres et al., unpub. data). Similarly, in earlier experiments with *K. brevis* and a different clay, Lewis et al. (2003) found that a PAC-modified phosphatic clay was non-toxic to infaunal amphipods (*Leptocheirus plumulosus* and *Ampelisca abdita*), grass shrimp embryos (*Palaemonetes pugio*) and larval sheepshead minnows (*Cyprinodon variegatus*). Moreover, animal mortality in the clay treatment of cultured *K. brevis* was not significantly different compared to untreated *K. brevis*, meeting the “no greater harm” criterion often used to evaluate the negative impacts of HAB control treatments.

In all the recent MC studies with *K. brevis*, a common finding was that during the flocculation and sedimentation process, some brevetoxin was released into the medium and was not adsorbed by the clay [e.g., Devillier et al. 2024]. This was evidenced by a decrease in parent brevetoxin and an increase in derivative toxins over time, a pattern that can be explained by toxin release after cell death and subsequent conversion of parent toxins to other forms (Pierce et al., 2011; Abraham et al., 2015). Furthermore, despite removal of 95 % or more of the cells in several hours, the total toxin in the tank water decreased only 34 %, with the difference being released, dissolved toxin. Although this release of toxin during flocculation and sedimentation was a concern, the experiments are still considered successful since most of the cells were killed or destroyed. In a treatment of a natural bloom, an equivalent result would suppress a bloom population and reduce future *K. brevis* development over the succeeding weeks or months, so a short-term release of toxin might be an acceptable outcome, particularly since the no-treatment option would include animal mortalities and other impacts due to the HAB itself.

More recent studies have turned to further modifications of the clay through the addition of algacide, oxidants, or other bioactive compounds (e.g., curcumin; Hall et al., 2024), and some of these either release less toxin during flocculation and cell death or chemically destroy or sequester the dissolved or particulate toxin. At this writing, modified clay formulations are being tested that remove >95 % of the *K. brevis* cells in 2 or 3 h, with 75–80 % toxin removal in 24 h (D. M. Anderson, unpub. data).

Large Scale Treatments: There have been no field-scale or large-scale treatments of clay dispersion for HAB control in the U.S. currently.

Regulatory Issues: Studies with MC and other modified clays in the U. S. have predominantly been conducted in small tubes, flasks, and mesocosm tanks. The next step in this development process will be pilot-scale (~2000 - 4000 m²) studies of natural *K. brevis* blooms in canal (physically constrained) sites to enable better controlled experiments. This step requires multiple permits and permit exceptions. Details are provided here so that those in the U.S. and other countries can learn about the challenging process needed to get approval for small-scale field trials. Locally, applications are needed to the Florida Department of Environmental Protection (DEP) for de minimus permit exceptions (i. e., impacts are expected to be small, so no permit is required). Approval is also required from several U.S. federal agencies with mandates relevant to the planned studies in marine waters, including the U.S. Army Corps of Engineers (navigation and changes in water depth) and the U.S. Fish and Wildlife Service (endangered species) and the National Oceanic and Atmospheric Administration (NOAA) National Marine Fisheries Service (protected/endangered species and critical fish habitat). It also is necessary to gain pre-approval for multiple possible treatment sites (typically canals or small embayments), given the unpredictability of *K. brevis* blooms. For each site, agreements are needed from owners of properties adjacent to the study area. Even with all local and state approvals, final clearance for clay dispersal pilot studies is currently awaiting determinations from the U.S. Environmental Protection Agency (EPA) under the FIFRA and FFDCA regulations described above.

Societal Issues: As noted above, long-standing opposition to clay dispersal for HAB control in FL has relaxed somewhat since the massive bloom of *K. brevis* in 2018 and is no longer a major impediment compared to the extended regulatory approval process for small-scale testing at a restricted field site.

Scalability and Breadth of Applicability: U.S. application of modified clays for marine HAB control is still in a testing or experimental stage. This is in part because more studies are needed on efficacy and impacts, but also because planned pilot-scale studies are currently stalled due to U.S. regulatory requirements.

6. Final perspectives

The societal, economic, geographic, and environmental impacts from HABs in marine waters have increased globally over the last 30 years (Hallegraeff et al., 2021), as has the demand for acceptable, effective, and scalable methods for controlling HABs in these systems. This review has provided a summary of the status of marine HAB control technologies and applications with a focus on those that have been attempted on relatively large scales, such as in mesocosm tanks or open marine waters. This represents a subset of many technologies that are being evaluated globally, but the relatively small number of case studies described here highlights the significant challenges that still constrain efforts to control HAB species in the field over large areas. These phenomena occur within complex planktonic assemblages, they are distributed throughout a water column that is mixing and advecting with tides and currents, and the blooms can span spatial scales sometimes reaching hundreds of km². As daunting as these challenges are, however, there are grounds for optimism. As highlighted here, our capabilities and understanding are substantially better and deeper than they were nearly 30 years ago

(Anderson, 1997) and prospects for continued advancement are good. Nevertheless, progress on bloom control technologies must continue to accelerate to match the mounting global scale of the HAB phenomena and its many impacts.

This compilation reveals some of the logistical and regulatory challenges that are commonly encountered. One view that emerges is that it is significantly easier to implement HAB control strategies on natural blooms in some nations/jurisdictions than in others. In part, this difference reflects the extraordinary social, cultural or economic value of some HAB-threatened resources and the need to protect them, as is the case with South Korea's 1.5 billion USD fish farming industry. But this difference also reflects varying national approaches to environmental protection and regulatory tolerances. One example is in Europe, where other than the treatment of an *Alexandrium ostenfeldii* bloom in the Netherlands (see above), there have been no significant bloom control efforts or studies, despite a long history of HAB impacts and research in the region. In our view, this reflects in part the effectiveness of shellfish monitoring programs and harvesting closures, which, though harmful, are short-lived with impacts that can be managed. Another reason may be a societal distrust of control technologies, perhaps linked to a lack of understanding of current capabilities.

Another example is the modified clay (MC) that has been used effectively on >20 occasions over large areas along the coast of China (Yu et al., 2017), but which has yet to receive regulatory approval for field testing in the U.S., despite significant effort. This discrepancy is notable because there have been many published environmental impact studies with MC (reviewed in Song et al., 2021) all reaching the conclusion that this technology has minimal negative impacts compared to those expected under the no-treatment option. Thus, the constraint in countries that focus on environmental protections is not necessarily with demonstrated dangers from the methodology, but rather the regulatory requirements that require the submission of multiple types of data, including ecotoxicological studies and residue analyses that are often far beyond the capabilities and resources of the scientists and engineers developing control strategies. In effect, substantial early investments are required by developers to generate and submit data to obtain the clearances for small-scale, in situ pilot studies that may ultimately demonstrate their method will fail to control blooms.

Thus, in some countries, well intentioned regulations designed to protect marine environments have impeded innovation and progress in the emerging field of marine HAB control. In many cases these regulations were not established to balance beneficial societal uses and environmental protection of marine ecosystems. As a result, there is often no clear pathway for advancing HAB control strategies. For example, in the U.S., broad environmental protections initially enacted to protect marine habitats or specific species (e.g. Pacific salmon) now govern the development of HAB control technologies intended to protect these resources. In other cases, rules enacted to regulate treatments to control harmful pests like insects or rodents are being applied to marine HABs.

One consequence in the U.S. is that investigators and end users may forego investing in the development of new ideas and turn instead to lists of "minimum risk" or exempt pesticides (or potentially inferior chemical solutions) in an attempt to control HABs, as these have little or no regulatory concerns compared to novel and potentially more effective compounds (see Section 5.2.3). Regulations have been established for good reason, but might be seen as too restrictive, particularly on research needed to advance HAB control methods.

Regulatory approaches to controlling other extreme natural phenomena that can quickly become an urgent threat to life, property and economy may offer useful lessons on how to balance societal benefits and environmental risks of effective methods of HAB control. For example, emergency responses to forest fires include large airborne dispersals of flame retardants - chemical tools that are routinely deployed but can pose environmental and health risks to plants and aquatic life (Gimenez et al., 2004).

Notably, there has been more rapid progress on control of freshwater

HABs versus marine HABs. Freshwater cyanobacteria control is operational with multiple established control strategies including chemical methods, mechanical/physical approaches, and biological methods, many of which are routinely implemented by water managers to protect drinking and recreational waters (Kibuye et al., 2021a,b; Pokrzywinski et al., 2022; Lefler et al., 2024; ITRC, 2020). These control methods have been tested, optimized, and standardized for cyanobacteria management, with proven effectiveness in reducing bloom magnitude, extent, and frequency with many being commercialized specifically for cyanobacteria control. One reason why marine HAB control has lagged freshwater control is that cyanoHABs are more uniform, widespread, and have universal societal impacts (e.g., drinking water supplies). In contrast, marine HAB control technology is harder to define because the problems are more diverse in causation, species, toxins, and impacts. A control technology developed for use against dense blooms of *K. brevis* (a neurotoxin producer) may not be appropriate, for example, for blooms of *Aureococcus anophagefferens*, the harmful, but non-toxic brown tide organism. Not only are these species markedly different in size, physiology, and habitat, but the resources impacted (and their value) differ dramatically as well. The diversity in marine HABs and their impacts may contribute to a poorly defined and fragmented market for control methods, greatly restricting technology development and implementation.

In countries where marine HAB control methods have been deployed to protect highly valued aquaculture fisheries, such as Japan, South Korea, and China, one common feature is the coordination and investment in developing control methodology by government entities. Much of Japan's HAB research, including the development of monitoring and control technology, is supported by the Fisheries Agency. Although the HcRNAV virus dispersal method (Case Study 5.2.2) is the only technology that has been put to practical use in Japan, the Japanese government continues to support the development of other control technologies. In South Korea, a "HAB Control Technology Development" program was supported by the National Institute of Fisheries Science under the Ministry of Ocean and Fisheries from 1997 to 2016. This led to the development of control methods such as clay dispersion devices and deep-water upwelling. Another program, the "HAB Removal System Development", was led by the South Korean Ministry of Science and Information and Communication Technology (MSIT) from 2013 to 2018. Algaecidal membranes, aquafarm filtering systems, and other related technologies were developed through this program. Korea also supported a public contest ("HAB Control Substance Development") organized in 2014 by the National Institute of Fisheries Science, which identified four types of modified clay (Case Study 5.4.2.1) that ultimately were approved for use.

In China, multiple authorities support HAB control research, including the Ministry of Science and Technology (MoST) and the National Science Foundation of China (NSFC). Prevention, Control, and Mitigation of HABs (PCMHAB), sponsored solely by MoST, has been in place since 2017. The PCMHAB program of China has focused mainly on the development, demonstration, commercialization of applicable technologies in monitoring, early warning, forecasting and emergency control of HABs. These include HABs causing extreme losses to the marine economy, such as the ichthyotoxic *Karenia mikimotoi*, and *Phaeocystis globosa*. In recent years, similar programs were proposed by other Ministries of China, including the Natural Resource Ministry and the Ministry of Ecology and Environment. These programs focus on much broader aspects of marine environmental protection, with HABs as one concern.

In contrast, investments in HAB control by the U.S., European Union and other countries have greatly lagged those of Japan, Korea and China. This trend is changing in the U.S., however, where the National Oceanic and Atmospheric Administration (NOAA) has implemented Congressionally authorized, national HAB competitive research programs for nearly 30 years, adding a specific focus on HAB control in 2009 with the creation of the NOAA Prevention, Control and Mitigation

of Harmful Algal Bloom (PCMHAB) program (74 Fed. Reg. 20465; <https://www.federalregister.gov/d/E9-10187>). In the ensuing years, PCMHAB investments explored the viability of several marine HAB control approaches and progressed two, algaecide IRI-160AA (5.2.3) and modified clay (5.4.2.3) to the field demonstration phase. NOAA and external partners created the U.S. Harmful Algal Bloom Control Technology Incubator (HAB-CTI) in 2022 to foster and help vet new and innovative ideas for HAB control and to help researchers navigate complex regulatory requirements governing in situ testing and later commercialization steps. This innovative program provides “seed money” for one-year, proof of concept projects which, if successful, may lead to future federal or state funding. One U.S. state program, the Florida Red Tide Mitigation and Technology Development Initiative (RTMTDI) has funded multiple potential control technologies specifically targeted on *K. brevis* HAB events. One of these is described in Section 5.3.4.

7. Recommendations

Globally, HABs threaten communities, businesses, and governments who are increasingly reliant on marine ecosystem services. Although there has been progress in HAB control research, there are few practical solutions for the majority of marine and estuarine HABs. Now is the time to accelerate research, testing, and implementation of HAB control methods to ensure continued safe access to vital marine resources. This paper summarizes the state of HAB control science to document viable options and highlights several methods that have been deployed in situ to control blooms of marine HAB species. Despite over three decades of research, only one effective bloom control option is in regular use (modified clay dispersal), and then only in two countries (China and South Korea). Some demonstrated and proven options are not in routine use (e.g. applications of naturally occurring algal virus HcRNAV in Japan and hydrogen peroxide in the Netherlands). Other options show promise but have not been adequately evaluated for scalability, cost effectiveness, or environmental impacts (e.g., alginate beads prepared with *Shewanella* sp. IRI-160 or IRI-160AA and modified clay in the U. S.). Still other promising approaches are stalled by societal concerns, regulatory hurdles or both. But the HAB research community is beginning to tackle the demand for marine and estuarine HAB control technologies, bolstered in some cases by increased investments by government agencies. However, current efforts are still far outshadowed by the breadth of the global HAB problem.

Accelerating progress towards a suite of control methods fitted to the most problematic HABs requires a reset of research perspectives, a reorganization of research funding, formal involvement of industry and commercial partners, and perhaps most importantly, a recognition that some major HABs are like other actionable extreme events (e.g., forest fires) regulations should allow for the development of viable control solutions. A worthy “moon-shot” approach to consider is to advance promising control efforts focusing on a small subset of HABs amenable to control, in reliably HAB-prone “test bed” field sites, with coordinated regulatory support, logistical help for short-term experiments, and expertise to help managers and the public weigh the benefits of HAB control versus the costs of no action. Here we present a list of recommendations under three broad categories to help shape this and other strategies to hasten the development of effective HAB control.

A) Identify which HAB phenomena are the most amenable to control

- 1) Identify HABs for which control efforts make sense both economically and practically. For example, in an area with routine monitoring for shellfish toxins, bloom control efforts might not be needed since the resource and its related industry are already protected to some degree by monitoring and harvesting restrictions. This might be the case for areas subject to paralytic shellfish poisoning outbreaks in the U.S., Europe, and many other areas of the world where blooms are frequent

and widespread, but where shellfish industries remain viable and productive because of short-duration closures or quarantine efforts. On the other hand, high-value resources such as fish farms, power or desalination plants, or even tourist areas might easily justify the cost and challenge of control efforts. In those cases, an additional consideration is the distribution and scale of the HAB. It may not be feasible to consider control of a marine HAB spanning hundreds of km along a coast, but it might well be possible to treat portions of those blooms that have entered small embayments, estuaries, or canals, or to attack the large marine bloom at hydrographic passes and other entryways into inland waterways to keep the species from spreading to new areas. The key is to keep expectations reasonable considering the characteristics of the impacted resource, the nature of the impacted region (hydrography, configuration), and the susceptibility of the HAB species to control efforts. Except for treatment of large-scale blooms in Korea and China, the most effective current control options can only treat blooms in small embayments or canals. The lessons learned from such applications will help improve our ability to expand to control solutions to more expansive blooms under more challenging circumstances.

- 2) Assess the socioeconomic footprint of HAB events to gauge the relative costs of bloom control against the value of the protected resource. The desire for HAB control is driven largely by the economic loss of resources (Trainer et al., 2020), so the greater the disruptions and cost, the greater the societal (and thus regulatory) willingness to explore control options. The value of the resource, risk of HAB-related disruptions to resource use, and implementation costs are all important factors that need to be understood and considered. There are challenges associated with assessments of social and economic HAB impacts (Suddleson and Hoagland, 2021) but a growing body of literature details improved methods to assess economic impacts and document HAB-related risks (Adams et al., 2018; Jin et al., 2020; Suddleson and Hoagland, 2021). Further, detailed studies of the total estimated implementation costs should be required for all promising HAB control approaches. An example is the South Korean study (e.g., Park et al., 2013) that provides an accounting of all relevant expenses, from the cost of clay to the labor and ship time for dispersal. Estimates of implementation costs of treatment technologies under consideration will help to determine if a control approach is justified by the socioeconomic benefit. Likewise, better efforts to assess the socioeconomic impacts of HABs and the costs of control methods will be key to driving investment in HAB control strategies. Further the creation of a standardized framework for cost-benefit analysis would be useful. This information is critical to determine which entities (e.g. government, businesses, individuals) or mix of entities will likely take on responsibilities (e.g. costs, liability) associated with implementing HAB control approaches and thus will help shape the emerging marine HAB control market.

B) Develop and test promising HAB control methodologies

- 1) Promote international collaborations on new control approaches and extend existing approaches to new organisms and habitats. Link the direct experience with HAB control in some nations to innovations in others to optimize the development of new strategies. International collaborations should be encouraged via the Intergovernmental Panel on Harmful Algae Blooms (IPHAB), its co-sponsors the UNESCO Intergovernmental Oceanographic Commission (IOC), and the Food and Agriculture Organization of the United Nations (FAO), as well as through multi-national regional ocean science bodies (e.g. the North Pacific Marine Science Organization [PICES]), international conferences (e.g. the

- International Conference on Harmful Algae [ICHA]), and international science programs (e.g. GlobalHAB). Harness the full capacity of scientific discovery by increasing the exchange of ideas, advances, and experiences (technical, logistical, and societal) to accelerate the use of marine control technologies.
- 2) Link scientists and engineers to work on control methodologies. Accelerating development of effective and logistically manageable approaches to HAB control hinges on synergy between science and engineering, which currently is rare in this field. New steps are needed to organize joint symposia and workshops to foster these interactions. Feedback on new approaches and results from field trials or full-scale implementation efforts will be essential, especially from application experiences in different habitats, so combining these workshops with training and reporting efforts from industry and resource managers would be invaluable.
 - 3) Increase investments in HAB control research at national and sub-national levels and promote partnerships with the private sector, including the insurance industry. Translating promising control methods from laboratory to field scales, and logistical and engineering needs (e.g., product licensing, storage, transport to affected areas, product delivery, and efficacy monitoring) require levels of investment that exceed those of normal science-funding agencies yet, in many cases, are far below the economic impact of recurrent HAB events. Attracting private sector investments in HAB control requires promotion of promising findings from small-scale field testing and a more robust pipeline of new ideas. Decisions by industries to make these investments depend on the commercial viability of the product or methodology. Involving companies that insure against HAB-related losses at early stages can help guide decision-making on the practical benefits of potential HAB control strategies.
 - 4) Explore combinations of existing and new technologies. While the effectiveness of the single-strategy HAB control approaches can vary widely, there has been little focus on the potential benefits of combining methods that use different mechanisms for control (e.g. remove cells vs. destroy toxins). A combined approach may lead to better outcomes faster than undertaking prolonged efforts to maximize the effectiveness of any single method.
 - 5) Create “incubators” where HAB control technologies can be tested and validated for larger-scale field evaluations (e.g., HAB-CTI and RTMTDI). A major roadblock to developing HAB control methods in many nations is the circular problem that methods cannot be field-tested until they are shown to have no, or manageable harmful effects, but obtaining this evidence requires that they be field-tested. Progress would be facilitated by the creation of sites for small, mesocosm- or field-scale testing of bloom control technologies in a controlled setting. These facilities should engage a research management process that follows a structured and tiered path, with decision thresholds to discontinue testing of technologies that fail one or more accepted field-feasibility criteria.
 - 6) Streamline regulatory processes governing in situ testing of HAB control technologies. Regulatory approvals for in situ testing often require extensive submissions to one or more agencies. To bolster innovation, the approval process could be simplified at national (e.g. HAB-CTI) and regional levels, not by weakening oversight but by building from existing regulatory criteria for similar treatments used in other environments and under different conditions (freshwaters, wastewater treatment, oil/gas/mining remediation, pesticides). This reorganization would allow the use of existing research data on products, greatly reducing the cost and complexity of developing HAB control in marine waters.
 - 7) Harness advances made in freshwater HAB control. HAB control in freshwater systems is far advanced compared to that in marine systems. Interactions between the two communities could help identify and develop methodologies for cell removal or suppression, in addition to practical and economical methods for dispersing algaecides over large areas.
 - 8) Severe HABs should be treated like other extreme events or natural disasters. As shown by Alvarez et al. (2024), some severe HABs have impacts that may exceed those of other extreme events, for example, hurricanes in Florida. For the purposes of emergency response, severe HABs should be treated like other extreme events. This is only a small subset of all HABs, however, so criteria should be developed to determine which are classified as extreme events.
- C) Gaining societal support for the research on, and implementation of HAB control.
- 1) Support social and behavioral science research on responsible development and implementation of control strategies. No bloom control approach is sustainable without social acceptance. Developing effective communication strategies to gain public awareness and trust hinges upon understanding the levels of public knowledge, attitudes and perceptions. This understanding, in turn, can guide the types of education, changes in laws, or economic incentives needed to promote acceptance of HAB control. All this is facilitated by strong coordination among researchers, stakeholders, community leaders, and decision-makers.
 - 2) Develop and encourage public and stakeholder co-development, outreach and support. The successes of HAB control should be shared widely with the public and stakeholders to gain support for these activities. For example, the successes in identifying new solutions for HAB control have been evident in Korea where funding competitions are open to the public to share and test ideas.

8. Synopsis

The growing array of global HABs and their impacts is large and varied, threatening human health and the health of marine and freshwater wildlife and ecosystems upon which many nations rely for food, recreation, tourism and a plethora of other goods and services. Bloom control strategies have moved from a little-studied area of HAB science to a major priority in several countries and regions. Though there are some proven methodologies now in use in some regions, capabilities to control HABs in marine systems are lacking in most nations. Clearly, not all HABs can be or should be controlled, as impacts may not be sufficiently severe, or in many cases, alternative strategies for managing impacts through mitigation strategies (e.g., toxin testing and harvest closures) are more appropriate. Decisions for the implementation of a control technology must weigh its costs and associated risks against the ecological and social impacts that will occur with the no-treatment option, yet the latter is often not considered by those opposing such efforts.

The bottom line is that for cases where HABs are causing extreme impacts on tourism, ecosystems, human health, fisheries, and aquaculture resources, among others, there is still a shortage of tools or approaches for effective bloom control. The need for acceptable control methods will only grow in the coming decades as societies increasingly rely on marine waters for food security and other critical resources.

Dedication

We dedicate this paper to our friend and colleague, Professor Ichiro Imai, whose visionary research across HAB science, including work on HAB control, inspires researchers around the world.

CRediT authorship contribution statement

Donald M. Anderson: Writing – review & editing, Writing – original draft, Conceptualization. **Mark L. Wells:** Writing – review & editing, Writing – original draft, Conceptualization. **Vera L. Trainer:** Writing – review & editing, Writing – original draft, Conceptualization. **Marc Suddleson:** Writing – review & editing, Writing – original draft, Conceptualization. **Kevin Claridge:** Writing – review & editing, Writing – original draft. **Kathryn J. Coyne:** Writing – review & editing, Writing – original draft. **Quay Dortch:** Writing – review & editing, Writing – original draft. **Christopher J. Gobler:** Writing – review & editing, Writing – original draft. **Cynthia A. Heil:** Writing – review & editing, Writing – original draft. **Nobuharu Inaba:** Writing – review & editing, Writing – original draft. **H. Dail Laughinghouse:** Writing – review & editing, Writing – original draft. **Jorge I. Mardones:** Writing – review & editing, Writing – original draft. **Natsuko Nakayama:** Writing – review & editing, Writing – original draft. **Taegyu Park:** Writing – review & editing, Writing – original draft. **Melissa B. Peacock:** Writing – review & editing, Writing – original draft. **Kaytee Pokrzywinski:** Writing – review & editing, Writing – original draft. **Heather Raymond:** Writing – review & editing, Writing – original draft. **Jennifer H. Toyoda:** Writing – review & editing, Writing – original draft. **Dean Trethewey:** Writing – review & editing, Writing – original draft. **Petra M. Visser:** Writing – review & editing, Writing – original draft. **Yanfei Wang:** Writing – review & editing, Writing – original draft. **Yongquan Yuan:** Writing – review & editing, Writing – original draft.

Declaration of competing interest

This Review Article, titled “Controlling harmful algal blooms (HAB) in marine waters: current status and future prospects” has not been published elsewhere and is not under consideration for publication elsewhere. This final, submitted version has been approved by all authors. All authors have made substantial contributions to the conception and design of the study, drafting the article, and revising the article.

Acknowledgements

This work is a result of two recent workshops, the first being held in Seattle, WA, from 21–22 October 2023 in association with the North Pacific Marine Science Organization (PICES) Annual Meeting and was titled (W3): GlobalHAB International Workshop on Solutions to Control HABs in Marine and Estuarine Waters. This workshop was held with support from the Global Harmful Algal Blooms (GlobalHAB) Programme and PICES. We thank those participants who helped with the initial brainstorming of this review, including: Javier Paredes Mella, Michelle Lepori-Bui, Colleen Kellogg, Ruoyu Guo, HoGeun Jang, Pengbin Wang, Natasha Melo Buckiewicz, Svetlana Esenkulova, Genki Terauchi, Yoichi Miyake, Megan Schulz, Takafumi Yoshida, West Bishop, Andrew Ross, Mandy Michaelson and Charles Trick. The second workshop was a 3.5-day HAB Control Writing Workshop, from February 27–March 1, 2024, held in Forks, WA, at the Olympic Natural Resources Center, a field facility of the University of Washington, and supported by the NOAA National Centers for Coastal Ocean Science and PICES. We thank these organizations for their support of this work. We acknowledge Dr. Zhiming YU, Dr. Xiuxian SONG and Dr. Xihua CAO for their help with this manuscript. DMA was supported by the Florida Red Tide Mitigation and Technology Development Initiative, State of Florida, Florida Fish and Wildlife Conservation Commission grant to Mote Marine Laboratory (initiative agreement #19153) and by funds provided by the NOAA PCMHAB Program through NOAA Grant. NA21NOS4780156. K.J.C, K.P. and Y.W. were supported by the PCMHAB Program through NOAA Grant NA20NOS4780185 and T.P. was funded by the National Institute of Fisheries Science, Korea (R2025040). This is PCMHAB publication number 75. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the author(s) and do not

necessarily reflect the views of NOAA or the Department of Commerce. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. Given their role as Editor and Associate Editor, neither Christopher Gobler nor Vera Trainer had any involvement in the peer review of this article and had no access to information regarding its peer review. Full responsibility for the editorial process for this article was delegated to another journal editor.

Data availability

No data was used for the research described in the article.

References

- Abraham, A., Plakas, S.M., Wang, Z., Jester, E.L., El Said, K.R., Granade, H.R., Henry, M. S., Blum, P.C., Pierce, R.H., Dickey, R.W., 2006. Characterization of polar brevetoxin derivatives isolated from *Karenia brevis* cultures and natural blooms. *Toxicon* 48 (1), 104–115. <https://doi.org/10.1016/j.toxicon.2006.04.015>.
- Abraham, A., El Said, K.R., Wang, Y., Jester, E.L., Plakas, S.M., Flewelling, L.J., Henry, M.S., Pierce, R.H., 2015. Biomarkers of brevetoxin exposure and composite toxin levels in hard clam (*Mercuraria* sp.) exposed to *Karenia brevis* blooms. *Toxicon* 96, 82–88.
- Adams, C.M., Larkin, S.L., Hoagland, P., Sancewich, B., 2018. Assessing the economic consequences of harmful algal blooms: a summary of existing literature, research methods, data, and information gaps. In: Shumway, S.E., Burkholder, J.M., Morton, S.L. (Eds.), *Harmful Algal Blooms: a Compendium Desk Reference*, pp. 337–354.
- Ahn, O., Petrell, R.J., Harrison, P.J., 1998. Ammonium and nitrate uptake by *Laminaria saccharina* and *Nereocystis luetkeana* originating from a salmon sea cage farm. *J. Appl. Phycol.* 10 (4), 333–340. <https://doi.org/10.1023/A:1008092521651>.
- Alacid, E., René, A., Gallisai, R., Paloheimo, A., Garcés, E., Kremp, A., 2020. Description of two new coexisting parasitoids of blooming dinoflagellates in the Baltic Sea: *Parvilucifera catillova* sp. nov. and *Parvilucifera* sp. (Perkinsea, Alveolata). *Harmful Algae* 100, 101944.
- Alvarez, S., Brown, C.E., Diaz, M.G., O’Leary, H., Solis, D., 2024. Non-linear impacts of harmful algal blooms on the coastal tourism economy. *J. Environ. Manage* 351, 119811.
- Amin, S.A., Hmelo, L.R., Van Tol, H.M., Durham, B.P., Carlson, L.T., Heal, K.R., Morales, R.L., Berthiaume, C.T., Parker, M.S., Djunaedi, B., Ingalls, A.E., 2015. Interaction and signaling between a cosmopolitan phytoplankton and associated bacteria. *Nature* 522 (7554), 98–101.
- Anabawati, H.M., Lee, W.H., Al-Anazi, A., Mohamed, M.M., Hassan, A., 2024. Advancements in biological strategies for controlling harmful algal blooms (HABs). *Water* 16 (2), 224.
- Anderson, D.M., 1997. Turning back the harmful red tide. *Nature* 388, 513–514.
- Anderson D.M. 2017. Harmful algal blooms. In: D.M. Anderson, S.F.E Boerlage, & M.B. Dixon (Eds.), *Harmful algal blooms (HABs) and desalination: a guide to impacts, monitoring and management. Manuals and Guide 78. IOC-UNESCO, Paris*, pp. 17–52.
- Anderson, D.M., Burkholder, J.M., Cochlan, W.P., Glibert, P.M., Gobler, C.J., Heil, C.A., Kudela, R.M., Parsons, M.L., Rensel, J.J., Townsend, D.W., Trainer, V.L., 2008. Harmful algal blooms and eutrophication: examining linkages from selected coastal regions of the United States. *Harmful Algae* 8 (1), 39–53.
- Anderson, D.M., Fensin, E., Gobler, C.J., Hoeglund, A.E., Hubbard, K.A., Kulis, D.M., Landsberg, J.H., Lefebvre, K.A., Provoost, P., Richlen, M.L., Smith, J.L., 2021. Marine harmful algal blooms (HABs) in the United States: history, current status and future trends. *Harmful Algae* 102, 101975.
- Archambault, M.C., Bricelj, V.M., Grant, J., Anderson, D.M., 2004. Effects of suspended and sedimented clays on juvenile hard clams, *Mercuraria mercenaria*, within the context of harmful algal bloom mitigation. *Mar. Biol.* 144, 553–565.
- Augyte, S., Yarish, C., Redmond, S., Kim, J.K., 2017. Cultivation of a morphologically distinct strain of the sugar kelp, *Saccharina latissima* forma *angustissima*, from coastal Maine, USA, with implications for ecosystem services. *J. Appl. Phycol.* 29 (4), 1967–1976. <https://doi.org/10.1007/s10811-017-1102-x>.
- Baden, D.G., Bourdelais, A.J., Jacocks, H., Michelliza, S., Naar, J., 2005. Natural and derivative brevetoxins: historical background, multiplicity, and effects. *Environ. Health Perspect.* 113 (5), 621–625. <https://doi.org/10.1289/ehp.7499>.
- Bai, X., Adolf, J.E., Bachvaroff, T., Place, A.R., Coats, D.W., 2007. The interplay between host toxins and parasitism by *Amoebophrya*. *Harmful Algae* 6 (5), 670–678.
- Balaji-Prasath, B., Wang, Y., Su, Y.P., Hamilton, D.P., Lin, H., Zheng, L., Zhang, Y., 2022. Methods to control harmful algal blooms: a review. *Environ. Chem. Lett.* 20 (5), 3133–3152.
- Bates, S.S., Hubbard, K.A., Lundholm, N., Montresor, M., Leaw, C.P., 2018. *Pseudo-nitzschia*, *Nitzschia*, and domoic acid: new research since 2011. *Harmful Algae* 79, 3–43.
- Bishop, W.M., Willis, B.E., Richardson, R.J., Cope, W.G., 2018. The presence of algae mitigates the toxicity of copper-based algacides to a nontarget organism. *Environ. Toxicol. Chem.* 37 (8), 2132–2142.
- Boesch, D.F., 1997. *Harmful Algal Blooms in Coastal Waters: Options for Prevention, Control and Mitigation* (No. 10). U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Coastal Ocean Office.

- Bohrerova, Z., Yousuf, Y., Crafton-Nelson, E., Cheng, C., Weaver, C.R., Weavers, L.K., 2023. Cyanobacteria mitigation using low power ultrasound for gas vesicle collapse. *AWWA Water Sci.* 5 (3).
- Brown, A.R., Lilley, M., Shuttler, J., Lowe, C., Artioli, Y., Torres, R., Berdalet, E., Tyler, C. R., 2019. Assessing risks and mitigating impacts of harmful algal blooms on mariculture and marine fisheries. *Rev. Aquac.* 12 (3), 1663–1688.
- Bolch, C.J., Hallegraeff, G.M., 1993. Chemical and physical treatment options to kill toxic dinoflagellate cysts in ships' ballast water. *J. Mar. Environ. Eng.* 1, 23–29.
- Burford, M.A., Gobler, C.J., Hamilton, D.P., Visser, P.M., Lurling, M., Codd, G.A., 2019. Solutions For Managing Cyanobacterial Blooms: A Scientific Summary For Policy Makers. IOC/UNESCO, Paris (IOC/INF-1382). Available from: <https://unesdoc.unesco.org/ark:/48223/pf0000372221.locale=en>.
- Burgunter-Delamare, B., Kleinjan, H., Frioux, C., Fremy, E., Wagner, M., Corre, E., Le Salver, A., Leroux, C., Leblanc, C., Boyen, C., Siegel, A., 2020. Metabolic complementarity between a brown alga and associated cultivable bacteria provide indications of beneficial interactions. *Front. Mar. Sci.* 7, 85.
- Burson, A., Matthijs, H.C., de Bruijne, W., Talens, R., Hoogenboom, R., Gerssen, A., Visser, P.M., Stomp, M., Steur, K., van Scheppingen, Y., Huisman, J., 2014. Termination of a toxic *Alexandrium* bloom with hydrogen peroxide. *Harmful Algae* 31, 125–135.
- Cao, X., Yu, Z., 2003. Extinguishment of harmful algae by organo-clay. *J. Appl. Ecol.* 14 (7), 1169–1172.
- Cao, X.H., Song, X.X., Yu, Z.M., 2004. Removal efficiency of red tide organisms by modified clay and its impacts on cultured organisms. *Huanjing Kexue* 25 (5), 148–152.
- GlobalHAB, 2023. Fish-Killing Marine Algal Blooms: causative Organisms, Ichthyotoxic Mechanisms, Impacts and Mitigation. In: Hallegraeff, G.M., et al. (Eds.), IOC Manuals and Guides, 93. UNESCO-IOC/SCOR, Paris, p. 96. <https://doi.org/10.25607/OBP-1964>.
- Chaffin, J.D., Berthold, D.E., Braig, E.C., Fuchs, J.D., Gabor, R.S., Jacquemin, S.J., Kuhn, H.E., Labus, L.D., Laughinghouse, H.D., Lefler, F.W., Mash, H.E., Raymond, H. A., Stanley, H., Taylor, A.T., Weavers, L.K., Wendel, S., 2024. Effectiveness of ozone nanobubble treatments on high biomass cyanobacterial blooms: a mesocosm experiment and field trial. *J. Environ. Manage* 372, 123406. <https://doi.org/10.1016/j.jenvman.2024.123406>.
- Chen, X., Wang, D., Wang, Y., Sun, P., Ma, S., Chen, T., 2022. Algicidal effects of a high-efficiency algicidal bacterium *Shewanella* Y1 on the toxic bloom-causing dinoflagellate *Alexandrium pacificum*. *Mar. Drugs* 20, 239. <https://doi.org/10.3390/md20040239>.
- Cheng, J., Jia, N., Chen, R., Guo, X., Ge, J., Zhou, F., 2022. High-resolution mapping of seaweed aquaculture along the Jiangsu coast of China using Google Earth Engine (2016–2022). *Remote Sens.* 14 (24), 6202.
- Chi, L., Ding, Y., He, L., Wu, Z., Yuan, Y., Cao, X., Song, X., Yu, Z., 2022. Application of modified clay in intensive mariculture pond: impacts on nutrients and phytoplankton. *Front. Mar. Sci.* 9, 976353.
- Chi, L., Jiang, K., Ding, Y., Wang, W., Song, X., Yu, Z., 2024. Uncovering nutrient regeneration, transformation pattern, and its contribution to harmful algal blooms in mariculture waters. *Sci. Total Environ.* 919, 170652.
- Choi, H.G., Kim, P.S., Lee, W.C., Yun, S.J., Kim, H.G., Lee, H.J., 1998. Removal efficiency of *Cochlodinium polykrikoides* by yellow loess. *Korean J. Fisher. Aquat. Sci.* 31 (1), 109–113.
- Chopin, T., Buschmann, A.H., Halling, C., Troell, M.F., Kautsky, N., Neori, A., Kraemer, G.P., Zertuche-González, J.A., Yarish, C., Neefus, C.D., 2001. Integrating seaweeds into marine aquaculture systems: a key toward sustainability. *J. Phycol.* 37, 975–986.
- Christian, D.K., Bergh, J.O., Thomas, E.D., 1995. Dechlorination equipment for shipboard pollution prevention. *Sea Technol.* 51–56.
- Chung, I.K., Oak, J.H., Lee, J.A., Shin, J.A., Kim, J.G., Park, K.S., 2013. Installing kelp forests/seaweed beds for mitigation and adaptation against global warming: Korean Project Overview. *ICES J. Mar. Sci.* 70, 1038–1044.
- Ciminiello, P., Dell'Aversano, C., Lacovo, E.D., Fattorusso, E., Forino, M., Tartaglione, L., Benedettini, G., Onorari, M., Serena, F., Battocchi, C., Casabianca, S., 2014. First finding of *Ostreopsis cf. ovata* toxins in marine aerosols. *Environ. Sci. Technol.* 48 (6), 3532–3540.
- Clement, A., Lincoque, L., Saldivia, M., Brito, C.G., Muñoz, F., Fernández, C., Pérez, F., Maluje, C.P., Correa, N., Moncada, K., Contreras, G., 2016. Exceptional summer conditions and HABs of *Pseudochattonella* in Southern Chile create record impacts on salmon farms. *Harmful Algae News* 53, 1–3.
- Coyne, K., Wang, Y., Johnson, G., 2022. Algicidal bacteria: a review of current knowledge and applications to control harmful algal blooms. *Front. Microbiol.* 13, 871177.
- Cruz-López, R., Maske, H., 2016. The vitamin B1 and B12 required by the marine dinoflagellate *Lingulodinium polyedrum* can be provided by its associated bacterial community in culture. *Front. Microbiol.* 7, 560.
- Cruz-Lopez, R., Maske, H., Yarimizu, K., Holland, N.A., 2018. The B-vitamin mutualism between the dinoflagellate *Lingulodinium polyedrum* and the bacterium *Dinoroseobacter shibae*. *Front. Mar. Sci.* 5, 274.
- Deng, L.L., Hayes, P.K., 2008. Evidence for cyanophages active against bloom-forming freshwater cyanobacteria. *Freshw. Biol.* 53 (6), 1240–1252.
- Deng, L., Shi, Z., 2015. Synthesis and characterization of a novel Mg–Al hydrotalcite-loaded kaolin clay and its adsorption properties for phosphate in aqueous solution. *J. Alloys. Compd.* 637, 188–196.
- Devillier, V., Hall, E.R., Heil, C.A., Frankle, J.D., Klass, S., Toyoda, J.H., Pierce, R., 2025. Lessons learned from mesocosm experiments with curcumin: pilot studies of a harmful algal bloom mitigation technique. *Limnol. Ocean Methods*. <https://doi.org/10.1002/lom3.10731>.
- Devillier, V.M., Hall, E.R., Anderson, D.M., Lewis, K.A., 2023. Exposure of blue crab (*Callinectes sapidus*) to modified clay treatment of *Karenia brevis* as a bloom control strategy. *Harmful Algae* 128, 102492.
- Devillier, V.M., Hall, E.R., Lovko, V., Pierce, R., Anderson, D.M., Lewis, K.A., 2024. Mesocosm study of PAC-modified clay effects on *Karenia brevis* cells and toxins, chemical dynamics, and benthic invertebrate physiology. *Harmful Algae* 134, 102609.
- Díaz-Alonso, A., Rodríguez, F., Riobó, P., Álvarez-Salgado, X., Teira, E., Fernández, E., 2024. Response of the toxic dinoflagellate *Alexandrium minutum* to exudates of the eelgrass *Zostera marina*. *Harmful Algae* 133, 102605.
- Ding, Y., Song, X., Cao, X., He, L., Liu, S., Yu, Z., 2021. Healthier communities of phytoplankton and bacteria achieved via the application of modified clay in shrimp aquaculture ponds. *Int. J. Environ. Res. Public Health* 18 (21), 11569.
- Ding, Y., Song, X.X., Yu, Z.M., 2022. Transcriptome profiles of genes related to growth and virulence potential in *Vibrio alginolyticus* treated with modified clay. *Microbiol. Res.* 262, 127095.
- Dong, X., Cao, X., Jiang, W., Song, X., Yu, Z., Yu, S., 2021. Profiles of and variations in aluminum species in PAC-MC used for the removal of blooming microalgae. *J. Environ. Sci.* 106, 76–82.
- Dorantes-Aranda, J.J., Seger, A., Mardones, J.I., Nichols, P.D., Hallegraeff, G.M., 2015. Progress in understanding algal bloom-mediated fish kills: the role of superoxide radicals, phycotoxins and fatty acids. *PLoS ONE*, 10 (7), e0133549. <https://doi.org/10.1371/journal.pone.0133549>.
- Duggins, D.O., 1980. Kelp beds and sea otters: an experimental approach. *Ecology* 61, 447–453.
- Dunga-Santos, J.C.R., Caspe, F.J.O., Tablizo, F.A., Purganan, D.J.E., Azanza, R.V., Onda, D.F.L., 2019. Algicidal potential of cultivable bacteria from pelagic waters against the toxic dinoflagellate *Pyrodinium bahamense* (Dinophyceae). *J. Appl. Phycol.* 31, 3721–3735.
- Durham, B.P., Dearth, S.P., Sharma, S., Amin, S.A., Smith, C.B., Campagna, S.R., Armbrust, E.V., Moran, M.A., 2017. Recognition cascade and metabolite transfer in a marine bacteria-phytoplankton model system. *Environ. Microbiol.* 19 (9), 3500–3513.
- FAO, 2020. The State of World Fisheries and Aquaculture. Sustainability in Action. <https://doi.org/10.4060/ca9229en>. Rome.
- Ferdouse, F., Holdt, S.L., Smith, R., Murúa, P., Yang, Z., 2018. The Global Status of Seaweed production, Trade and Utilization, 124. FAO Globefish Research Programme.
- Fernández, P.A., Leal, P.P., Henríquez, L.A., 2019. Co-culture in marine farms: macroalgae can act as chemical refuge for shell-forming molluscs under an ocean acidification scenario. *Phycologia* 58 (5), 542–551. <https://doi.org/10.1080/00318884.2019.162857>.
- Fernando, B.M., Lefler, F.W., Kennedy, A., Berthold, D.E., May, L.R., Laughinghouse, H. D., Indest, K.J., 2025. Algicidal effects of tryptoline, tryptamine, and other microbial metabolites on target and non-target freshwater cyanobacteria and freshwater indicator organisms. *Ecotoxicol. Environ. Saf.* 292, 117918.
- Fei, C., Booker, A., Klass, S., Vidyaratna, N.K., Ahn, S.H., Mohamed, A.R., Arshad, M., Glibert, P.M., Heil, C.A., Martínez Martínez, J., Amin, S.A., 2025. Friends and foes: symbiotic and algicidal bacterial influence on *Karenia brevis* blooms. *ISMe Commun.* 5 (1), 164.
- Gallardo-Rodríguez, J.J., Astuya-Villalón, A., Llanos-Rivera, A., Avello-Fontalba, V., Ulloa-Jofré, V., 2019. A critical review on control methods for harmful algal blooms. *Rev. Aquac.* 11 (3), 661–684.
- Gao, G., Gao, L., Jiang, M., Jian, A., He, L., 2022. The potential of seaweed cultivation to achieve carbon neutrality and mitigate deoxygenation and eutrophication. *Environ. Res. Lett.* 17, 014018.
- Gao, Y., Yu, Z., Song, X., 2007a. Impact of modified clays on the infant oyster (*Crassostrea gigas*). *Mar. Sci. Bull. Chinese edition* 26 (3), 53.
- Gao, Y., Yu, Z., Song, X., 2007b. The influence of organic modified clay on nutrients and main water quality index in sea water. *Mar. Sci. Qingdao-Chinese Edition* 31 (8), 30.
- Gerphagnon, M., Latour, D., Colombet, J., Sime-Ngando, T., 2013. Fungal parasitism: life cycle, dynamics and impact on cyanobacterial blooms. *PLoS ONE* 8 (4), e06894.
- Gharbia, H.B., Yahia, O.K.D., Cecchi, P., Masseret, E., Amzil, Z., Hervé, F., Rovillon, G., Nouri, H., M'Rabet, C., Couet, D., Triki, H.Z., Laabir, M., 2017. New insights on the species-specific allelopathic interactions between macrophytes and marine HAB dinoflagellates. *PLoS ONE* 12 (11), 1–28. <https://doi.org/10.1371/journal.pone.0187963>.
- Gimenez, A., Pastor, E., Zarate, L., Planas, E., Arnaldos, J., 2004. Long-term forest fire retardants: a review of quality, effectiveness, application and environmental considerations. *Int. J. Wildland. Fire* 13 (1), 1–15.
- Gleason, F.H., Jephcott, T.G., Küpper, F.C., Gerphagnon, M., Sime-Ngando, T., Karpov, S. A., Guillou, L., Van Ogtrop, F.F., 2015. Potential roles for recently discovered chytrid parasites in the dynamics of harmful algal blooms. *Fungal. Biol. Rev.* 29 (1), 20–33.
- Gobler, C.J., Sunda, W.G., 2012. Ecosystem disruptive algal blooms of the brown tide species, *Aureococcus anophagefferens* and *Aureoumbra lagunensis*. *Harmful Algae* 14, 36–45.
- Grasso, C.R., 2018. Effects of the bacterial Algicide IRI-160AA on the Microbial Community Composition of the Delaware Inland Bays. Master's Thesis, University of Delaware.
- Grasso, C.R., Pokrzywinski, K.L., Waechter, C., Rycroft, T., Zhang, Y., Aligata, A., Kramer, M., Lamsal, A., 2022. A review of cyanophage–host relationships: highlighting cyanophages as a potential cyanobacteria control strategy. *Toxins* 14 (6), 385.
- Gregg, M.D., Hallegraeff, G.M., 2007. Efficacy of three commercially available ballast water biocides against vegetative microalgae, dinoflagellate cysts and bacteria. *Harmful Algae* 6 (4), 567–584.

- Gregg, M., Rigby, G., Hallegraeff, G.M., 2009. Review of two decades of progress in the development of management options for reducing or eradicating phytoplankton, zooplankton and bacteria in ship's ballast water. *Aquat. Invasions* 4 (3), 521–565.
- HAB RDDTT, 2008. Harmful Algal Bloom Research, Development, Demonstration, and Technology Transfer National Workshop Report. In: Dortch, Q., Anderson, D.M., Ayres, D.L., Glibert, P.M. (Eds.). Woods Hole, Massachusetts.
- Hall, E.R., Heil, C.A., Frankle, J.D., Klass, S., Devillier, V., Lovko, V., Toyoda, J.H., Pierce, R., 2024. Mitigation of *Karenia brevis* cells and brevetoxins using curcumin, a natural supplement. *Water* 16 (10), 1458.
- Hallegraeff, G.M., 2010. Ocean climate change, phytoplankton community responses, and harmful algal blooms: a formidable predictive challenge. *J. Phycol.* 46 (2), 220–235.
- Hallegraeff, G.M., Anderson, D.M., Belin, C., Bottein, M.Y.D., Bresnan, E., Chinain, M., Enevoldsen, H., Iwataki, M., Karlson, B., McKenzie, C.H., Sunesen, I., 2021. Perceived global increase in algal blooms is attributable to intensified monitoring and emerging bloom impacts. *Commun. Earth. Environ.* 2 (1), 117.
- Hanic, L.A., Sekimoto, S., Bates, S.S., 2009. Oomycete and chytrid infections of the marine diatom *Pseudo-nitzschia pungens* (Bacillariophyceae) from Prince Edward Island, Canada. *Botany* 87 (11), 1096–1105.
- Hansen, P.J., 2002. Effect of high pH on the growth and survival of marine phytoplankton: implications for species succession. *Aquatic Microbial Ecology* 28 (3), 279–288. <https://doi.org/10.3354/ame028279>.
- Hardman, R.C., Cooper, W.J., Bourdelais, A.J., Gardinali, P., Baden, D.G., 2004. Brevetoxin degradation and by-product formation via natural sunlight. In: Steidinger, K.A., et al. (Eds.), *Harmful Algae 2002: Proceedings of the Xth International Conference on Harmful Algae*. St. Pete Beach, Florida, USA. October 21–25, 2002.
- Hare, C.E., Demir, E., Coyne, K.J., Cary, S.C., Kirchner, D.L., Hutchins, D.A., 2005. A bacterium that inhibits the growth of *Pfiesteria piscicida* and other dinoflagellates. *Harmful Algae* 4 (2), 221–234.
- Heisler, J., Glibert, P.M., Burkholder, J.M., Anderson, D.M., Cochlan, W.P., Dennison, W. C., Dortch, Q., Gobler, C.J., Heil, C.A., Humphries, E., Lewitus, A.J., Magnien, R., Marshall, H.G., Sellner, K., Stockwell, D.A., Stoecker, D.K., Suddleson, M., 2008. Eutrophication and harmful algal blooms: a scientific consensus. *Harmful Algae* 8 (1), 3–13. <https://doi.org/10.1016/j.hal.2008.08.006>.
- Hu, J., Berthold, D.E., Wang, Y., Xiao, X., Laughinghouse IV, H.D., 2022. Treatment of the red tide dinoflagellate *Karenia brevis* and brevetoxins using USEPA-registered algacides. *Harmful Algae* 120, 102347.
- Hurd, C.L., Gattuso, J.P., Boyd, P.W., 2024. Air-sea carbon dioxide equilibrium: will it be possible to use seaweeds for carbon removal offsets? *J. Phycol.* 60, 4–18. <https://doi.org/10.1111/jpy.13405>.
- Hurd, C.L., Law, C.S., Bach, L.T., Britton, D., Hovenden, M., Paine, E.R., Raven, J.A., Tamsitt, V., Boyd, P.W., 2022. Forensic carbon accounting: assessing the role of seaweeds for carbon sequestration. *J. Phycol.* 58, 347–353.
- Ibrahim, N.H., Iqbal, A., Mohammad-Noor, N., Razali, R.M., Sreekantan, S., Yanto, D.H. Y., Mahadi, A.H., Wilson, L.D., 2022. Photocatalytic remediation of harmful *Alexandrium minutum* bloom using hybrid chitosan-modified TiO₂ films in seawater: a lab-based study. *Catalysts* 12 (7), 707.
- Ichikawa, S., Wakao, Y., Fukuyo, Y., 1992. Extermination efficacy of hydrogen peroxide against cysts of red tide and toxic dinoflagellates, and its adaptability to ballast water of cargo ships. *Nippon Suisan Gakkaishi* 58 (12), 2229–2233 (in Japanese, with English summary).
- Imai, I., Kimura, S., 2008. Resistance of the fish-killing dinoflagellate *Cochlodinium polykrikoides* against algicidal bacteria isolated from the coastal Sea of Japan. *Harmful Algae* 7 (3), 360–367.
- Imai, I., Yamaguchi, M., Hori, Y., 2006a. Eutrophication and occurrences of harmful algal blooms in the Seto Inland Sea, Japan. *Plankt. Benthos Res.* 1 (2), 71–84. <https://doi.org/10.3800/pbr.1.71>.
- Imai, I., Fujimaru, D., Nishigaki, T., Kurosaki, M., Sugita, H., 2006b. Algicidal bacteria isolated from the surface of seaweeds from the coast of Osaka Bay in the Seto Inland Sea, Japan. *Afr. J. Mar. Sci.* 28 (2), 319–323.
- Imai, I., Inaba, N., Yamamoto, K., 2021. Harmful algal blooms and environmentally friendly control strategies in Japan. *Fish. Sci.* 87, 437–464.
- Inaba, N., 2024. Toward the establishment of Nature-based Solution (NbS) using seagrasses and macroalgae to control harmful algal bloom. In: Kurniawan, T.A., Anouzla, A. (Eds.), *Algae as a Natural Solution For Challenges in Water-Food-Energy Nexus*. Springer Singapore Springer Nature, Singapore, pp. 91–106.
- Inaba, N., Trainer, V.L., Onishi, Y., Ishii, K.I., Wyllie-Echeverria, S., Imai, I., 2017. Algicidal and growth-inhibiting bacteria associated with seagrass and macroalgae beds in Puget Sound, WA, USA. *Harmful Algae* 62, 136–147.
- Inaba, N., Nagai, S., Sakami, T., Watanabe, T., Araki, K., Kawasaki, S., Imai, I., 2018. Temporal variability of algicidal and growth-inhibiting bacteria at an eelgrass bed in the Ariake Sea, Japan. *Bioremediat. J.* 22 (3–4), 112–125.
- Inaba, N., Trainer, V.L., Nagai, S., Kojima, S., Sakami, T., Takagi, S., Imai, I., 2019. Dynamics of seagrass bed microbial communities in artificial *Chattonella* blooms: a laboratory microcosm study. *Harmful Algae* 84, 139–150.
- Inaba, N., Kodama, I., Nagai, S., Shiraiishi, T., Matsuno, K., Yamaguchi, A., Imai, I., 2020. Distribution of harmful algal growth-limiting bacteria on artificially introduced *Ulva* and natural macroalgal beds. *Appl. Sci.* 10 (16), 5658.
- ITRC (Interstate Technology & Regulatory Council), 2020. Strategies For Preventing and Managing Harmful Cyanobacterial Blooms (HCB-1). Interstate Technology & Regulatory Council, HCB Team, Washington, D.C.. www.itrcweb.org/management-and-control-strategies-for-hcbs/.
- Jeong, H.J., Kim, H.R., Kim, K.I., Kim, K.Y., Park, K.H., Kim, S.T., Yoo, Y.D., Song, J.Y., Kim, J.S., Seong, K.A., Yih, W.H., 2002. NaOCl produced by electrolysis of natural seawater as a potential method to control marine red-tide dinoflagellates. *Phycologia* 41 (6), 643–656.
- Jeong, H.J., Kim, J.S., Yoo, Y.D., Kim, S.T., Kim, T.H., Park, M.G., Lee, C.H., Seong, K.A., Rang, N.S., Shim, J.H., 2003. Feeding by the heterotrophic dinoflagellate *Oxyrrhis marina* on the red-tide raphidophyte *Heterosigma akashiwo*: a potential biological method to control red tides using mass-cultured grazers. *J. Eukaryot. Microbiol.* 50 (4), 274–282.
- Jeong, H.J., Kim, J.S., Du Yoo, Y., Kim, S.T., Song, J.Y., Kim, T.H., Seong, K.A., Kang, N. S., Kim, M.S., Kim, J.H., Kim, S., 2008. Control of the harmful alga *Cochlodinium polykrikoides* by the naked ciliate *Strombidinopsis jeokjo* in mesocosm enclosures. *Harmful Algae* 7 (3), 368–377.
- Jiang, W., Yu, Z., Cao, X., Jiang, K., Yuan, Y., Anderson, D.M., Song, X., 2021. Effects of soluble organics on the settling rate of modified clay and development of improved clay formulations for harmful algal bloom control. *Environ. Pollut.* 289, 117964.
- Jiang, K., Yu, Z., Cao, X., Song, X., Zang, X., Chi, L., Jiang, W., 2023. An optimization strategy for highly efficient flocculation and capture of algal cells: controlling dosing patterns of modified clay. *Environ. Technol. Innov.* 32, 103359.
- Jiang, K.Q., Song, X.X., Chi, L.B., Cao, X.H., Yu, Z.M., 2025. A novel comb-like polymer polyaluminum-chitosan modified clay (AlnCTS/clay) for efficiently controlling miniaturized red tide organisms. *J. Environ. Chem. Eng.* 13 (3), 116400.
- Jin, D., Moore, S., Holland, D., Anderson, L., Lim, W.A., Kim, D., Jardine, S., Martino, S., Gianella, F., Davidson, K., 2020. 2. Evaluating the economic impacts of harmful algal blooms: issues, methods, and examples. *PICES Sci. Rep.* (59), 5–41.
- Johnson, G., 2023. Investigating algicidal amines as agents for chemical control of toxic dinoflagellate *Karenia brevis*. Master's Thesis. University of Delaware.
- Jung, K.S., 2000. Redtide-Phytoplankton Disinfection using Ultraviolet Radiation. M.S. Thesis. Chosun University, Gwangju.
- Kang, S.J., Lim, S.I., Lee, B.H., 2001. The removal of red tide organisms by using microscreen and ozone. *J. Korea Technol. Soc. Water Waste Water Treat* 9, 11–17.
- Kasprzak, P., Gonsiorczyk, T., Grossart, H.P., Hupfer, M., Koschel, R., Petzoldt, T., Wauer, G., 2018. Restoration of a eutrophic hard-water lake by applying an optimised dosage of poly-aluminium chloride (PAC). *Limnologia* 70, 33–48.
- Kaya, K., Liu, Y.-D., Shen, Y.-W., Xiao, B.-D., Sano, T., 2005. Selective control of toxic *Microcystis* water blooms using lysine and malonic acid: an enclosure experiment. *Environ. Toxicol.* 20 (2), 170–178. <https://doi.org/10.1002/tox.20092>.
- Kibuye, F.A., Zamyadi, A., Wert, E.C., 2021a. A critical review on operation and performance of source water control strategies for cyanobacterial blooms: part I-chemical control methods. *Harmful Algae* 109, 102099. <https://doi.org/10.1016/j.hal.2021.102099>.
- Kibuye, F.A., Zamyadi, A., Wert, E.C., 2021b. A critical review on operation and performance of source water control strategies for cyanobacterial blooms: part II-mechanical and biological control methods. *Harmful Algae* 109, 102119. <https://doi.org/10.1016/j.hal.2021.102119>.
- Kidwell, D.M., 2015. Mitigation of harmful algal blooms: the way forward. In: North Pacific Marine Science Organization, 23. PICES Press. <https://dev.pices.int/publications/pices-press/volume23/2015-v23-n2-pp-22-24-HABs-mitigation.pdf>.
- Kidwell, D.M., Callender, R., Conrad, C.F., Jasinski, P.H., Baker, S.S.L.M., Dortch, Q., 2015. Programmatic Environmental Assessment For the Prevention, Control, and Mitigation of Harmful Algal Blooms Program. National Ocean Service. <https://repository.library.noaa.gov/view/noaa/12618>.
- Kim, M.J., Jeong, S.Y., Lee, S.J., 2008. Isolation, identification, and algicidal activity of marine bacteria against *Cochlodinium polykrikoides*. *J. Appl. Phycol.* 20, 1069–1078.
- Kim, J.K., Kraemer, G.P., Yarish, C., 2015. Use of sugar kelp aquaculture in Long Island Sound and the Bronx River Estuary for nutrient extraction. *Mar. Ecol. Prog. Ser.* 531, 155–166. <https://doi.org/10.3354/meps11331>.
- Kim, J.K., Stekoll, M., Yarish, C., 2019. Opportunities, challenges and future directions of open-water seaweed aquaculture in the United States. *Phycologia* 58 (5), 446–461. <https://doi.org/10.1080/00318884.2019.1625611>.
- Kim, S.J., 2000. Removal of red tide organisms: flocculation of red tide organisms by using loess. *J. Kor. Fish. Soc.* 33, 455–462.
- Kinley-Baird, C., Calomeni, A., Berthold, D.E., Lefler, F.W., Barbosa, M., Rodgers, J.H., Laughinghouse IV, H.D., 2021. Laboratory-scale evaluation of algacide effectiveness for control of microcystin-producing cyanobacteria from Lake Okeechobee, Florida (USA). *Ecotoxicol. Environ. Saf.* 207, 111233.
- Klemencić, P., Krivograd Klemencić, A., 2021. Effect of ultrasonic algae control devices on non-target organisms: a review. *Acta Biol. Sloven.* 64 (1), 5–17.
- Landsberg, J.H., Flewelling, L.J., Naar, J., 2009. *Karenia brevis* red tides, brevetoxins in the food web, and impacts on natural resources: decadal advancements. *Harmful Algae* 8 (4), 598–607.
- Lapointe, B.E., Brewton, R.A., Herren, L.W., Wang, M., Hu, C., McGillicuddy Jr., D.J., Lindell, S., Hernandez, F.J., Morton, P.L., 2021. Nutrient content and stoichiometry of pelagic *Sargassum* reflects increasing nitrogen availability in the Atlantic Basin. *Nature* 21 (12), 306. <https://doi.org/10.1038/s41467-021-23135-7>.
- Lapointe, M., Barbeau, B., 2020. Understanding the roles and characterizing the intrinsic properties of synthetic vs. natural polymers to improve clarification through interparticle bridging: a review. *Sep. Purif. Technol.* 231, 115893.
- Laurens, L.M.L., Lane, M., Nelson, R.S., 2020. Sustainable seaweed biotechnology solutions for carbon capture, composition, and deconstruction. *Trend Biotechnol.* 38, 1232–1244.
- Lawrence, J.E., Chan, A.M., Suttle, C.A., 2001. A novel virus (HaNIV) causes lysis of the toxic bloom-forming alga *Heterosigma akashiwo* (Raphidophyceae). *J. Phycol.* 37 (2), 216–222.
- Lefler, F.W., Berthold, D.E., Barbosa, M., Laughinghouse IV, H.D., 2022. The effects of algacides and herbicides on a nuisance *Microcystis wesenbergii* dominated bloom. *Water* 14 (11), 1739. <https://doi.org/10.3390/w14111739>.

- Lefler, F.W., Barbosa, M., Berthold, D.E., Roten, R., Bishop, W., Laughinghouse IV, H.D., 2024. Microbial community response to granular peroxide-based algicide treatment of a cyanobacterial harmful algal bloom in lake Okeechobee, Florida (USA). *Toxins* 16, 206. <https://doi.org/10.3390/toxins16050206>.
- Lepelletier, F., Karpov, S.A., Alacid, E., Le Panse, S., Bigeard, E., Garcés, E., Jeanthon, C., Guillou, L., 2014. *Dinomyces arenysensis* gen. et sp. nov. (Rhizophytiales, Dinomycetaceae fam. nov.), a chytrid infecting marine dinoflagellates. *Protist* 165 (2), 230–244.
- Lewis, M.A., Dantin, D.D., Walker, C.C., Kurtz, J.C., Greene, R.M., 2003. Toxicity of clay flocculation of the toxic dinoflagellate, *Karenia brevis*, to estuarine invertebrates and fish. *Harmful Algae* 2 (4), 235–246.
- Li, Z., Lin, S., a, X., Tan, J., Pan, J., Yang, H., 2014a. A freshwater bacterial strain, *Shewanella* sp. Lzh-2, isolated from Lake Taihu and its two algicidal active substances, hexahydropyrrrole [1, 2-a] pyrazine-1, 4-dione and 2, 3-indolinedione. *Appl. Microbiol. Biotechnol.* 98, 4737–4748.
- Li, P., Song, Y., Yu, S., 2014b. Removal of *Microcystis aeruginosa* using hydrodynamic cavitation: performance and mechanisms. *Water Res.* 62, 241–248.
- Li, D., Kang, X., Chu, L., Wang, Y., Song, X., Zhao, X., Cao, X., 2021. Algicidal mechanism of *Raoultella ornithinolytica* against *Microcystis aeruginosa*: antioxidant response, photosynthetic system damage and microcystin degradation. *Environ. Pollut.* 287, 117644.
- Li, H., Yu, Z., Cao, X., Song, X., 2023. Chitosan modification and its synergism with clay to mitigate harmful algal blooms. *Environ. Technol. Innov.* 29, 103028.
- Lim, C.C., Yoon, J., Reynolds, K., Gerald, L.B., Ault, A.P., Heo, S., Bell, M.L., 2023. Harmful algal bloom aerosols and human health. *Environ. Bio Med.* 93.
- Lin, W., Li, D., Sun, Z., Tong, Y., Yan, X., Wang, C., Zhang, X., Pei, G., 2020. A novel freshwater cyanophage vB_MeLS-Me-ZS1 infecting bloom-forming cyanobacterium *Microcystis elabens*. *Mol. Biol. Rep.* 47, 7979–7989.
- Liu, M., Huang, J., Huang, M., 2023. The environmental toxicity of halloysite clay and its composites. *Clay Composites: Environmental Applications*, pp. 559–574.
- Liu, Y., 2016. Mechanisms and Methods to Increase the Algae Removal Efficiency of Modified Clays. Ph.D. thesis. Institute of Oceanology, Chinese Academy of Sciences.
- Liu, Y., Cao, X., Yu, Z., Song, X., Qiu, L., 2016a. Controlling harmful algae blooms using aluminum-modified clay. *Mar. Pollut. Bull.* 103 (1–2), 211–219.
- Liu, Y., Cao, X., Yu, Z., Song, X., Qiu, L., 2016b. Flocculation of harmful algal cells using modified clay: effects of the properties of the clay suspension. *J. Appl. Phycol.* 28, 1623–1633.
- Liu, Z., Yu, Z., Cao, X., Jiang, W., Yuan, Y., Song, X., 2022. An environmentally friendly material for red tide algae removal: performance and mechanism. *Front. Mar. Sci.* 9, 1013471.
- Long, M., Peltekis, A., González-Fernández, C., Hegaret, H., Bailleul, B., 2021. Allelochemicals of *Alexandrium minutum*: kinetics of membrane disruption and photosynthesis inhibition in a co-occurring diatom. *Harmful Algae* 103, 101997.
- Lovås, S.M., Torum, A., 2001. Effect of the kelp *Laminaria hyperborea* upon sand dune erosion and water particle velocities. *Coast. Engin.* 44, 37–63.
- Lu, G., Song, X., Yu, Z., Cao, X., Yuan, Y., 2015. Effects of modified clay flocculation on major nutrients and diatom aggregation during *Skeletonema costatum* blooms in the laboratory. *Chin. J. Oceanol. Limnol.* 33 (4), 1007–1019.
- Lürling, M., Tolman, Y., 2014a. Beating the blues: is there any music in fighting cyanobacteria with ultrasound? *Water Res.* 66, 361–373.
- Lürling, M., Tolman, Y., 2014b. Effects of commercially available ultrasound on the zooplankton grazer daphnia and consequent water greening in laboratory experiments. *Water Res.* 66 (11), 3247–3263.
- Lürling, M., Meng, D.B., Faassen, E.J., 2014. Effects of hydrogen peroxide and ultrasound on biomass reduction and toxin release in the cyanobacterium, *Microcystis aeruginosa*. *Toxins* 6 (12), 3260–3280.
- Mao, L., Huang, J., Mao, H., Xu, M., Zhang, W., 2022. Self-floating capsule of algicidal bacteria *Bacillus* sp. HL and its performance in the dissolution of *Microcystis aeruginosa*. *J. Environ. Manage* 320, 115837.
- Mardones, J.I., Flores-Leñero, A., Pinto-Torres, M., Paredes-Mella, J., Fuentes-Alburquenque, S., 2023. Mitigation of marine dinoflagellates using hydrogen peroxide (H₂O₂) increases toxicity towards epithelial gill cells. *Microorganisms* 11, 83.
- Marinho, G.S., Holdt, S.L., Birkeland, M.J., Angelidaki, I., 2015. Commercial cultivation and bioremediation potential of sugar kelp, *Saccharina latissima*, in Danish waters. *J. Appl. Phycol.* 27 (5), 1963–1973. <https://doi.org/10.1007/s10811-014-0519-8>.
- Marvin, K.T., Lansford, L.M., Wheeler, R.S., 1961. Effects of copper ore on the ecology of a lagoon. U. S. Fish Wildlife Serv. Fish. Bull. 61, 153–160.
- Marvin, K.T., Proctor, R.R., 1964a. Preliminary results of the systematic screening of 4306 compounds as red tide toxicants. U.S. Fish Wildlife Serv. Data Rep. 2, 85.
- Marvin, K.T., Proctor, R.R., 1964b. Laboratory evaluation of red-tide control agents. *Fish. Bull.* 66 (1), 163–164.
- Matthijs, H.C.P., Visser, P.M., Reeze, B., Meeuse, J., Slot, P.C., Wijn, G., Talens, R., Huisman, J., 2012. Selective suppression of harmful cyanobacteria in an entire lake with hydrogen peroxide. *Water Res.* 46, 1460–1472.
- Mayali, X., Azam, F., 2004. Algicidal bacteria in the sea and their impact on algal blooms. *J. Eukaryot. Microbiol.* 51, 139–144.
- McClintock, T.A., Handa, A., Fredheim, A., Lien, E., Reitan, K.I., 2010. Controlled artificial upwelling in a fjord to stimulate non-toxic algae. *Aquac. Eng.* 42 (3), 140–147.
- McKindles, K.M., McKay, R.M.L., Bullerjahn, G.S., Frenken, T., 2023. Interactions between chytrids cause variable infection strategies on harmful algal bloom forming species. *Harmful Algae* 122, 102381.
- Mehrotra, T., Dev, S., Banerjee, A., Chatterjee, A., Singh, R., Aggarwal, S., 2021. Use of immobilized bacteria for environmental bioremediation: a review. *J. Environ. Chem. Eng.* 9 (5), 105920.
- Mei, Z., Zhang, Z., Zhao, C., Xu, M., Li, M., 2010. Dynamics of phytoplankton and water quality with control of cyanobacterial bloom in Lake Xuanwu, Nanjing. *J. Lake Sci.* 22 (1), 44–48.
- Meng, X.J., Song, X.X., Zhang, Y., Song, W.J., Zhang, P.P., Shen, H.H., Yu, Z.M., 2022. Effect of modified clay on paralytic shellfish poisoning in *Mizuhopecten yessoensis*. *J. Oceanol. Limnol.* 53, 616–624.
- Meyer, N., Bigalke, A., Kaulfuß, A., Pohnert, G., 2017. Strategies and ecological roles of algicidal bacteria. *FEMS Microbiol. Rev.* 41 (6), 880–899.
- Mittler, R., 2002. Oxidative stress, antioxidants and stress tolerance. *Trends. Plant Sci.* 7 (9), 405–410.
- Mizumoto, H., Tomaru, Y., Takao, Y., Shirai, Y., Nagasaki, K., 2007. Intraspecies host specificity of a single-stranded RNA virus infecting a marine photosynthetic protist is determined at the early steps of infection. *J. Virol.* 81 (3), 1372–1378.
- Na, G.H., Choi, W.J., Chun, Y.Y., 1996. A study on red tide control with loess suspension. *J. Aquacult.* 9 (3), 239–245.
- Nagasaki, K., Yamaguchi, M., 1997. Isolation of a virus infectious to the harmful bloom causing microalga *Heterosigma akashiwo* (Raphidophyceae). *Aqu. Microb. Ecol.* 13 (2), 135–140.
- Nakayama, N., Hamaguchi, M., 2016. Multiplex reverse transcription quantitative PCR detection of a single-stranded RNA virus HcRNAV infecting the bloom-forming dinoflagellate *Heterocapsa circularisquama*. *Limnol. Oceanogr.* 14 (6), 370–380.
- Nakayama, N., Hamaguchi, M., 2022. The importance of the genetic diversity of the HcRNAV ssRNA virus in the viral-based bloom control of the dinoflagellate *Heterocapsa circularisquama*. *Aquaculture* 546, 737318.
- Nakayama, N., Fujimoto, A., Kawami, H., Tomaru, Y., Hata, N., Nagasaki, K., 2013. High interaction variability of the bivalve-killing dinoflagellate *Heterocapsa circularisquama* strains and their single-stranded RNA virus HcRNAV isolates. *Microb. Environ.* 28 (1), 112–119.
- Nakayama, N., Hamaguchi, M., Yamaguchi, H., Masuda, K., Fujiwara, M., 2020. Evaluation of a virus-based control method to protect cultured oysters from the harmful dinoflagellate *Heterocapsa circularisquama*. *Aquaculture* 529, 735625.
- National Institute of Fisheries Science (NIFS), 2013. Monitoring, Management and Mitigation of Red Tide. Annual Report of NIFS on Red Tide of Korea, Busan, Korea (written in Korean).
- Neori, A., Chopin, T., Troell, M.F., Buschmann, A.H., Kraemer, G.P., Halling, C., Shpigler, M., Yarish, C., 2004. Integrated aquaculture: rationale, evolution and state of the art emphasizing seaweed biofiltration in modern mariculture. *Aquaculture* 231 (1–4), 361–391. <https://doi.org/10.1016/j.aquaculture.2003.11.015>.
- Norderhaug, K.M., Christie, H., Fosså, J.H., Fredriksen, S., 2005. Fish-macrofauna interactions in a kelp (*Laminaria hyperborea*) forest. *J. Mar. Biol. Assoc. UK* 85, 1279.
- Notification no. 2024-760 of Ministry of Ocean and Fisheries, 2024. Guidelines For Red Tide Monitoring, Forecasting and Mitigation, pp. 1–17.
- Novoveská, L., Robertson, A., 2019. Brevetoxin-producing spherical cells present in *Karenia brevis* bloom: evidence of morphological plasticity? *JMSE* 7 (2), 24. <https://doi.org/10.3390/jmse7020024>.
- Ohara, S., Yano, R., Furuya, K., Sato, T., Ikeda, S., Koike, K., 2023. The effects of sea-bottom plowing on phytoplankton assemblages: a case study of northern Hiroshima Bay, the Seto Inland Sea of Japan. *Front. Mar. Sci.* 10, 1222810.
- Onishi, Y., Tuji, A., Yamaguchi, A., Imai, I., 2020. Distribution of growth-inhibiting bacteria against the toxic dinoflagellate *Alexandrium catenella* (Group I) in Akkeshi-Ko Estuary and Akkeshi Bay, Hokkaido, Japan. *Appl. Sci.* 11 (1), 172.
- Owen, D.P., 2015. Acclimation of red tide dinoflagellate *Karenia brevis* to higher temperatures results in abnormal morphology and changes in growth rates. Retrieved from http://purl.flvc.org/fsu/fd/FSU_migr_uhm-0515-P.
- Paerl, H.W., Otten, T.G., Kudela, R.M., 2018. Mitigating the expansion of harmful algal blooms across the freshwater-to-marine continuum. *Environ. Sci. Technol.* 52, 5519–5529. <https://doi.org/10.1021/acs.est.7b05950>.
- Pal, M., Yesankar, P.J., Dwivedi, A., Qureshi, A., 2020. Biotic control of harmful algal blooms (HABs): a brief review. *J. Environ. Manage* 268, 110687.
- Park, M.G., Yih, W., Coats, D.W., 2004. Parasites and phytoplankton, with special emphasis on dinoflagellate infections 1. *J. Eukaryot. Microbiol.* 51 (2), 145–155.
- Park, T.G., Lim, W.A., Park, Y.T., Lee, C.K., Jeong, H.J., 2013. Economic impact, management and mitigation of red tides in Korea. *Harmful Algae* 30, S131–S143.
- Park, J., Church, J., Son, Y., Kim, K.-T., Lee, W.H., 2017. Recent advances in ultrasonic treatment: challenges and field applications for controlling harmful algal blooms (HABs). *Ultrason. Sonochem.* 38, 326–334.
- Park, M., Shin, S.K., Do, Y.H., Yarish, C., Kim, J.K., 2018. Application of open water integrated multi-trophic aquaculture to intensive monoculture: a review of the current status and challenges in Korea. *Aquaculture* 497, 174–183.
- Pierce, R.H., Henry, M.S., 2008. Harmful algal toxins of the Florida red tide (*Karenia brevis*): natural chemical stressors in South Florida coastal ecosystems. *Ecotoxicology* 17, 623–631.
- Pierce, R.H., Henry, M.S., Blum, P.C., Osborn, S.E., Cheng, Y.S., Zhou, Y., Irvin, C.M., Bourdelaes, A.J., Naar, J., Baden, D.G., 2011. Compositional changes in neurotoxins and their oxidative derivatives from the dinoflagellate, *Karenia brevis*, in seawater and marine aerosol. *J. Plankton. Res.* 33 (2), 343–348.
- Pokrzywinski, K.L., Place, A.R., Warner, M.E., Coyne, K.J., 2012. Investigation of the algicidal exudate produced by *Shewanella* sp. IRI-160 and its effect on dinoflagellates. *Harmful Algae* 19, 23–29.
- Pokrzywinski, K.L., Tilney, C.L., Modla, S., Caplan, J.L., Ross, J., Warner, M.E., Coyne, K.J., 2017a. Effects of the bacterial algicide IRI-160AA on cellular morphology of harmful dinoflagellates. *Harmful Algae* 62, 127–135.
- Pokrzywinski, K.L., Tilney, C.L., Warner, M.E., Coyne, K.J., 2017b. Cell cycle arrest and biochemical changes accompanying cell death in harmful dinoflagellates following exposure to bacterial algicide IRI-160AA. *Sci. Rep.* 7 (1), 45102.

- Pokrzywinski, K.L., Bishop, W.M., Grasso, C.R., Fernando, B., Sperry, B.P., Berthold, D.E., Laughinghouse IV, H.D., VanGoethm, E., Volk, K., Heilman, M., Getsinger, K., 2022. Evaluation of a peroxide-based algicide product for cyanobacteria control: a mesocosm trial in Lake Okeechobee, FL, USA. *Water* 14 (2), 169.
- Purcell, D., Parsons, S.A., Jefferson, B., Holden, S., Campbell, A., Wallen, A., Chipps, M., Holden, B., Ellingham, A., 2013. Experiences of algal bloom control using green solutions barley straw and ultrasound, an industry perspective. *Water Environ. J.* 27, 148–156.
- Qiu, L., Yu, Z., Cao, X., Song, X., Liu, Y., Zhong, Y., 2017. Removal efficiencies for *Phaeocystis globosa* and *Prorocentrum donghaiense* with modified clay. *Oceanol. Limnol. Sin.* 48 (05), 982–989.
- Qiu, L., Yu, Z., Cao, X., Ji, H., Song, X., 2020. The mechanism of a new type of modified clay controlling *Phaeocystis globosa* growth. *J. Oceanol. Limnol.* 38 (4), 1270–1282.
- Randhawa, V., Thakkar, M., Wei, L., 2012. Applicability of hydrogen peroxide in brown tide control: culture and microcosm studies. *PLoS ONE* 7 (10), e47844.
- Regulation, E.U., 2012. No 528/2012 of the European Parliament and of the Council of 22 May 2012 concerning the making available on the market and use of biocidal products. *Off. J. Eur. Union L* 167, 1–123.
- Rong, C., Zhou, K., Li, S., Xiao, K., Xu, Y., Zhang, R., Yang, Y., Zhang, Y., 2022. Isolation and characterization of a novel cyanophage encoding multiple auxiliary metabolic genes. *Viruses* 14 (5), 887.
- Rothäusler, E., Gomez, I., Hinojosa, I.A., Karsten, U., Tala, F., Thiel, M., 2011. Psychological performance of floating giant kelp *Macrocystis pyrifera* (Phaeophyceae) latitudinal variability in the effects of temperature and grazing. *J. Phycol.* 47, 269–281.
- Roth, P.B., Twiner, M.J., Mikulski, C.M., Barnhorst, A.B., Doucette, G.J., 2008. Comparative analysis of two algalicidal bacteria active against the red tide dinoflagellate *Karenia brevis*. *Harmful Algae* 7 (5), 682–691.
- Rounsefell, G.A., Evans, J.E., 1958. Large-Scale Experimental Tests of Copper Sulfate as a Control for the Florida Red Tides. Department of the Interior, Fish and Wildlife Service, U.S. Special Scientific Report, Fisheries No. 270.
- Ruangrit, K., Phinyo, K., Chailungka, S., Duangian, K., Naree, A., Thasana, J., Kamopas, W., Seangpong, S., Pekkoh, J., Noirungsee, N., 2025. Enhanced nitrate removal in aquatic systems using biochar immobilized with algicidal *Bacillus* sp. AK3 and denitrifying *Alcaligenes* sp. M3: a synergistic approach. *PLoS ONE* 20 (3), e0318416.
- Seger, A., Park, T.G., Hallegraef, G.M., 2017. Assessment of the efficacy of clay flocculation in Korean fish farm waters: *Cochlodinium* cell removal and mitigation of ichthyotoxicity. *Harmful Algae* 61, 46–55.
- Seger, A., Hallegraef, G., 2022. Application of clay minerals to remove extracellular ichthyotoxins produced by the dinoflagellates *Karlodinium veneficum* and *Karenia mikimotoi*. *Harmful Algae* 111, 102151.
- Sellner, K.G., Rensel, J.E., 2018. Prevention, control, and mitigation of harmful algal bloom impacts on fish, shellfish, and human consumers. In: Shumway, S.E., Burkholder, J.M., Morton, S.L. (Eds.), *Harmful Algal Blooms: A Compendium Desk Reference*, pp. 435–492.
- Sengco, M.R., 2009. Prevention and control of *Karenia brevis* blooms. *Harmful Algae* 8 (4), 623–628.
- Sengco, M.R., Anderson, D.M., 2004. Controlling harmful algal blooms through clay flocculation. *J. Eukaryot. Microbiol.* 51 (2), 169–172.
- Sengco, M.R., Li, A., Tugend, K., Kulis, D., Anderson, D.M., 2001. Removal of red-and brown-tide cells using clay flocculation. I. Laboratory culture experiments with *Gymnodinium breve* and *Aureococcus anophagefferens*. *Mar. Ecol. Prog. Ser.* 210, 41–53.
- Seo, K.S., Lee, C.K., Park, Y.T., Lee, Y., 2008. Effect of yellow clay on respiration and phytoplankton uptake of bivalves. *Fish. Sci.* 74, 120–127.
- Seymour, J.R., Amin, S.A., Raina, J.B., Stocker, R., 2017. Zooming in on the phycosphere: the ecological interface for phytoplankton–bacteria relationships. *Nat. Microbiol.* 2 (7), 1–12.
- Shetty, K.G., Huntzicker, J.V., Rein, K.S., Jayachandran, K., 2010. Biodegradation of polyether algal toxins—Isolation of potential marine bacteria. *J. Environ. Sci. Health Part A* 45 (14), 1850–1857. <https://doi.org/10.1080/10934529.2010.520510>.
- Shi, X., Zou, Y., Zheng, W., Liu, L., Xie, Y., Ma, R., Chen, J., 2022. A novel algicidal bacterium and its effects against the toxic dinoflagellate *Karenia mikimotoi* (Dinophyceae). *Microbiol. Spectr.* 10 (3), e00429–22.
- Shi, J., Wang, W., Wang, F., Lei, S., Shao, S., Wang, C., Li, G., An, T., 2023. Efficient inactivation of harmful algae *K. mikimotoi* by a novel algicidal bacterium via a rare direct contact pathway: performances and mechanisms. *Sci. Total Environ.* 892, 164401.
- Shirot, A., 1989. Red tide problem and countermeasures. II. *Int. J. Aqua. Fish. Technol.* 1, 195–223.
- Shumway, S.E., Frank, D.M., Ewart, L.M., Ward, E.J., 2003. Effect of yellow loess on clearance rate in seven species of benthic, filter-feeding invertebrates. *Aquac. Res.* 34 (15), 1391–1402.
- Siclar, L.R., 2019. Evaluation of the Acute and Chronic Toxicity of the Modified Clay Product (In Spanish), Scientific and Technical Report by University of Valparaíso, Chile, p. 41.
- Simons, V.E., Coyne, K.J., Warner, M.E., Dolan, M.M., Cohen, J.H., 2021. Effects of a bacteria-produced algicide on non-target marine invertebrate species. *Sci. Rep.* 11 (1), 583.
- Simons, V.E., Targgett, T.E., Gaffney, P.M., Coyne, K.J., 2025. Bacteria-produced algicide for field control of toxic dinoflagellates does not cause a cortisol stress response in two estuarine fish species. *Mar. Biotechnol.* 27, 29. <https://doi.org/10.1007/s10126-024-10383-z>.
- Smale, D.A., Burrows, M.T., Moore, P., O'Connor, N., Hawkins, S.J., 2013. Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective. *Ecol. Evol.* 3, 4016–4040, 38.
- Song, X., Yu, Z., Gao, Y., 2003. Removal of different species of red tide organisms with an effective clay-complex system. *J. Appl. Ecol.* 14 (7), 1165–1168.
- Song, X., Zhang, Y., Yu, Z., 2021. An eco-environmental assessment of harmful algal bloom mitigation using modified clay. *Harmful Algae* 107, 102067.
- Song, W., Song, X., Shen, H., Ding, Y., Cheng, R., Yu, Z., 2023. Degradation of paralytic shellfish toxins during flocculation of *Alexandrium pacificum* by an oxidized modified clay: a laboratory experiment. *Ecotoxicol. Environ. Saf.* 253, 114667.
- Suddleson, M., Hoagland, P., 2021. In: *Proceedings of the Workshop on the Socio-Economic Effects of Harmful Algal Blooms in the United States*. U.S. National Office for Harmful Algal Blooms, Woods Hole Oceanographic Institution. <https://repository.library.noaa.gov/view/noaa/33455>.
- Sun, X.X., Choi, J.K., 2004. Recovery and fate of three species of marine dinoflagellates after yellow clay flocculation. *Hydrobiologia* 519, 153–165.
- Suslick, K.S., Flannigan, D.J., 2008. Inside a collapsing bubble: sonoluminescence and the conditions during cavitation. *Ann. Rev. Phys. Chem.* 59, 659–683.
- Sylvers, L.H., Gobler, C.J., 2021. Mitigation of harmful algal blooms caused by *Alexandrium catenella* and reduction in saxitoxin accumulation in bivalves using cultivable seaweeds. *Harmful Algae* 105, 102056.
- Sylvers, L.H., Gobler, C.J., 2023. Cultivable seaweeds eliminate the lethal effects of the harmful alga, *Margalefidinium polykrikoides*, on early life stage fish. *Aquaculture* 574, 739676.
- Sylvers, L.H., Gobler, C.J., 2025. Inhibition of cosmopolitan toxic diatom, *Pseudo-nitzschia*, by seaweeds. *Limnol. Oceanogr.* 70, 2591–2602. <https://doi.org/10.1002/lno.70127>.
- Tang, Y., Gobler, C.J., 2011. The green macroalgae, *Ulva lactuca*, inhibits the growth of seven common harmful algal bloom species via allelopathy. *Harmful Algae* 10 (5), 480–488.
- Tang, Y., Kang, Y., Berry, D.L., Gobler, C.J., 2014. The ability of the red macroalgae, *Porphyra purpurea* (Rhodophyceae) to inhibit the proliferation of seven common harmful microalgae. *J. Appl. Phycol.* 27 (1), 531–544.
- Teagle, H., Hawkins, S.J., Moore, P.J., Smale, D.A., 2017. The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *J. Exp. Mar. Biol. Ecol.* 492, 81–98.
- Ternon, E., Wang, Y., Coyne, K.J., 2018. Small polar molecules: a challenge in marine chemical ecology. *Molecules* 24 (1), 135.
- Tilney, C.L., Pokrzywinski, K.L., Coyne, K.J., Warner, M.E., 2014a. Effects of a bacterial algicide, IRI-160AA, on dinoflagellates and the microbial community in microcosm experiments. *Harmful Algae* 39, 210–222.
- Tilney, C.L., Pokrzywinski, K.L., Coyne, K.J., Warner, M.E., 2014b. Growth, death, and photobiology of dinoflagellates (Dinophyceae) under bacterial-algicide control. *J. Appl. Phycol.* 26, 2117–2127.
- Trainer, V.L. (Ed.), 2020. *GlobalHAB: Evaluating, Reducing and Mitigating the Cost of Harmful Algal Blooms: A Compendium of Case Studies*. North Pacific Marine Science Organization, Victoria, BC, Canada, p. 107. <https://doi.org/10.25607/OBP-1709> (PICES Scientific Report No. 59).
- Tomaru, Y., Hata, N., Masuda, T., Tsuji, M., Igata, K., Masuda, Y., Yamatogi, T., Sakaguchi, M., Nagasaki, K., 2007. Ecological dynamics of the bivalve-killing dinoflagellate *Heterocapsa circularisquama* and its infectious viruses in different locations of western Japan. *Environ. Microbiol.* 9 (6), 1376–1383.
- Tullos, D., Skinner, M.M., Paerl, H.W., Preece, E.P., 2025. A practitioner-informed decision tree for selecting harmful cyanobacteria bloom control and mitigation techniques. *Wiley Interdiscip. Rev.* 12 (2), e70005. <https://doi.org/10.1002/wat2.70005>.
- Vanderklift, M.A., Wernberg, T., 2008. Detached kelps from distant sources are a food subsidy for sea urchins. *Oecologia* 157, 327–335.
- Velo-Suarez, L., Brosnahan, M.L., Anderson, D.M., McGillicuddy Jr, D.J., 2013. A quantitative assessment of the role of the parasite *Amoebophrya* in the termination of *Alexandrium fundyense* blooms within a small coastal embayment. *PLoS ONE* 8 (12), e81150.
- Wahl, M., Schneider Covachá, S., Saderne, V., Hiebenthal, C., Müller, J.D., Pansch, C., Sawall, Y., 2018. Macroalgae may mitigate ocean acidification effects on mussel calcification by increasing pH and its fluctuations. *Limnol. Oceanogr.* 63 (1), 3–21. <https://doi.org/10.1002/lno.10608>.
- Wang, Y., 2021. Bacterial algicides: application strategies and cellular response of target organisms. University of Delaware, p. 318. Ph.D. Thesis.
- Wang, Y., Coyne, K.J., 2020. Immobilization of algicidal bacterium *Shewanella* sp. IRI-160 and its application to control harmful dinoflagellates. *Harmful Algae* 94, 101798.
- Wang, Y., Coyne, K.J., 2022. Metabolomic insights of the effects of bacterial algicide IRI-160AA on dinoflagellate *Karlodinium veneficum*. *Metabolites* 12 (4), 317.
- Wang, Y., Coyne, K.J., 2023. Transcriptome profiling reveals a global response in harmful dinoflagellate *Karlodinium veneficum* to naturally-occurring bacterial algicides. *Front. Mar. Sci.* 10, 1112913.
- Wang, Y., Coyne, K.J., 2024. Molecular insights into the synergistic effects of putrescine and ammonium on dinoflagellates. *Int. J. Mol. Sci.* 25 (2), 1306.
- Wang, Y., Holland, W.C., Hounshell, A.G., Kennedy, A., Pokrzywinski, K., Coyne, K.J., 2025. Non-target effects of a harmful algal bloom biocontrol technology (DinoSHIELD) in an *in-situ* mesocosm experiment. *Harmful Algae*, 102984.
- Wang, Z.F., Yu, Z.M., Song, X.X., Cao, X.H., 2014a. Effects of modified clay on the infant of *Patinopsetta yessoensis* for HABs control. *Mar. Environ. Sci.* 33 (6), 817–821.
- Wang, Z.F., Yu, Z.M., Song, X.X., Cao, X.H., Liu, K., 2014b. Impact of modified clay on the growth of the infant *Apostichopus japonicus* Selenka in HABs controlling. *Oceanol. Limnol. Sin.* 45 (2), 233–238.

- Wang, Z., Song, X., Zhang, Y., Yu, Z., Tang, X., 2019. Effects of modified clay on *Mercenaria mercenaria*. *Oceanol. Limnol. Sin.* 50, 692–699.
- Wang, M., Chen, S., Zhou, W., Yuan, W., Wang, D., 2020. Algal cell lysis by bacteria: a review and comparison to conventional methods. *Algal. Res.* 46, 101794.
- Wang, M., Cao, X., Zhang, B., Mu, Q., Song, X., Yu, Z., 2023a. Single source with series modifications: new method for preparing modified clay to control harmful algae blooms. *Mater. Des.* 232, 112077.
- Wang, M., Zhang, B., Cao, X., Li, F., Song, X., Yu, Z., 2023b. Influence of algal organic matter on algal removal efficiency by flocculation of modified clay. *J. Mar. Sci. Eng.* 11 (3), 613.
- Watson, S.E., Taylor, C.H., Bell, V., Bellamy, T.R., Hooper, A.S., Taylor, H., Jouault, M., Kille, P., Perkins, R.G., 2024. Impact of copper sulphate treatment on cyanobacterial blooms and subsequent water quality risks. *J. Environ. Manage.* 366, 121828.
- Weenink, E.F., Kraak, M.H., van Teulingen, C., Kuijt, S., van Herk, M.J., Sigon, C.A., Piel, T., Sandrini, G., Leon-Groeters, M., de Baat, M.L., Huisman, J., 2022. Sensitivity of phytoplankton, zooplankton and macroinvertebrates to hydrogen peroxide treatments of cyanobacterial blooms. *Water Res.* 225, 119169.
- Weisberg, R.H., Liu, Y., Lembke, C., Hu, C., Hubbard, K., Garrett, M., 2019. The coastal ocean circulation influence on the 2018 West Florida Shelf *K. brevis* red tide bloom. *J. Geophys. Res.* 124 (4), 2501–2512.
- Wells, M.L., Trainer, V.L., Smayda, T.J., Karlson, B.S., Trick, C.G., Kudela, R.M., Ishikawa, A., Bernard, S., Wulff, A., Anderson, D.M., Cochlan, W.P., 2015. Harmful algal blooms and climate change: learning from the past and present to forecast the future. *Harmful Algae* 49, 68–93.
- Wu, J., Nyborg, W.L., 2008. Ultrasound, cavitation bubbles and their interaction with cells. *Adv. Drug Deliv. Rev.* 60 (10), 1103–1116.
- Wu, P., Yu, Z., 2007. Extinguishment of harmful algae by organo-clay modified by gemini surfactant. *Environ. Sci.* 28 (1), 80–86.
- Wu, P., Yu, Z.M., Song, X.X., 2006. Extinguishment of harmful algae by organo-clay modified by alkyl glucoside quaternary ammonium compound. *Huanjing Kexue* 27 (11), 2164–2169.
- Xu, C., Yu, S., Hu, J., Effiong, K., Ge, Z., Tang, T., Xiao, X., 2022. Programmed cell death process in freshwater *Microcystis aeruginosa* and marine *Phaeocystis globosa* induced by a plant derived allelochemical. *Sci. Total Environ.* 838, 156055. <https://doi.org/10.1016/j.scitotenv.2022.156055>.
- Yarimizu, K., Cruz-López, R., Carrano, C.J., 2018. Iron and harmful algae blooms: potential algal-bacterial mutualism between *Lingulodinium polyedrum* and *Marinobacter algicola*. *Front. Mar. Sci.* 5, 180.
- Yokote, M., Honjo, T., 1985. Morphological and histochemical demonstration of glycocalyx on the cell surface of *Chattonella antiqua*, a “naked flagellate”. *Experientia* 41, 1143–1145.
- Yoshida, N., Ikeda, R., Okuno, T., 2006. Identification and characterization of heavy metal-resistant unicellular alga isolated from soil and its potential for phytoremediation. *Bioresour. Technol.* 97 (15), 1843–1849.
- Young, C.S., Gobler, C.J., 2018. The ability of macroalgae to mitigate the negative effects of ocean acidification on four species of North Atlantic bivalve. *Biogeosciences* 15 (20), 6167–6183. <https://doi.org/10.5194/bg-15-6167-2018>.
- Young, C.S., Sylvers, L.H., Tomasetti, S.J., Lundstrom, A., Schenone, C., Doall, M.H., Gobler, C.J., 2022. Kelp (*Saccharina latissima*) mitigates coastal ocean acidification and increases the growth of North Atlantic bivalves in lab experiments and on an oyster farm. *Front. Mar. Sci.* 9, 513.
- Yu, Z.M., Zou, J.Z., Ma, X.N., 1994a. A new method to improve the capability of clays for removing red tide organisms (In Chinese). *Oceanol. Limnol. Sin.* 25 (2), 226–232.
- Yu, Z.M., Zou, J.Z., Ma, X.N., 1994b. Application of clays to removal of red tide organisms: coagulation of red tide organisms with clays. *Chinese J. Oceanol. Limnol.* 25 (3), 193–200.
- Yu, Z.M., Zou, J.Z., Ma, X.N., 1994c. A more effective clay for removing red tide organisms. *J. Nat. Disast.* 3, 105–109.
- Yu, Z.M., Ma, X.N., Xie, Y., 1995. Study of main nutrients adsorption on clays in seawater. *Oceanol. Limnol. Sin.* 26 (2), 208–214.
- Yu, Z., Sun, X., Song, X., Zhang, B., 1999. Clay surface modification and its coagulation of red tide organisms. *Chin. Sci. Bull.* 44, 617–620.
- Yu, Z., Song, X., Cao, X., Liu, Y., 2017. Mitigation of harmful algal blooms using modified clays: theory, mechanisms, and applications. *Harmful Algae* 69, 48–64.
- Yu, Z., Tang, Y., Gobler, C.J., 2023a. Harmful algal blooms in China: history, recent expansion, current status, and future prospects. *Harmful Algae* 129, 102499.
- Yu, Q., Yu, Z., Song, X., Cao, X., Jiang, W., Chu, Y., 2023b. The synthesis of an acrylamide copolymer and its synergistic effects on clay flocculation of red tide organisms. *J. Environ. Manage.* 332, 117326.
- Zhang, P., Song, X., Zhang, Y., Zhu, J., Shen, H., Yu, Z., 2022. Assessing the effect of modified clay on the toxicity of *Karenia mikimotoi* using marine medaka (*Oryzias melastigma*) as a model organism. *Toxics* 10 (3), 105.
- Zhang, D., You, F., He, Y., Te Shu, H., Gin Karina, Y.-H., 2020a. Isolation and characterization of the first freshwater cyanophage infecting *Pseudanabaena*. *J. Virol.* 94. <https://doi.org/10.1128/Jvi.00682-20>.
- Zhu, X., Dao, G., Tao, Y., Zhan, X., Hu, H., 2021. A review on control of harmful algal blooms by plant-derived allelochemicals. *J. Hazard. Mater.* 401, 123403. <https://doi.org/10.1016/j.jhazmat.2020.123403>.
- Zhu, J., Yu, Z., Cao, X., Jiang, W., He, L., Zang, X., Song, X., 2024. Double effects of mitigating cyanobacterial blooms using modified clay technology: regulation and optimization of the microbial community structure. *Front. Microbiol.* 15, 1480069.
- Zhu, J., Yu, Z., He, L., Cao, X., Liu, S., Song, X., 2018. Molecular mechanism of modified clay controlling the brown tide organism *Aureococcus anophagefferens* revealed by transcriptome analysis. *Environ. Sci. Technol.* 52 (12), 7006–7014.
- Zhu, J., Yu, Z., He, L., Jiang, Y., Cao, X., Song, X., 2023. The molecular mechanisms and environmental effects of modified clay control algal blooms in aquacultural water. *J. Environ. Manage.* 337, 117715. <https://doi.org/10.1016/j.jenvman.2023.117715>.
- Zang, X., Yu, Z., Song, X., Cao, X., Jiang, K., 2024. Insights into the differential removal of various red tide organisms using modified clay: influence of biocellular properties and mechanical interactions. *Harmful Algae* 138, 102695.
- Zhang, F., Fan, Y., Zhang, D., Chen, S., Bai, X., Ma, X., Xie, Z., Xu, H., 2020b. Effect and mechanism of the algicidal bacterium *Sulfobacter porphyrae* ZFX1 on the mitigation of harmful algal blooms caused by *Prorocentrum donghaiense*. *Environ. Poll.* 263, 114475.
- Zhang, P., Song, X., Li, J., Yu, Z., 2019b. Effects of modified clay on Atlantic salmon (*Salmo salar*). *Oceanol. Limnol. Sin.* 50, 216–223.
- Zhang, Y., Song, X., Shen, H., Cao, X., Yuan, Y., Wu, Z., Yu, Z., 2020c. The effects of modified clay on abalone (*Haliotis discus hannai*) based on laboratory and field experiments. *Environ. Toxicol. Chem.* 39 (10), 2065–2075.
- Zhang, Y., Song, X., Yu, Z., Zhang, P., Cao, X., Yuan, Y., 2019a. Impact assessment of modified clay on embryo-larval stages of turbot *Scophthalmus maximus* L. *J. Oceanol. Limnol.* 37 (3), 1051–1061.