Invasive Mussels and Harmful Algal Blooms: Interactions and Detection Methods

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14. ABSTRACT
Both quagga (*Dreissena rostriformis bugensis*) and zebra (*Dreissena polymorpha*) (QM/ZM) and harmful algal blooms (HABs) are topics of concern in the western United States. As QM/ZM continue to spread into new waterbodies, there is more opportunity for potential interactions between these invasive mussels and algae communities. Understanding how these two separate issues impact each other is important for researchers and water managers. This scooping proposal was a literature review to assess the research that has been performed. Appendix A contains a list of State and Federal web based HAB resources. Appendix B contains selected abstracts that show the connections between HABs and QM/ZM. Some of interactions involve QM/ZM feeding on algae, water quality impacts, and algal impacts on mussel fertility. Understanding the interactions between QM/ZM and algal blooms is important as both issues continue to increase.

15. SUBJECT TERMS
Harmful algal bloom, quagga mussel, zebra mussel, water quality

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The mission of the Bureau of Reclamation is to manage, develop, and protect water and related resources in an environmentally and economically sound manner in the interest of the American public.

Disclaimer

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Peer Review

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Acronyms and Abbreviations

Reclamation	Bureau of Reclamation
Eco Lab	Ecological Research Laboratory
HAB	Harmful Algal Bloom
QM	Quagga Mussel (*Dreissena rostriformis bugensis*)
ZM	Zebra Mussel (*Dreissena polymorpha*)

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Executive Summary

Quagga (*Dreissena rostriformis bugensis*) and zebra (*Dreissena polymorpha*) mussels (QM/ZM) and harmful algal blooms are topics of concern in the western United States. As QM/ZM continue to spread into new waterbodies, there is more opportunity for potential interactions between these invasive mussels and algae communities. Algal blooms and harmful algal blooms (HABs), where toxins are produced, seem to be increasing each summer. Understanding how these two separate issues impact each other is important for researchers and water managers. This scooping proposal was a literature review to assess the research that has been performed. Appendix A contains a list of State and Federal web based HAB resources. Appendix B contains select abstracts that show the connections between HABs and QM/ZM.

Some key HAB and QM/ZM interactions are:

- ZM can selectively reject feeding on the blue-green algae microcystis.
- QM/ZM are known to increase phosphorus and nitrogen levels in a water column, which in turn contributes to algal blooms.
- QM/ZM can bioaccumulate the toxin, microcystin, in their tissues.
- QM/ZM fertility and sperm motility can be impacted by cyanobacteria.
- There are financial implications for landowners with increased algal blooms occurring following the infestation of QM/ZM.

As HAB events continue to occur, and in some cases are exacerbated by the presence of QM/ZM it is also important for Reclamation to know and understand the different methods for both algal identification and toxin analysis. HAB analysis ranges from field testing with dip stick tests to analytical methods that require specialized equipment. Some of the assays use quantitative polymerase chain reaction (qPCR) which is a technology that the Ecological Research Laboratory at the Reclamation Technical Service Center has experience with and could use to analyze HAB samples.

Research that explores the interactions between algal blooms and QM/ZM will continue to be of interest to Reclamation researchers. One potential research topic to explore is the occurrence of algal blooms in water bodies where suspect QM/ZM have been found but an adult population has not occurred. Part of this future project would be to collect algal monitoring data from State websites and map it to the locations with QM/ZM monitoring is occurring. Moving forward it is important to consider the interactions of algal blooms and QM/ZM.

1.Introduction

Since the arrival of invasive dreissenid mussels in the Great Lakes from Eurasia over twenty years ago, there has been research on how these invasive mussel impact algal blooms, and in particular harmful algal blooms where toxins are produced. This literature review will address two questions. First, what are the interactions between harmful algal blooms (HABs) and invasive dreissenid mussels? Second, what are the current detection methods for HABs and their toxins? And can these HAB detection methods be performed at the Ecological Research Laboratory (Eco Lab). Understanding the connections between invasive mussels and algal blooms is important because of the impact these events have on water quality and the environment. This literature review is the first step to determining the best pathway forward to studying dreissenid mussels and algal blooms.

2. Literature Review

1.1 Invasive Mussels

Over twenty years ago, two invasive bivalves, quagga and zebra mussels, arrived in the Great Lakes of North America. In 2007, quagga mussels (QM) were first detected in Lake Mead and have since spread throughout the lower Colorado River system and into other waterbodies in the western United States. Zebra mussels (ZM) are found at only a few sites west of the Mississippi and are mainly found in the eastern United States. Over the last few years ZM have begun to be found in waterbodies throughout Texas. Both invasive mussel species can cause significant impacts to the environment, and to infrastructure such as dams, water intakes, and water treatment facilities. An extensive monitoring program has been developed by Reclamation that uses both microscopy and environmental DNA (eDNA) to analyze samples from across the western United States to perform early detection for both organisms. The Eco Lab, Denver, CO, has for over ten years performed early detection for both QM/ZM. For Reclamation, the focus of the impacts of QM/ZM has been on the issues that these invaders cause to infrastructure. This has led to research into the best practices and technologies to keep QM/ZM from setting within facilities, mitigation methods after settlement has occurred, and early detection methods.

The ecological dynamics of a waterbody can be severely altered with the establishment of QM/ZM populations. Cuhel and Aguilar (Yauck, 2009) have shown that in Lake Michigan's food web there were decreases in phytoplankton, zooplankton, and scavengers/decomposers (Figure 1) following the introduction of QM/ZM. Where previously, the biomass from these producers would flow to fish, now with the arrival of QM/ZM the bulk of the biomass is within the invasive mussels. QM/ZM consume the phytoplankton, which changes the food web and opens opportunities for other species, such as algae and invasive plants, to find a new niche.

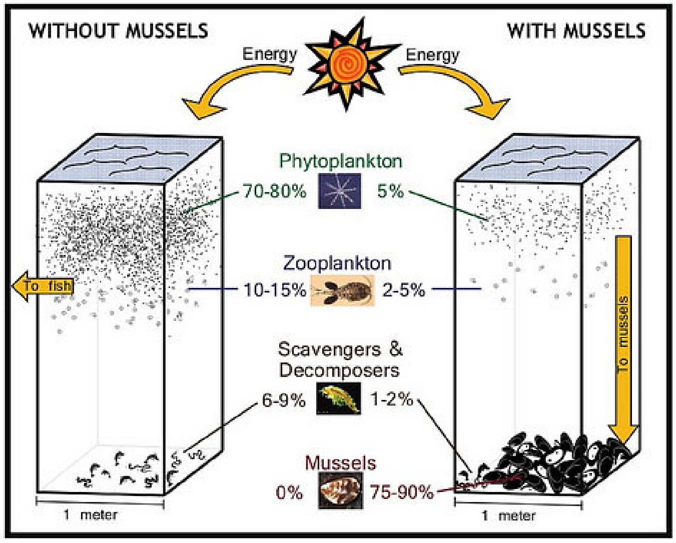

Figure 1: Impact of QM/ZM on a water column (Yauck, 2009).

In 2021, researchers showed that QM are now the primary regulator of phosphorus cycling in four of the Great Lakes (Li et al., 2021). QM can pull large amounts of phosphorus out of the water and into their tissues. This has led to the phosphorus cycle now being regulated by the changes in QM populations. Other researchers found that the presence of QM/ZM lead to reduced diatom and cyanobacteria abundances, and increased soluble reactive phosphorus (Reynolds & Aldridge, 2021). Increased phosphorus is also a cause of algal blooms and HABs. Thus, when a large mussel die-off occurs, phosphorus is released back into the water, and an algal bloom could then occur. QM/ZM are known to increase the concentrations of both nitrogen and phosphorus in water columns (Turner, 2010). Studies have found that QM/ZM can alter phosphorus, nitrogen, and carbon cycles in waterbodies (Marzocchi et al., 2021). QM/ZM can cause massive shifts in water quality and chemistry which in turn could lead to algal blooms and HABs.

1.2 Harmful Algal Blooms

Algal bloom research is focused on detection, causes, prevention, and mitigation (Glibert & Burkholder, 2018; Sellner, Doucette, & Kirkpatrick, 2003). It is important to note that not all algal blooms result in toxins being produced, but the impacts of a non-toxin producing algal bloom to the waterbody can still be significant. Fresh water algal blooms can be caused by several different species of phytoplankton with cyanobacteria or blue green algae (*Microcystis*) causing the most issues. Harmful algal blooms occur when toxins are produced, and the three most common toxins that are produced are microcystin, cylindrospermopsin, and anatoxin-a. Each toxin has different health impacts, for example microcystin is a liver toxin which can impact terrestrial animals (dogs, cattle, humans) and aquatic animals (fish kills) differently. Once an algal bloom or HAB is detected in a waterbody, an advisory or closing of public swim beaches is usually implemented by the water manager.

Figure 2 shows the impact of an algal bloom that does not produce toxins in a waterbody. Excessive phosphorus and nitrogen from agriculture are washed into a waterbody, this allows aquatic plants to flourish, and then an algal bloom occurs which depletes the oxygen in the water.

The bloom covers the waterbody, which in turn prevents sunlight from reaching aquatic plants. The plants die and decompose which further depletes the oxygen. With the lowered oxygen levels, aquatic organisms then start to die off. When a toxin producing HAB occurs, the algae release toxins into the water that can lead to large fish kills and other aquatic life being impacted. Each summer many lakes in the United States are impacted by both algal blooms and HAB events which in turn leads to restrictions on recreation and environmental impacts. Appendix A contains a list of HAB resources from both Federal and State agencies.

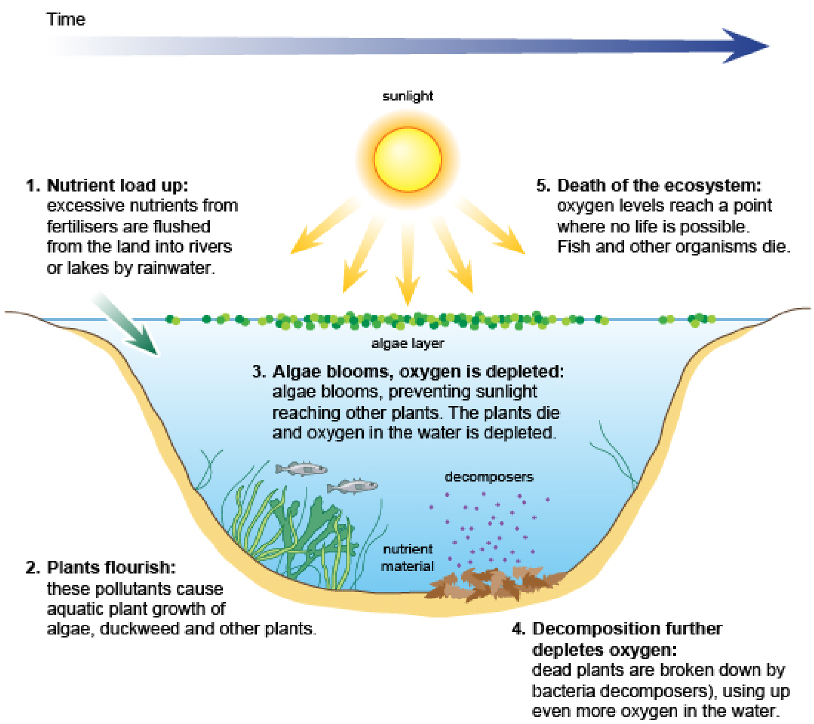

Figure 2: Impacts of an algal bloom on the ecosystem. From: http://biobunch.blogspot.com/2016/08/algal-blooms-ecological-cascades.html

1.3 HAB and Mussel Interactions

There are several different areas of research into HABs and QM/ZM interactions. Appendix B contains the abstracts of several publications that highlight how HABs and QM/ZM interact. The key points are:

- ZM can selectively reject feeding on the blue-green algae microcystis.
- QM/ZM are known to increase phosphorus and nitrogen levels in a water column, which in turn contributes to algal blooms.
- QM/ZM can bioaccumulate the toxin, microcystin, in their tissues.
- QM/ZM fertility and sperm motility can be impacted by cyanobacteria

- There are financial implications for landowners with increased algal blooms following the infestation of QM/ZM.

Mussel Feeding and Microcystis

There are several publications by the same group of NOAA researchers that detail the interactions between ZM and microcystis blooms in Saginaw Bay, Lake Huron. The first publication in 1994 showed that ZM can selectively ingest microcystis through three different mechanisms: expel the algae as pseudofeces, screen out large algal colonies before they get into the mussels siphon, and slow their pumping rate (H A Vanderploeg et al., 1995). The authors hypothesized that by using these mechanisms to selectively reject ingesting microcystis, ZM contributed to algal bloom formation. Additional studies showed that microcystis became abundant following ZM establishment in Saginaw Bay (H. A. Vanderploeg et al., 2001). Feeding experiments showed that ZM's could selectively reject microcystis in favor of Cryptomonas, one of their favorite foods (Henry A. Vanderploeg et al., 2013). This research group has done extensive feeding experiments with ZM and microcystis. By selectively rejecting microcystis, ZM cause an increase in the concentration of this algae in a waterbody, which in turn could lead to an HAB event.

Several studies have shown that adult ZM are able to bioaccumulate microcystin in their tissues either when microcystis is the sole food source or from when the toxins are bound to sediment particles (Paldavičiene, Zaiko, Mazur-Marzec, & Razinkovas-Baziukas, 2015; Pires et al., 2004). Pires et al. (2004) showed that somehow the mussels were protected against the accumulation of harmful amounts of microcystin and showed that the amount of microcystin accumulated in the mussels was high enough to cause liver damage in diving ducks. By accumulating the toxins, the mussels were decreasing the mortality in ducks in the shallow lakes in the Netherlands. Paldavičiene et al. (2015) found that in years where no HABs were detected in the water, ZM tissue still contained microcystin toxin most likly from resuspened sediment particles that had microcystin residuals. The implication is that QM/ZM are able to bioaccumulate microcystin toxin which in turn could help protect other wildlife and serve as a filter system to remove HAB toxins from a waterbody. Additional feeding studies are needed to better understand the conditions where QM/ZM selectively reject microcystis, and the conditions where these mussels are able to accumulate algal toxins in their tissues.

Water Quality

QM/ZM are both known to increase the concentrations of nitrogen and phosphorus in the water column (Turner, 2010), which can promote algal blooms. There are field observations that phosphorus availability impacts microcystis response to QM/ZM invasions (Sarnelle, White, Horst, & Hamilton, 2012). Sarnelle et al. (2012) showed that ZM had positive effects on *M. aeruginosa* at low phosphorus concentrations, but at high phosphorous levels ZM had negative impacts on the algae in a closed system. Field studies are needed to better understand QM/ZM, phosphorus, and algal bloom interactions.

Impacts of Cyanobacteria on QM fertility

Two publications have shown that QM spawning, fertilization, and sperm motility can be impacted by cyanobacteria (Boegehold, Alame, Johnson, & Kashian, 2019; Boegehold, Johnson, & Kashian, 2019). Both studies were done in the laboratory by inducing spawning in QM, via serotonin, and used cyanobacteria cultures. In the first paper, only one of the cultures inhibited spawning, while six cultures were able to impact fertilization. The second paper showed that QM sperm motility decreased when exposed to various cyanobacteria cultures. Both publications show that cyanobacteria can negatively impact QM fertility and sperm motility. Also, the authors suggest that understanding the mechanism by which cyanobacteria inhibit spawning and fertilization could lead to a potential control method for QM/ZM. Further research is needed determine the mechanism by which these interactions take place and to assess in an open water system the impacts of cyanobacteria and their toxins on QM/ZM fertility.

Additional Interactions

Changes in property values can also be impacted by the presence of QM/ZM and increased algae. Limburg et al. (2010) conducted a survey of business and homeowners about the impact of QM/ZM on water clarity and the production of nuisance algae (Cladopora and Microcysts) along Lake Ontario and in the Western St. Lawrence River in New York. Increased water clarity was considered a positive outcome, while the presence of increased algae was a negative impact. Both businesses and homeowners reported decrease in property values due to increased algae presence.

1.4 HAB Detection Methods

The detection methods for algal blooms and HABs in a waterbody range from observational to specialized laboratory analysis. Once a potential algal bloom or HAB event is observed, then further testing can be performed to determine the species of algae involved, and if toxins have been produced. Initial monitoring for potential toxins can be done by commercially available dipstick tests. These tests are available for anatoxin-a, cylindrospermopsin, and microcystin, and can be used on site to determine the toxin concentration. If the toxins are below the detection limit of the dip tests, then analytical tests can be used to determine the toxin concentrations.

Additional HAB testing can be broken down into three areas- cyanobacteria identification and measurements, molecular analysis, and toxin analysis. Once an algal bloom or HAB is suspected it is necessary to determine the species of algae and if toxins have been produced. Microscopy can be used to determine the genus/species and cell density. Laboratory tests can be done to determine chlorophyll-a and phycocyanin concentrations based on Standard Methods, which have been performed in the Eco Lab. Molecular analysis can be used for the identification of cyanobacteria species with 16S/18S next generation DNA sequencing or rapid tests for the toxin producing genes (such as microcystin) with qPCR. The Eco Lab has a qPCR instrument and could perform assays for the toxin producing genes as well as algal identification by molecular methods using published methods.

The EPA has developed analytical procedures for the detection of cyanotoxins in drinking and freshwater (Appendix B). The methods include the use of ELISA (enzyme linked immunosorbent assays) and LC-MS (liquid chromatography mass spectrometry). There are multiple commercial laboratories that can perform HAB identification and toxin testing using microscopy, molecular methods, and analytical tests. These laboratories can provide sample collection bottles and results within 24 hours depending on the test performed. Some of the toxins that can be tested for include:

microcystin, nodularin, cylindrospermopsin, saxitoxin, and anatoxin-a. The commercial laboratories can perform the EPA recommended tests to document the HAB event and determine if toxins have been produced.

HAB monitoring continues to expand with the Cyanobacteria Assessment Network (CyAn), which is a multiagency project to develop an early warning system to detect HABs in waterbodies in the United States (Appendix B). As part of this a web app, CyAN has been developed to provide satellite data on over 2,000 lakes and reservoirs. CyAN is an important resource for water managers across the United States because it allows them to use satellite data to determine if the waterbodies they manage have a potential bloom occurring. Once the satellite data shows a potential bloom, sampling of the site can begin. CyAN will allow water managers to make faster and better-informed management decisions. As new technologies emerge, new HAB detection and testing methods will continue to be developed.

1.5 Conclusion

There are many different interactions between algal blooms and QM/ZM. Some of the interactions have been defined: QM/ZM grazing, nutrient cycling, and impacts of algal toxins on mussel fertility. Researchers are continuing to study these interactions. There are most likely additional interactions occurring that have yet to be defined or understood.

How do algal blooms impact Reclamation's QM/ZM monitoring program? One future research topic is to assess the waterbodies where QM/ZM monitoring is taking place and determine which sites have algal blooms occurring. If the algal toxins can impact QM/ZM fertility, then it could be possible at sites where only single suspects have been found, the invasive mussel population could not establish due to the presence of the algal toxins. It is important to continue to study at the connections between QM/ZM and algal blooms so that we can better understand the long-term impacts both these events have on Reclamation waters.

Algal blooms are a growing area of interest for agencies at both the local, State, and Federal levels. Monitoring, detection, and mitigation the impacts of algal blooms and HABs where toxins are produced are all active areas of research for these organisms. Determining how Reclamation will address algal blooms is an ongoing topic of discussion between Reclamation researchers. A survey of Reclamation area offices is currently underway to assess algal research needs and will help guide future research. Both QM/ZM and algal blooms will be ongoing issues for Reclamation in the coming years.

1.6 Data

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This final report is also stored in the TSC Folder: Z:\DO\TSC\Jobs\DO_NonFeature\Science and Technology PNG-2021-Invasive Mussels and Harmful Algal Blooms: Interactions and Detection methods. This final report has also been uploaded to Reclamations RISE Database.

Point of contact: Jacque Keele, jkeele@usbr.gov, 303-445-2187
Data description: Final report for a scooping project.
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Appendix A: List of online HAB resources

Table AB-1: List of Federal HAB resources

Agency	Website
CDC	https://wwwn.cdc.gov/norsdashboard/
CyAN	https://www.epa.gov/water-research/cyanobacteria-assessment-network-application-cyan-app
EPA	https://www.epa.gov/cyanohabs
EPA- Extensive list of resources	https://www.epa.gov/cyanohabs/federal-agencies-and-organizations-habs-resources
NOAA	https://coastalscience.noaa.gov/research/stressor-impacts-mitigation/habhrca/
U.S. National Office for Harmful Algal Blooms	https://hab.whoi.edu/regions-resources/

Table AB-2: List of State HAB resources covering Reclamation's boundaries

State	Website
Arizona	https://azdeq.gov/AZHAB
California	http://www.mywaterquality.ca.gov/habs/resources/field.html
Colorado	https://cdphe.colorado.gov/toxic-algae
Idaho	https://www.deq.idaho.gov/water-quality/surface-water/cyanobacteria-harmful-algal-blooms/
Kansas	https://www.kdheks.gov/algae-illness/index.htm
Montana	https://dphhs.mt.gov/publichealth/Epidemiology/hab/
North Dakota	https://deq.nd.gov/WQ/3_Watershed_Mgmt/8_HABS/Habs.aspx
Nebraska	https://deq-iis.ne.gov/zs/bw/
New Mexico	https://www.env.nm.gov/surface-water-quality/nutrients/

Oklahoma	https://www.deq.ok.gov/state-environmental-laboratory-services/environmental-public-health-information/harmful-algal-blooms/
Texas	https://tpwd.texas.gov/landwater/water/environconcerns/hab/
South Dakota	https://denr.sd.gov/dfta/wp/habs.aspx
Utah	https://deq.utah.gov/water-quality/harmful-algal-blooms-home
Wyoming	https://health.wyo.gov/publichealth/infectious-disease-epidemiology-unit/disease/harmful-algal-blooms/

*Note- HAB monitoring, and reporting are housed in both environmental and health departments.

Table AB-3: List of non-governmental HAB resources

Group	Website
Harmful Algae Information System	http://haedat.iode.org/
International Society for the Study of Harmful Algae	https://issha.org
Fisheries and Oceans Canada	https://www.dfo-mpo.gc.ca/index-eng.html

Appendix B: Select abstracts on the interactions between invasive mussels and harmful algal blooms

[1] **P. M. Armenio, C. M. Mayer, S. A. Heckathorn, T. B. Bridgeman, and S. E. Panek, "Resource contributions from dreissenid mussels to the benthic algae Lyngbya wollei (Cyanobacteria) and Cladophora glomerata (Chlorophyta),"** ***Hydrobiologia*****, vol. 763, no. 1, pp. 35–51, 2016.**

Dreissena spp. (zebra and quagga mussels) are invasive to North America and increase light to the benthos, provide hard structure for algal attachment, and may contribute limiting nutrients to benthic algae, thereby facilitating algal blooms. We conducted experiments to determine how Dreissena affect nutrient stoichiometry and growth of Lyngbya wollei and Cladophora glomerata, two benthic algal species recently increasing in biomass in parts of the Laurentian Great Lakes, combined with a field survey to determine the likelihood of L. wollei co-occurrence with Dreissena. L. wollei had a significantly higher concentration of carbon, nitrogen, phosphorus, potassium, and sulfur when grown with live Dreissena. C. glomerata had greater biomass in tanks with live Dreissena, but did not have significant increases in nutrient concentration like L. wollei did. Neither algal species increased in growth due to the added structure of Dreissena shells. L. wollei biomass was greater in the presence of Dreissena during 1 year (of two) of our field survey. This field survey also showed that L. wollei and Dreissena are likely to co-occur. These results suggest that Dreissena provide several nutrients to benthic algae, and these added resources can promote algal growth and consequently blooms.

[2] **A. G. Boegehold, K. Alame, N. S. Johnson, and D. R. Kashian, "Cyanobacteria reduce motility of quagga mussel (Dreissena rostriformis bugensis) sperm,"** ***Environ. Toxicol. Chem.*****, vol. 38, no. 2, pp. 368–374, 2019.**

The temporal expansion of harmful algal blooms, primarily associated with cyanobacteria, may impact aquatic organisms at vulnerable life-history stages. Broadcast spawning species release gametes into the water column for external fertilization, directly exposing sperm to potential aquatic stressors. To determine if cyanobacteria can disrupt reproduction in freshwater broadcast spawners, we evaluated sublethal effects of cyanobacteria exposure on quagga mussel (Dreissena rostriformis bugensis) sperm. In laboratory studies, sperm were collected after inducing mussels to spawn using serotonin and exposed to 11 cultures of cyanobacteria including Anabaena flos-aquae, Aphanizomenon flos-aquae, Dolichospermum lemmermannii, Gloeotrichia echinulata, 5 cultures of Microcystis aeruginosa, M. wesenbergii, and Planktothrix suspensa. Sperm motility, using endpoints of cumulative distance traveled and mean velocity, was calculated for a minimum of 10 individual sperm using a novel optical biotracking assay method. The distance and velocity at which sperm traveled decreased when exposed to Aphanizomenon flos-aquae and 2 M. aeruginosa cultures. Our findings indicate that cyanobacteria impede the motility of quagga mussel sperm, which can potentially result in reproductive impairments to mussels and potentially other broadcast spawning species. Environ Toxicol Chem 2019;38:368–374. © 2018 SETAC.

[3] **A. G. Boegehold, N. S. Johnson, and D. R. Kashian, "Dreissenid (quagga and zebra mussel) veligers are adversely affected by bloom forming cyanobacteria,"** ***Ecotoxicol.***

***Environ. Saf.*, vol. 182, 2019.**

Quagga (Dreissena rostriformis bugensis) and zebra (D. polymorpha) mussels are broadcast spawners that produce planktonic, free swimming veligers, a life history strategy dissimilar to native North American freshwater bivalves. Dreissenid veligers require highly nutritious food to grow and survive, and thus may be susceptible to increased mortality rates during harsh environmental conditions like cyanobacteria blooms. However, the impact of cyanobacteria and one of the toxins they can produce (microcystin) has not been evaluated in dreissenid veligers. Therefore, we exposed dreissenid veligers to eleven distinct cultures (isolates) of cyanobacteria representing Anabaena, Aphanizomenon, Dolichospermum, Microcystis, and Planktothrix species and the cyanotoxin microcystin to determine the lethality of cyanobacteria on dreissenid veligers. Six-day laboratory bioassays were performed in microplates using dreissenid veligers collected from the Detroit River, Michigan, USA. Veligers were exposed to increasing concentrations of cyanobacteria and microcystin using the green algae Chlorella minutissima as a control. Based on dose response curves formulated from a Probit model, the LC50 values for cyanobacteria used in this study range between 15.06 and 135.06 μg/L chlorophyll-a, with the LC50 for microcystin-LR at 13.03 μg/L. Because LC50 values were within ranges observed in natural waterbodies, it is possible that dreissenid recruitment may be suppressed when veliger abundances overlap with seasonal cyanobacteria blooms. Thus, the toxicity of cyanobacteria to dreissenid veligers may be useful to include in models forecasting dreissenid mussel abundance and spread.

[4] **J. Li, V. Ianaiev, A. Huff, J. Zalusky, T. Ozersky, and S. Katsev, "Benthic invaders control the phosphorus cycle in the world's largest freshwater ecosystem," *Proc. Natl. Acad. Sci. U. S. A.*, vol. 118, no. 6, 2021.**

The productivity of aquatic ecosystems depends on the supply of limiting nutrients. The invasion of the Laurentian Great Lakes, the world's largest freshwater ecosystem, by dreissenid (zebra and quagga) mussels has dramatically altered the ecology of these lakes. A key open question is how dreissenids affect the cycling of phosphorus (P), the nutrient that limits productivity in the Great Lakes. We show that a single species, the quagga mussel, is now the primary regulator of P cycling in the lower four Great Lakes. By virtue of their enormous biomass, quagga mussels sequester large quantities of P in their tissues and dramatically intensify benthic P exchanges. Mass balance analysis reveals a previously unrecognized sensitivity of the Great Lakes ecosystem, where P availability is now regulated by the dynamics of mussel populations while the role of the external inputs of phosphorus is suppressed. Our results show that a single invasive species can have dramatic consequences for geochemical cycles even in the world's largest aquatic ecosystems. The ongoing spread of dreissenids across a multitude of lakes in North America and Europe is likely to affect carbon and nutrient cycling in these systems for many decades, with important implications for water quality management.

[5] **K. E. Limburg, V. A. Luzadis, M. Ramsey, K. L. Schulz, and C. M. Mayer, "The good, the bad, and the algae: Perceiving ecosystem services and disservices generated by zebra and quagga mussels," *J. Great Lakes Res.*, vol. 36, no. 1, pp. 86–92, 2010.**

Dreissenid (zebra and quagga) mussels are widely recognized as having strong, adverse ecological and economic impacts, e.g., biofouling and loss of water column primary production. We assessed perceptions and values associated with two less often considered ecological outcomes of dreissenid mussel influences on coastal ecosystems along Lake Ontario and the western St. Lawrence River in New York State. One, the generation of water clarity through filtration, we define as an ecosystem service; the other, the production of large amounts of nuisance algae (e.g., Cladophora and Microcystis) is defined as an ecosystem disservice. Surveys of business owners and homeowners quantified their preferences and the formation of values regarding these products of zebra mussel influence. Water clarity increased greatly, particularly in the eastern portion of Lake Ontario, and algal problems increased throughout. Businesses attributed increases and decreases in revenues associated with water clarity and algae; homeowners reported analogous changes in property values. Water clarity was positively associated, and algae negatively associated, with changes in revenues and property values. Threshold responses of costs as functions of filamentous algae were evident. Given the likely continued influx of invasive species due to human activities, further development of the ecosystem service concept should consider potential "goods" and "bads" of invasives and their influence on ecosystem and social system resiliency. © 2009 Elsevier B.V. All rights reserved.

[6] A. Paldavičiene, A. Zaiko, H. Mazur-Marzec, and A. Razinkovas-Baziukas, "Bioaccumulation of microcystins in invasive bivalves: A case study from the boreal lagoon ecosystem," ***Oceanologia*****, vol. 57, no. 1, pp. 93–101, 2015.**

In the current study we present the first report on the bioaccumulation of microcystins (MC) in zebra mussel Dreissena polymorpha from the eutrophic brackish water Curonian Lagoon. The bioaccumulation capacity was related to age structure of mussels and ambient environmental conditions. We also discuss the relevant implications of these findings for biomonitoring of toxic cyanobacteria blooms in the Curonian Lagoon and potential consequences for D. polymorpha cultivation activities considered for the futures as remediation measure. Samples for the analysis were collected twice per year, in June and September, in 2006, 2007 and 2008, from two sites within the littoral zone of the lagoon. The highest microcystin concentrations were measured in mussels larger than 30 mm length and sampled in 2006 (when a severe toxic cyanobacteria bloom occurred). In the following years, a consistent reduction in bioaccumulated MC concentration was noticed. However, certain amount of microcystin was recorded in mussel tissues in 2007 and 2008, when no cyanotoxins were reported in the phytoplankton. Considering high depuration rates and presence of cyanotoxins in the bottom sediments well after the recorded toxic blooms, we assume mechanism of secondary contamination when microcystin residuals could be uptaken by mussels with resuspended sediment particles.

[7] L. M. D. Pires ***et al.*****, "Assimilation and depuration of microcystin-LR by the zebra mussel, Dreissena polymorpha,"** ***Aquat. Toxicol.*****, vol. 69, no. 4, pp. 385–396, 2004.**

Zebra mussels (Dreissena polymorpha) are an important component of the foodweb of shallow lakes in the Netherlands, amongst others in Lake IJsselmeer, an international important wetland. Large numbers of ducks feed on these mussels in autumn and winter. The mussels are filter feeders and are exposed to high densities of cyanobacteria in summer and autumn. Mussels and cyanobacteria both thrive in Lake IJsselmeer. Apparently, the mussels are somehow protected against accumulation of harmful quantities of cyanobacterial toxins. In this study, we investigated the assimilation of the cyanobacterial toxin microcystin-LR (MC-LR) in zebra mussels when fed the toxic cyanobacterium Microcystis aeruginosa as sole food or in a mixture with the eustigmatophyte Nannochloropsis limnetica. After 3 weeks of assimilation we studied the depuration of MC-LR during 3 weeks when the food of the mussels was free of cyanobacteria. These assimilation/depuration experiments were combined with grazing experiments, using the same food treatments. Microcystins were analyzed using liquid chromatography-mass spectrometry (LC-MS); in addition, covalently bound MC were analyzed using the MMPB method. The mussels showed higher clearance rates on Microcystis than on Nannochloropsis. No selective rejection of either phytoplankton species was observed in the excretion products of the mussels. Zebra mussels fed Microcystis as single food, assimilated microcystin-LR relatively fast, and after 1 week the maximum value of free unbound microcystin assimilation (ca. 11 μg g DW -1) was attained. For mussels, fed with the mixed food, a maximum of only 3.9 μg g DW -1 was recorded after 3 weeks. Covalently bound MC never reached high values, with a maximum of 62% of free MC in the 2nd week of the experiment. In the depuration period microcystin decreased rapidly to low values and after 3 weeks only very low amounts of microcystin were detectable. The amount of toxin that accumulated in the mussels would appear to be high enough to cause (liver) damage in diving ducks. However, death by exposure to microcystin seems unlikely. Mussels seem efficient in minimizing the assimilation of microcystin. If it were not for this, mass mortalities of ducks in shallow lakes in the Netherlands would presumably occur on a much more widespread scale than is currently observed. © 2004 Elsevier B.V. All rights reserved.

[8] **O. Sarnelle, J. D. White, G. P. Horst, and S. K. Hamilton, "Phosphorus addition reverses the positive effect of zebra mussels (Dreissena polymorpha) on the toxic cyanobacterium, Microcystis aeruginosa,"** ***Water Res.*****, vol. 46, no. 11, pp. 3471–3478, 2012.**

We tested the hypothesis that zebra mussels (Dreissena polymorpha) have positive effects on the toxin-producing cyanobacterium, Microcystis aeruginosa, at low phosphorus (P) concentrations, but negative effects on M. aeruginosa at high P, with a large-scale enclosure experiment in an oligotrophic lake. After three weeks, mussels had a significantly positive effect on M. aeruginosa at ambient P (total phosphorus, TP ∼10 μg L-1), and a significantly negative effect at high P (simulating a TP of ∼40 μg L-1 in lakes). Positive and negative effects were strong and very similar in magnitude. Thus, we were able to ameliorate a negative effect of Dreissena invasion on water quality (i.e., promotion of Microcystis) by adding P to water from an oligotrophic lake. Our results are congruent with many field observations of Microcystis response to Dreissena invasion across ecosystems of varying P availability. © 2012 Elsevier Ltd.

[9] **C. B. Turner, "Influence of zebra (dreissena polymorpha) and quagga (dreissena rostriformis) mussel invasions on benthic nutrient and oxygen dynamics,"** ***Can. J. Fish. Aquat. Sci.*****, vol. 67, no. 12, pp. 1899–1908, 2010.**

Although invasive zebra (Dreissena polymorpha) and quagga (Dreissena rostriformis) mussels are known to increase water column concentrations of nitrogen and phosphorus, the relative roles of direct nutrient release by the mussels and mussel-induced alterations to sediment fluxes are little understood. In short-term microcosm experiments comparing the presence and absence of mussels on sediments from Oneida Lake, New York, USA, both dreissenid species approximately doubled benthic oxygen consumption and fluxes of ammonium. The impact on soluble reactive phosphate (SRP) flux varied from 40% to 140% depending on whether mussels were located in the water column or directly on sediments. The additional flux was attributable directly to release by the mussels, with fluxes from the sediments remaining largely unchanged. However, mussels located directly on sediment surfaces released twice as much SRP as mussels located higher in the water column, with a molar N:P ratio as low as 4:1. The high rate of SRP release by mussels on sediment, possibly caused by mobilization of iron-bound phosphorus from sediment particles in the anoxic guts of the mussels, could contribute to observed increases in SRP, abundance of nuisance algae such as Cladophora, and abundance and toxicity of the cyanobacteria Microcystis in dreissenid invaded ecosystems.

[10] **H. A. Vanderploeg** ***et al.*****, "Do zebra mussels promote blue-green and metaphyton blooms in Saginaw Bay, and do these blooms affect the mussels?," in** ***Proceedings of***

***the 38th Conference of the International Association of Great Lakes Research.*, 1995, p. 113.**
After a clear-water phase in spring 1994, a bloom of Microcystis persisted and mussels (Dreissena polymorpha) fed very low rates throughout summer and fall in the inner bay. Videographic observations with a Schlieren optical pathway showed that the mussels did not stop pumping, but exhibited a number of mechanisms to reduce ingestion of Microcystis colonies: (1) mussels filtered at an apparently normal rate, but expelled filtered algae as loosely consolidated pseudofeces; (2) mussels screened out large colonies on tentacles guarding the entrance to the siphon; and (3) mussels occasionally slowed pumping rate in conjunction with mechanisms (1) and (2). We hypothesized these mechanisms of selective rejection contributed to bloom formation. Other mechanisms considered included: (1) blue-green algae are spatially segregated from the mussels because of their positive buoyancy, and (2) the N/P ratio excreted by the mussels promotes growth of blue-greens. Metaphyton growth would be promoted because of increased water clarity, nutrient excretion by the mussels, and the metaphyton being too large to be filtered by the mussels. Blue-green algae may contribute to the lower growth rates of mussels in the inner bay.

[11] **H. A. Vanderploeg *et al.*, "Zebra mussel (Dreissena polymorpha) selective filtration promoted toxic Microcystis blooms in Saginaw Bay (Lake Huron) and Lake Erie," *Can. J. Fish. Aquat. Sci.*, vol. 58, no. 6, pp. 1208–1221, 2001.**
Microcystis aeruginosa, a planktonic colonial cyanobacterium, was not abundant in the 2-year period before zebra mussel (Dreissena polymorpha) establishment in Saginaw Bay (Lake Huron) but became abundant in three of five summers subsequent of mussel establishment. Using novel methods, we determined clearance, capture, and assimilation rates for zebra mussels feeding on natural and laboratory M. aeruginosa strains offered alone or in combination with other algae. Results were consistent with the hypothesis that zebra mussels promoted blooms of toxic M. aeruginosa in Saginaw Bay, western Lake Erie, and other lakes through selective rejection in pseudofeces. Mussels exhibited high feeding rates similar to those seen for a highly desirable food alga (Cryptomonas) with both large (>53 µm) and small (<53 µm) colonies of a nontoxic and a toxic laboratory strain of M. aeruginosa known to cause blockage of feeding in zooplankton. In experiments with naturally occurring toxic M. aeruginosa from Saginaw Bay and Lake Erie and a toxic isolate from Lake Erie, mussels exhibited lowered or normal filtering rates with rejection of M. aeruginosa in pseudofeces. Selective rejection depended on "unpalatable" toxic strains of M. aeruginosa occurring as large colonies that could be rejected efficiently while small desirable algae were ingested.

[12] **H. A. Vanderploeg, T. H. Johengen, and J. R. Liebig, "Feedback between zebra mussel selective feeding and algal composition affects mussel condition: Did the regime changer pay a price for its success?," *Freshw. Biol.*, vol. 54, no. 1, pp. 47–63, 2009.**
1. We investigated the role of algal composition on pumping, clearance, assimilation, pseudofaeces and faeces production, feeding time budgets, and condition of zebra mussels from spring to autumn at two sites in Saginaw Bay (Lake Huron) and one site in western Lake Erie. Size-fractioned chlorophyll was used to distinguish between feeding on small (<53 µm) and large (>53 µm) size fractions, and mussel feeding behaviour was quantified by video observations. 2. Mussel pumping, clearance and assimilation rates varied among sites, particularly during summer, when phytoplankton composition varied considerably among sites. Lowest values were seen at the inner-bay site of Saginaw Bay, low to moderate values at the outer-bay site of Saginaw Bay, and high values at the Lake Erie site. Clearance, pumping and assimilation rates were all highly positively correlated (R2 = 0.76) with per cent

contribution of flagellates to total algal biomass and negatively correlated with per cent of Microcystis aeruginosa (R2 = 0.63). The negative effects on pumping rate (as determined by clearance rate on the <53 μm fraction) of Microcystis, which occurred in the >53 μm fraction, could be mitigated by the presence of flagellates in the <53 μm fraction. 3. Visual observations of mussel feeding showed evidence for poor seston quality during summer negatively affecting feeding rates. High faeces production during times of low assimilation rate was suggestive of poor assimilation efficiency and/or viable gut passage of grazing resistant algae. Long periods of time not filtering by the mussels during some Microcystis blooms and lack of production of a filtering current during one experiment were suggestive of intoxication from microcystin or other secondary compounds. 4. Clearance and feeding rates of the mussels in Saginaw Bay were high during spring and autumn and very low in summer, particularly at the inner-bay site. Condition of the mussels (mass : length ratio) was highest in spring and lowest during summer. This seasonal variation probably reflected high food assimilation rate during autumn and spring and low assimilation rate and reproduction during summer. The condition of mussels throughout the year was higher at the outer-bay than the inner-bay site, reflecting better feeding conditions at the former. Mussel selective feeding may have been responsible for the poor quality of food at the inner bay site; therefore, we postulate that a regime shift in phytoplankton composition promoted by the mussels fed back into lowered condition of the mussels. © 2008 Blackwell Publishing Ltd.

[13] **H. A. Vanderploeg, J. R. Liebig, T. F. Nalepa, G. L. Fahnenstiel, and S. A. Pothoven, "Dreissena and the disappearance of the spring phytoplankton bloom in Lake Michigan,"** ***J. Great Lakes Res.*****, vol. 36, no. SUPPL. 3, pp. 50–59, 2010.**

We determined the clearance rates of the profunda morph of the quagga mussel (Dreissena bugensis) using seston and Cryptomonas ozolini, a high-quality algal food, for the temperature range 1-7°C, which is the full temperature range this morph is likely to experience during isothermal conditions or in the hypolimnion of deep lakes. Experiments at 3°C with the shallow-water morph of the quagga and the zebra mussel provided very similar results. The clearance rates were combined with dreissenid abundance in 0-30. m, 30-50. m, 50-90. m, and > 90m depth zones of the southern basin of Lake Michigan to calculate a maximum (using Cryptomonas) and minimum (using seston) fraction of the water column cleared (FC) per day in the different depth zones at 3°C to determine dreissenid impact on the spring phytoplankton bloom from 1994 to 2008. Starting in 2003 or 2004 with the replacement of zebra mussels by quagga mussels in shallow water and expansion of quagga mussel biomass in deep water, FC began to exceed likely phytoplankton growth in the 30-50. m zone. In 2007-2008, FC greatly exceeded likely phytoplankton growth by a factor of about 5 in the 30- to 50-m depth zone, where dreissenids were extremely abundant. Low FC in the offshore region led to the hypothesis of a mid-depth carbon (C) and phosphorous (P) sink caused by mussel uptake of seston-associated C and P that affected not only the mid-depth region, but also the offshore region "downstream" of the mid-depth zone. © 2010.

[14] **H. A. Vanderploeg** ***et al.*****, "Role of Selective Grazing by Dreissenid Mussels in Promoting Toxic Microcystis Blooms and Other Changes in Phytoplankton Composition in the Great Lakes," in** ***Quagga and Zebra Mussels: Biology, Impacts, and Control, Second Edition*****, 2013, pp. 509–524.**

We investigated the feeding response of zebra and quagga mussels to Microcystis aeruginosa strains from culture collection and from natural seston from Saginaw Bay (Lake Huron), western Lake Erie, and enclosures from Gull Lake, an inland lake in Michigan. These experiments were done to evaluate the roles of strain identity, toxin concentration (microcystin), colony size, and environmental phosphorus concentrations as they affect ingestion or selective rejection of Microcystis in pseudofeces and potential Microcystis bloom promotion through the selective-rejection process. A combination of traditional feeding experiments with mussels confined in beakers and videotaping of mussel behavior was used. We measured changes in Microcystis concentration in the feeding experiments using changes in chlorophyll and the toxin associated with Microcystis (microcystin) in small (<53 μm) and large (>53 μm) size fractions. In natural seston, most colonies fell within the large size fraction. Overall, there were complex interactions that could not be simply explained by microcystin concentration, colony size, or environmental P concentration. Experiments with toxic and nontoxic strains from culture collection indicated different reasons for rejection. In one nontoxic strain having colonies in both the small and large fractions, small colonies were ingested, while large colonies were not. In another nontoxic strain, consisting only of large colonies, no colonies were ingested; however, when the colonies were broken apart by sonication, no small colonies or even single cells were ingested. Video observations showed that both of these strains were readily captured and rejected in pseudofeces after a large number were collected. Mussels fed upon the small colonies of a moderately toxic strain, whereas for another less toxic strain, no feeding occurred. When mussels were induced to feed on this latter strain by adding Cryptomonas-a favorite food of mussels-to the suspension, one of the mussels showed extreme sensitivity to Microcystis by rejecting each colony as they entered the incurrent siphon. Experiments with Microcystis having moderate microcystin concentration from both the low P (Saginaw Bay) and high P (Maumee Bay) sites in the Great Lakes were rejected. Microcystis from enclosures in Gull Lake was ingested despite having very high microcystin concentrations. Whether the selective-rejection process results in a Microcystis bloom depends on both mussel abundance and environmental P concentration as they affect mortality and growth rate of algae competing with Microcystis, as well as the composition of different Microcystis strains (genetic identities) that can coexist at the same time in the same water body. Questions for future research and research approaches to understand these complex interactions are outlined.

[15] F. Yuan, R. A. Krebs, and A. N. Wagner, "Identifying the influence of zebra and quagga mussels on sedimentary phosphorus dynamics in western Lake Erie," *Hydrobiologia*, vol. 848, no. 8, pp. 1897–1909, 2021.

Dreissenid mussels can alter nutrient cycling and algal productivity in many freshwater ecosystems. But their effects on sedimentary phosphorus dynamics remain largely undefined. Here, we report evidence that dreissenids affect the concentrations of five sedimentary phosphorus fractions and total phosphorus. During our study, zebra mussels were still common and coexisted with quagga mussels in many parts of the basin. The relative abundances varied across the basin, which we characterized as five west-to-east alternating zones where zebra mussels dominated zones I (coastal) and III, quagga mussels dominated zones II and IV, and few dreissenids were present in zone V. The phosphorus fractions exhibited variation concordant with and therefore potentially influenced by dreissenids. Concentrations of all fractions and TP were consistently greater in sediments where quagga mussels dominated than in sediments where zebra mussels dominated. The responses to the absence versus presence of dreissenids were mixed, with Res-P being significantly affected, NaCl-Pi and HCl-Pi being moderately affected, and NaOH-Pi being least affected. Although such dreissenid effects were somewhat altered by in-lake biogeochemical cycling and transfer, we found that elevated levels of NaCl-Pi in dreissenid-present sediments, especially in quagga-dominated sediments, could be linked to recent eutrophication and harmful algal blooms in the basin.