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Aquatic Invasive Species in the Great Lakes Region: An Overview

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ABSTRACT
Aquatic invasive species (AIS) are of concern in North America due to their devastating impacts on ecosystems and economies. The Great Lakes region is particularly vulnerable to AIS introduction and establishment with at least 184 nonindigenous species reported in this region from a large number of taxa including viruses, bacteria, diatoms, protozoa, arthropods, mollusks, fish, and plants. Representative species from these groups were explored, describing the features of their natural history and current efforts in prevention and control. Specifically, five AIS that are expected to spread to novel areas in the region are discussed: viral hemorrhagic septicemia virus and heterosporis (pathogens affecting fish), starry stonewort (an alga), zebra mussels (a bivalve), and carps (fishes). Novel strategies for AIS control include next-generation sequencing technologies, gene editing, mathematical modeling, risk assessment, microbiome studies for biological control, and human-dimension studies to address tensions related to AIS management. Currently, AIS research is evolving to adapt to known technologies and develop novel technologies to understand and prevent AIS spread. It was found that AIS control in this region requires a multidisciplinary approach focusing on the life history of the species (e.g., pheromones), adaptive management of anthropogenic structures (e.g., bubble curtains), and the integration of human dimensions to develop efficient management plans that integrate local citizens and management agencies.

KEYWORDS
Aquatic invasive species; Great Lakes; starry stonewort; heterosporis; zebra mussels

Introduction

Aquatic invasive species (AIS) have devastating effects on ecosystems as well as on local and national economies worldwide (Lovell et al., 2006). The Great Lakes region represents the largest freshwater body in the world, and the area is known for its rich biodiversity and economic importance (Mills et al., 1993). This region, however, has fragile ecosystems that have demonstrated a high vulnerability to AIS (Elsayed et al., 2006; Lumsden et al., 2007). At least 184 nonindigenous species have been reported within the Great Lakes region, across a vast range of taxonomic groups such as viruses, bacteria, diatoms, protozoa, arthropods, mollusks, fish, and plants (NOAA, 2016). Resulting AIS damage estimates can be up to $138 million per year; however, upon considering other side effects such as sport fishing losses, the negative impact of AIS in the Great Lakes may exceed $800 million annually (Rothlisberger et al., 2012). In this region, where aquatic ecosystems are an integral part of the economy and culture, tens of millions of dollars are spent annually on the prevention, control, and management of AIS (Rosaen et al., 2012; MNDNR, 2015).

Given the biological and economic impacts of AIS, this contribution presents an overview of the current knowledge, existing prevention and control research, and future steps in finding science-based solutions to AIS problems affecting the Great Lakes region of the U.S. Investigations across AIS taxa are key to improve detection, prevention, and control strategies. Fortunately, most invasive species share ecological features that promote their invasiveness and can in turn help us predict their spread, including ecological plasticity, high reproductive potential, habitat generalism, and favorable response to human-mediated dispersal and disturbance (Lockwood et al., 2006). Here, AIS research is explained for four main groups: microorganisms, plants, invertebrates and vertebrate animals. Representative species from different taxonomic groups were included with emphasis on AIS with ongoing expansion in the Great

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Lakes region. Viral hemorrhagic septicemia virus and heterosporis (microorganisms), starry stonewort (alga), zebra mussels (invertebrate animals), and carps (vertebrate animals) are described. This review aims to include critical information about the taxonomy, natural history, current research efforts, and future need for investigation for AIS that have potential to spread to non-infested areas in the Great Lakes region. This information may help fisheries biologists, environmental managers, and aquaculture professionals to be aware of the ongoing invasion process in this region. Finally, opportunities for future AIS research are discussed. Strategic research can be used to better inform management efforts and the allocation of limited resources among detection, prevention, and control activities.

Microorganism: Viral hemorrhagic septicemia virus

Outbreaks of viral hemorrhagic septicemia virus (VHSv; *Novirhabdovirus*) cause mortality in aquaculture facilities and in wild fish populations, especially in salmonids (Wolf, 1988; Kim and Faisal, 2011; Figure 1). Indeed, rainbow trout (*Oncorhynchus mykiss*) are considered the most important reservoir and propagator of the virus and are responsible for outbreaks in many countries around the world (Wolf, 1988; Smail and Snow, 2011). Furthermore, several other economically important fish species have experienced outbreaks in farm facilities (Ross et al., 1994; Garver et al., 2013). Based on the structural composition of the VHSv nucleoprotein and glycoprotein, four genotypes have been identified (genotype I–IV) (Einer-Jensen et al., 2004; Snow et al., 2004).

VHSv causes a disease that presents in both acute and chronic forms, with clinical and pathological signs depending on the stage of the disease (Wolf, 1988; Lovy et al., 2012). VHSv displays a variety of clinical and pathological alterations, including internal lesions; serous or sanguinolent edema; petechiae and hemorrhage in visceral organs, muscles, and brain; external lesions comprising ocular and skin hemorrhage exophthalmia, skin darkening, and pale gills. Also, some behavioral alterations appear, including anorexia, lethargy, and erratic swimming (Skall et al., 2005; Lovy et al., 2013; Cornwell et al., 2014; Munro et al., 2015).

Given the known risk factors and potential for catastrophic losses of farmed and wild fish populations, the management response in the Great Lakes region has

Figure 1. Fish kill in the Great Lakes region due to VHSv. Photo credit: Andy Noyes, Department of Environmental Conservation, State of New York.

largely focused on preventing overland spread (VHSv Expert Panel, 2010). This has included regulatory inspections prior to interstate movements of live fish or gametes as outlined by the U.S. Department of Agriculture – Animal and Plant Health Inspection Service's Federal Order (USDA-APHIS, 2008). The Federal Order was lifted in 2014; however, current state requirements within the Great Lakes region meet or exceed those standards and have been considered, at least in part, responsible for the slower than expected rate of invasion (Faisal et al., 2012). Additional precautions, such as egg disinfection (Groocock et al, 2013), disinfection of frozen baitfish (Phelps et al., 2013), and disease-free baitfish certifications (Vollmar et al., 2014) have been implemented to varying degrees to reduce risk of spread. Vaccines for VHSv have not been widely used in production facilities in the region and vaccine applications for wild fish populations has not been realistic.

Current efforts

Designing effective plans for VHSv prevention requires an accurate understanding of its distribution and abiotic and biotic preferences. Studying pathogen associations with their host and environment is essential to infectious disease prevention (Johnson et al., 2015). These relationships represent factors that shape the pathogen's distribution and may include the viral cycle, environmental features, host abundance, distribution (Figure 2), and susceptibility towards infection in the native and invaded range (Chow and Suttle, 2015). The factors involved in the organisms' presence within an environment are either *abiotic factors*, which include ecological variables related to physical phenomena (e.g., temperature, bathymetry, light, chemical compounds, among others) that limit the organism's distribution or *biotic factors*, which account for interspecies interactions (e.g., parasite–host dynamics, immunity, predation by phages, among others) that allow or limit virus development and transmission (Hurst, 2011).

The ecology of VHSv is constrained to the ecosystem used by the host and the host's internal environment (Hurst, 2011). For instance, its abiotic and biotic characteristics vary between free-living and parasitic phases. The virus cycle requires entry of the virus into susceptible cells of the host, viral replication using the cell's internal mechanisms, and exit from the cell or host (Nerland et al., 2011). This is accomplished by efficient vertical and horizontal transmission routes (Hurst, 2011) together with inherent capacity of the virus to survive in the aquatic environment (Nerland et al., 2011) and evade the host's immune system (Workenhe et al., 2010). Understanding the factors limiting or facilitating VHSv occurrence is crucial to anticipate and prevent its spread. A recent study explored the biogeography of VHSv across the Great Lakes region focusing on the abiotic components associated with VHSv occurrence, and found that temperature, bathymetry, and primary

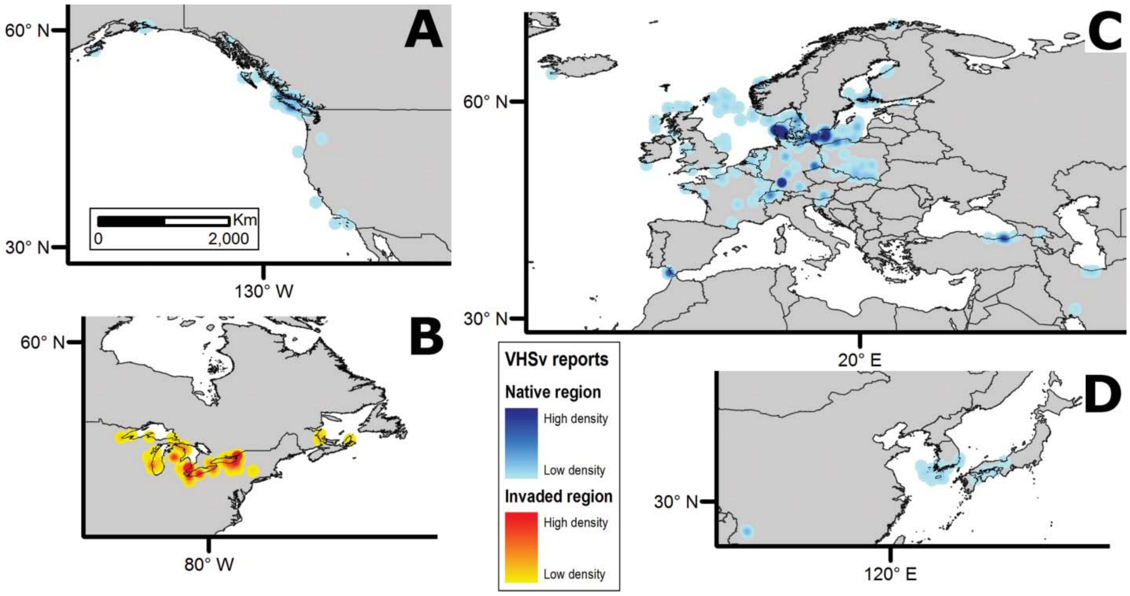

Figure 2. Hotspot areas of Viral Hemorrhagic Septicemia virus (VHSv) reports. Density of VHSv reports in its native (blue-white range) and invaded distributions (red-yellow range) across the west coast of North America (A), Europe (B), the Great Lakes Region of North America (C), and Asia (D). Continuous values estimated based on a Kernel Density Estimation from original VHSv reports in ArcGIS software version 10.3.1 (ESRI, Redlands CA) with one-degree bandwidth. Sources: http://www.fishpathogens.eu and http://gis.nacse.orgnfo/vhsv.

productivity can be associated with VHSv presence (Escobar et al., 2016). Studies focusing on VHSv tolerance to temperature have shown that it tends to maintain its biological cycle between 0 and 20°C *in vitro*, however the capacity to infect differs within this range: the optimal infective temperature is between 10 and 14°C (Estepa and Coll, 1997; Gaudin et al., 1999; Isshiki et al., 2002; Vo et al., 2015). At low temperatures (i.e., $\leq 5°C$), infection occurred at a slower rate and at temperatures of approximately 25°C, infection did not occur (Isshiki et al., 2001; Vo et al., 2015). Temperature affects the virus' capacity to infect and use the host's cells by influencing the viral protein functionality, which is principally linked to fusion activity (Gaudin et al., 1999). These previous studies *in vitro* correlate with infection studies *in vivo* in which, depending on the genotype and species used, mortalities occurred between 8 and 25°C; suggesting a narrow temperature range to facilitate the disease. Optimal *in vivo* temperature for VHSv development is approximately 14°C in several species (Goodwin and Merry, 2011; Avunje et al., 2012; Goodwin et al., 2012), but some marine isolates exhibit greater mortalities between 8 and 10°C (Isshiki et al., 2002; Hershberger et al., 2013). This may be due to the fact that the infectivity of a virus strain may be enhanced by, and fish immunity compromised at, particular temperature ranges (Sano et al., 2009). These temperature–response differences seen between experimental designs may be explained partly by the greater biological complexity in experiments *in vivo*, principally related to immune response, in contrast to studies *in vitro*, which do not involve sophisticated immune components (Workenhe et al., 2010).

Future steps

Like other invasive species, a clear demarcation of the species range is critical to effective management. Although research and surveys have greatly informed the current status of VHSv in the Great Lakes region, many questions remain. At least 30 species have been found positive to VHSv in the Great Lakes region (Escobar et al., 2016), and it is necessary to identify further vulnerable fish species as well as transmission pathways, focusing on areas where susceptible species inhabit. Another important area of research is identifying which wild species are potential VHSv reservoirs. Surveys have detected key species in endemic areas (Mortensen et al., 1999; King et al., 2001; Skall et al., 2005; Frattini et al., 2006; Garver et al., 2013; Kim et al., 2013; Moreno et al., 2014; Ogut and Altuntas, 2014); however, additional effort is needed to identify important species in areas where VHSv has recently been detected or is still absent. This will allow researchers and managers to determine ideal "sentinel" fish species for long-term VHSv monitoring to inform early warning systems. Finally, a thorough evaluation of the >10 years of diagnostic testing history is needed to redefine the ongoing strategy for regulatory inspection and surveillance to ensure continued protection while minimizing costs (Gustafson et al., 2010).

Microorganism: Heterosporis

Heterosporis sutherlandae was initially detected by Sutherland et al. (2000) and D. Cloutman (personal communication) in the skeletal muscles of yellow perch (*Perca flavescens*) in the Great Lakes region. It is not clear if this microsporidian parasite is native or invasive but it has been reported in 45 waterbodies in the Great Lakes region, and has been identified as a disease of concern by the Great Lakes Fishery Commission (Phelps et al., 2015). Susceptible species include fishes important to aquaculture and sport fishing, such as walleye (*Sander vitreus*), rainbow trout (*Oncorhynchus mykiss*), and baitfish (Miller, 2009).

Members of the genus *Heterosporis* are spore-forming, unicellular, fish parasites that damage the skeletal muscle of susceptible fish hosts. Fish are exposed to the parasite by consuming infected fish or coming into contact with free-living spores in the water (Lom and Nilsen, 2003; Diamant et al., 2010; Al-Quraishy et al., 2012; Phelps et al., 2015). As the infection progresses, spores form intracellular sporphorous vesicles that rupture to release additional spores into the tissue (Figure 3). The result is a concave appearance of the fish, and a fillet that appears white or freezer-burned, has a soft and mushy texture, and is considered unfit for human consumption (Lom et al., 2000; Phelps et al., 2015). Spores are resistant

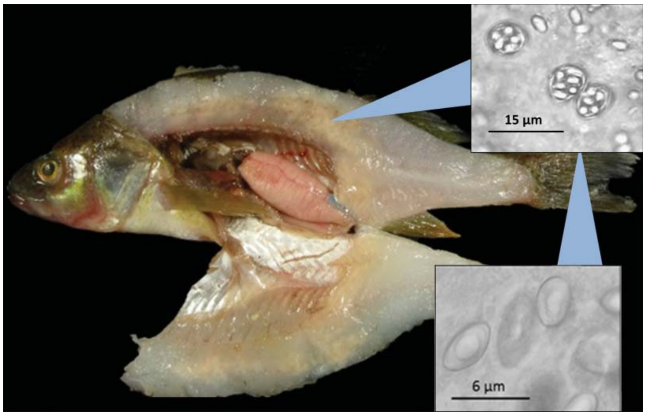

Figure 3. Heterosporis infection. Yellow perch (*Perca flavescens*) from Leech Lake with *H. sutherlandae* and characteristic muscle lesions; spores and sporophorous vesicles 400× (first insert) and spores at 1000× (second inset).

to standard laboratory disinfection procedures and can survive outside of a host for up to six months (Miller, 2009).

Current efforts

Current research has identified *H. sutherlandae* as unique with less than 96% rRNA gene sequence identity to other *Heterosporis* species, and has confirmed infection in yellow perch, northern pike (*Esox lucius*) and walleye (*Sander vitreus*) from inland lakes in Minnesota and Wisconsin (Phelps et al., 2015). Field collection is underway to identify host-specific factors (such as weight or age) or environmental factors (such as temperature) which may influence the spread or severity of *H. sutherlandae*. Concurrent laboratory infection trials are estimating pathogen transmission and virulence, and measuring physiological effects on the host of *H. sutherlandae* infection (M. Tomamichel, personal communication). A yield model is also in development using parameters estimated from experimental and field observations to predict the loss of harvest of yellow perch due to *H. sutherlandae* (P. Venturelli, personal communication).

Future steps

This parasite poses a threat to both farmed fish and wild populations. Because of the resistant nature of spores, *H. sutherlandae* could be difficult to eradicate in either a farm or natural environment. Once established, the pathogen could reduce harvest yield significantly. In addition, it would be difficult to prevent transfer to naïve populations by human or natural vectors. Therefore, the broad areas with potential to spread *H. sutherlandae* within fish populations in the region make it necessary to develop informed, evidence-based management and monitoring strategies (Escobar et al., 2017).

Alga: Starry stonewort

Starry stonewort (*Nitellopsis obtusa*; family Characeae) is a dioecious green alga that gets its namesake from the starchy, star-shaped bulbils that develop on its stem nodes and rhizoids for asexual reproduction (Bharathan, 1987; Lambert, 2009; Figure 4). Sexual reproduction via oospores is less prevalent in the dioecious taxa of Characeae, but starry stonewort has been documented to reproduce sexually under eutrophic conditions (Bharathan, 1983). Interestingly, only male specimens have been documented in starry stonewort's invaded range to date (Sleith et al., 2015). This suggests it is relying exclusively on the asexual growth of bulbils and fragments for its spread. Starry stonewort is a charophyte, but it is similar to many invasive macrophytes in its ability to form monocultures and persist at nuisance growth levels in the littoral zone (Hackett et al., 2014).

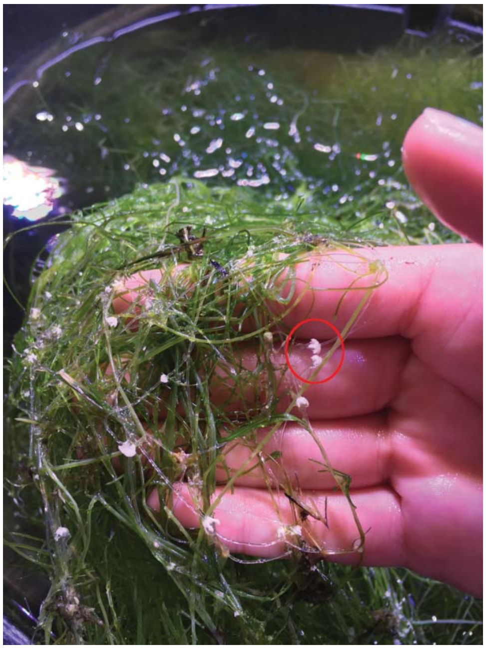

Figure 4. Starry stonewort (Nitellopsis obtusa). Note the bulbils (white structure inside red circle) attached to rhizoids (green structures). This image corresponds to a captive alga population under study at Minnesota Aquatic Invasive Species Research Center.

Starry stonewort is native to Europe and Asia (Kato et al., 2014), and is established as an invasive species in many lakes of the Great Lakes basin (Escobar et al., 2016; Figure 5). The introduction of starry stonewort to North America is widely hypothesized to be from the ballast water of transatlantic ships (Hackett et al., 2014). Starry stonewort was first documented in New York in the St. Lawrence River system in 1978, and subsequent invasion have since been documented in Michigan (1983), Indiana (2008), Pennsylvania (2012), Wisconsin (2014), Vermont (2015), and Minnesota (2015) (Sleith et al., 2015; Escobar et al., 2016; Kippt et al., 2017).

Starry stonewort is used in many cytological studies due to its large cell size, but research on the ecology and biology of this species is severely underrepresented in the literature (Hackett et al., 2014). Initial detection of starry stonewort has often occurred inadvertently during routine plant surveys or from citizen reports to state agencies (Hackett et al., 2014; Kipp et al., 2014). For example, the first confirmed report of starry stonewort in Minnesota showed that growth of the alga spanned 53 acres of a lake, suggesting it may have persisted there for some time without being reported (MNDNR, 2015). Starry stonewort is very similar in appearance to native

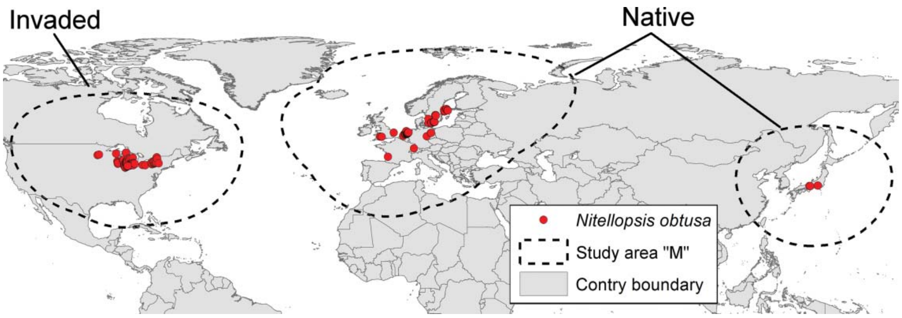

Figure 5. Native and invaded ranges of starry stonewort (Nitellopsis obtusa). Occurrences of starry stonewort (red points) resembling the global distribution of the species including the native and invade range of North America. Figure from Escobar et al. (2016) (Creative Commons Attribution 4.0 International License).

Muskgrasses (*Chara*; family Characeae), which further complicates identification and early detection efforts. Detection of starry stonewort on a case-by-case basis could limit the opportunity for early detection and rapid response management strategies. A coarse-scale ecological niche model of starry stonewort, based on climatic variables, has identified areas suitable for its establishment and further expansion across North America (Escobar et al., 2016).

Current efforts

Current research involves studying starry stonewort's ability to grow and spread, as well as assessing the efficacy of current chemical and mechanical management strategies used for its control. It is uncertain how long bulbils and fragments of starry stonewort can remain viable out of water; research to quantify these parameters is ongoing at the Minnesota Aquatic Invasive Species Research Center (MAISRC) at the University of Minnesota and includes desiccation trials for bulbils and fragments, complemented with field experiments to determine the survival of the alga in boats and, in turn, spread by boater-assisted movement. Quantifying the desiccation tolerances of aquatic invasive plants is useful for characterizing expansion risk and preventing spread, and it has been investigated for other species including Eurasian watermilfoil (*Myriophyllum spicatum*) and curly-leaf pondweed (*Potamogeton crispus*) (Bruckerhoff et al., 2015). These experiments will inform management decisions regarding the placement and efficiency of boat launch monitoring personnel (Bruckerhoff et al., 2015). This information will be key to limiting and/or preventing further starry stonewort spread. Site characteristics of known starry stonewort occurrences are being aggregated to define the ecological parameters needed for its establishment. Because so little is known about starry stonewort, adaptive management is critical for ongoing treatments. The outcomes of starry stonewort treatments in Minnesota are being monitored in the field and in the lab. Starry stonewort was treated in Lake Koronis (Stearns County, MN, USA) during the summer of 2016 by mechanical harvest and algaecide applications. Bulbils from treated areas and an untreated control area were collected to asses sprouting, and field surveys were conducted to monitor biomass and bulbil density. Results of this research showed that although biomass was reduced following treatment, bulbils retained sprouting ability regardless of treatment (Glisson et al., in review).

Future steps

While there are many anecdotal observations regarding the impacts of starry stonewort, scientific conclusions backed by research and robust data are lacking. There are still major gaps of knowledge for this species, which hinders effective management. Applied ecological research is needed to understand starry stonewort's impacts on native plant communities, fish populations, and ecosystem functions. An effective control for this species, especially one that is capable of inducing bulbil mortality, is needed and collaborations between entities of invaded states may accelerate research leading to quicker management turnarounds.

Invertebrates: Zebra mussels

Benefiting from shipping traffic, commercial fishing, and the creation of canals connecting inland lakes, zebra mussels (*Dreissena polymorpha*) started to spread in Europe almost two centuries ago (Karatayev et al., 1998, 2003). The species was then introduced to North America, first into the Great Lakes in the mid-1980s in ballast water discharge of transatlantic boats (Hebert et al., 1989; Carlton 2008). By 2010, zebra mussels were found in more than 600 lakes and rivers across 26 U.S. states (Benson, 2014) and are one of the world's most economically and ecologically damaging aquatic invasive species. Costs associated with the control and management of zebra mussels in the hydropower industry and drinking water treatment plants (e.g., of mechanical and chemical treatments to remove mussels, training of personnel, reconstruction and retrofitting, lost production, among others) were estimated to be about $18 million per year from 1989 to 2005 throughout North America (Connelly et al., 2007; Chakraborti et al., 2014). Zebra mussels clog the water intake pipes of industrial facilities (Prescott 2010), compete with and smother native bivalve species (Karatayev et al., 1997; Lucy et al., 2014), and restructure aquatic food webs (Bootsma and Liao, 2014; Higgins and Vander Zanden, 2010; Mayer 2010). The dispersal ability and invasiveness of zebra mussels are due to their high fecundity, highly dispersive planktonic larval stage, attachment of adults to hard substrata via byssal threads, and from the ability of these mussels to reach such high densities that their total filtering capacity can remove 50% or more of the biomass of phytoplankton at the base of aquatic food webs (Hebert et al., 1989; Mackie, 1991; Higgins and Vander Zanden, 2010; Strayer, 2010).

Current efforts

Although the cumulative number of infested lakes has reached a plateau in several U.S. states in recent years (Figure 6), the number of infested lakes is increasing yearly in Minnesota (and perhaps Wisconsin) where zebra mussels continue to actively spread to new inland lakes. As a consequence, there is the potential to benefit greatly from targeted prevention in the Great Lakes region. Investigating the sources and pathways of zebra mussel spread is a key approach to prevent further introduction and is essential for effective measures to be taken (Estoup and Guillemaud, 2010).

To identify pathways of spread, population genetics is a powerful tool that has proven its ability to infer sources and routes of invasion in many cases of invasion worldwide, across diverse taxa. This is true despite recent arrival and short histories of many of the studied invasions (Lombaert et al., 2010; Ascunce et al., 2011; Rius et al., 2012; Perdereau et al., 2013). Traditional population genetic analyses (Weir and Cockerham, 1984; Saitou and Nei, 1987; Pritchard et al., 2000; Paetkau et al., 2004) coupled with approximate Bayesian computation analyses (Beaumont et al., 2002), a major step forward in the field (Miller et al., 2005; Pascual 2007), have allowed researchers to begin to draw inferences about the source waterbodies responsible for invasion outbreaks, and to evaluate useful contrasts of alternative invasion scenarios along with the statistical confidence in the scenarios preferred. In the Great Lakes region, these tools are now helping to identify waterbodies that serve as sources for spreading zebra mussels to new inland lakes, which may provide insight into important spread mechanisms or vectors (e.g., spread by veliger larvae in water moved from lake to lake by fishing boats, or by adult and juvenile mussels transported on boat lifts and other equipment). For instance, Mallez and McCartney (in review [Invasion population genetic model testing succeeds at small spatial scales: testing scenarios of spread for zebra mussels between Minnesota lakes]) have provided unexpected insights into the absence of large inland lakes (previously thought to be "super-spreaders") contributing to secondary spread and have started to examine the causes of the clustering of zebra mussel invasions – a pattern common in both European and North American invaded ranges (Kraft et al., 2002; Johnson et al., 2006).

Ongoing research aims also to develop rational approaches to population control in open waters, using molluscicides that are known to be highly toxic to zebra mussel adults and larvae, with relatively few nontarget effects if used responsibly (M. McCartney, personal communication). Across the United States, a handful of treatment attempts using both mechanical and chemical methods, and targeted at early stage invasions, have either successfully controlled (i.e., suppressed population growth and recruitment) or extirpated small infestations, thereby preventing explosive population growth (Wimbush, 2009; Fernald and Watson, 2014). These findings motivated a recent treatment attempt of a small isolated infestation in Christmas Lake in Minnesota (Lund et al., in press) that has not yet eradicated the zebra mussel population but has generated considerable new information about how to best conduct and evaluate the effectiveness of pesticide treatment efforts. Four ongoing open-water treatment attempts in Minnesota by the Minnesota Department of Natural Resources and MAISRC will provide more information to develop ways to best evaluate the outcomes and use them to improve zebra mussel management efforts. Just a few years ago, management was not considered to be an option for zebra mussel invasions, but attitudes may be slowly changing as this new research moves forward.

Future steps

The small geographic scale of the ongoing investigations into the population genetics of zebra mussel in the Great Lakes region makes inferences particularly challenging, as does the fast spread to inland lakes (post-2005). So far, analysis has focused on typical numbers of standard markers (i.e., nine microsatellite loci; S. Mallez and M. McCartney, personal communication). Studies conducted at MAISRC have turned to Single Nucleotide Polymorphisms (SNPs) and high-throughput genotyping

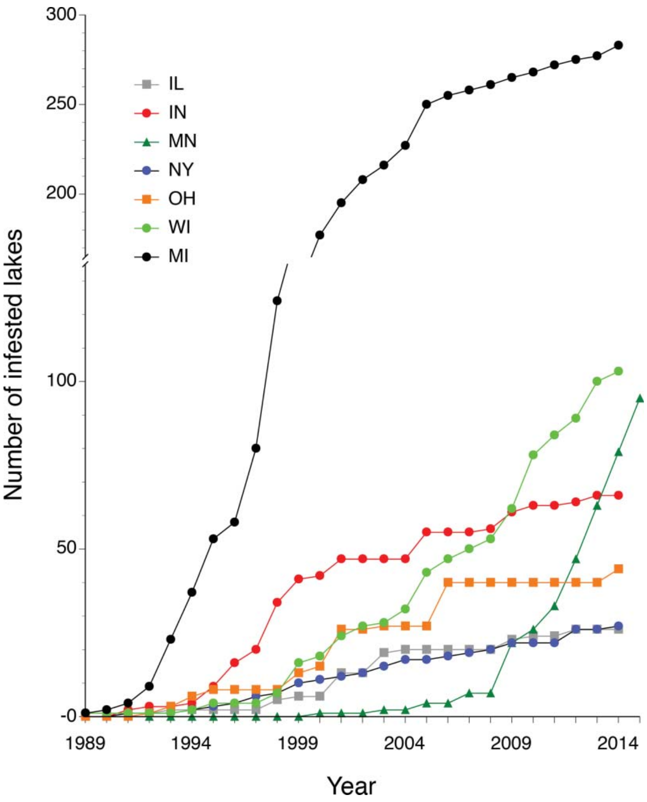

Figure 6. Pattern of spread of zebra mussels to U.S. inland lakes. The cumulative number of infested lakes is plotted against the year of infestation. The earliest date with confirmed presence of Zebra mussels was used as the date of first infestation. Only the U.S. states having more than 25 infested lakes are shown. They are: Illinois (IL), Indiana (IN), Minnesota (MN), New York (NY), Ohio (OH), Wisconsin (WI) and Michigan (MI). Data from Minnesota were obtained from the MN Department of Natural Resources. Data from other states were obtained from the US Geological Survey. From Mallez & McCartney, in review. The top trace shows the state with the greatest number of lakes infested (> 250, Michigan). This trace is shown with an axis break in order to be able to expand the scale for all the other states, with fewer lakes infested (< 100), so that their pattern of infestation can be viewed on the same figure panel.

by Next Generation Sequencing technologies known as Sequence Based Genotyping (Andrews et al., 2016), which is capable of generating large numbers of SNPs covering the entire genome. SNPs can detect finer genetic structure than typical genetic markers (e.g., microsatellite, Jeffries et al., 2016), and when several to hundreds of thousands of SNPs are assayed, these markers can provide geographic resolution at a scale similar to that of a U.S. state (Elhaik et al., 2014). The genomic resources from ongoing studies, including the sequence of the zebra mussel reference genome (M. McCartney and S. Mallez, personal communication), will create other opportunities such as identifying genes that control processes that could be targeted with gene-editing technologies (Gantz and Bier, 2015).

Vertebrates: Common carp

The common carp or (*Cyprinus carpio*) is one of the most invasive and ecologically destructive fishes in the world (Vilizzi et al., 2015). It is one of nine species of fish included among the world's 100 worst invaders (http://www.issg.orgnfo/worst100_species.html). Native to Eurasia, common carp have been introduced to all continents except Antarctica (Balon, 1995). Although the common carp is ubiquitous in many regions of the world, it is especially widespread and abundant in North America and Australia, where its biomass commonly exceeds 400 kg/ha (Bajer et al., 2009; Matsuzaki et al., 2009). Common carp feed in benthic sediments sorting out edible items (insect larvae, plant seeds, etc.) using a specialized sensory organ (palatal organ) and cross-current filtration. By aggressively feeding in the lake bottom, common carp uproot aquatic vegetation, increase turbidity, and increase transport of nutrients from the sediments into the water column (Zambrano et al., 2001; Bajer et al., 2009). Excessively abundant (>100 kg/ha), common carp can "flip" shallow lakes from a clear water state with submerged aquatic vegetation into turbid systems that lack aquatic vegetation and are dominated by algae and cyanobacteria (Zambrano et al., 2001). This leads to reduced numbers of waterfowl, amphibians (often through predation on tadpoles), insects, and possibly also fish. Lakes that lack aquatic vegetation also have reduced capacity to store or transform nutrients, thus carp contribute to excessive nutrient export out of watersheds they invade. It has been estimated that common carp are a major factor of degradation of 70% of lakes within the Great Plains Ecoregion in North America.

Current efforts

In North America, common carp are managed primarily by physical removal, treating lakes with nonspecific fish toxin (i.e., rotenone), and water draw-downs. Winter seining is the most effective form of removal because common carp form dense winter aggregations that can be located using telemetry and removed using large seine nets (Bajer et al., 2011; Figure 7). This strategy can be very effective and selective but is limited to lakes in which common carp only infrequently produce young due to native fish predation (Lechelt and Bajer, 2016). The use of rotenone and draw-downs are applied less often as they kill all fish in lakes and particularly for the draw-downs, are possible only in lakes with engineered outlets. In Australia, where physical removal is not effective due to large, connected river systems and high rates of recruitment, common carp control has focused on

Figure 7. Winter seining for carp in a lake in Minnesota after baiting using corn in a square drilled through the ice.

developing genetic technologies (e.g., daughterless, female-lethality) and the use of pathogens (Cyprinid herpesvirus-3, KHV) both of which remain in developmental stages (McColl et al., 2014; Thresher et al., 2014). Overall, aside from lakes in which common carp can be controlled using winter removal or those that can be dewatered/poisoned, there are no sustainable common carp control strategies.

Future steps

New understanding of the life history and cognitive abilities of common carp offers new control possibilities. Biocontrol appears to be a viable strategy in many lakes in the Great Lakes region and across other temperate regions of North America. Indeed, studies of common carp recruitment showed that in some lakes in Minnesota, common carp are unable to produce young because native predatory fishes, such as the bluegill sunfish (*Lepomis macrochirus*) that consumes common carp eggs and larvae. As common carp evolved spawning migrations that access predator-free habitats, such as shallow marshes prone to winter hypoxia, predator escape was achieved (Bajer and Sorensen, 2010; Bajer et al., 2012, 2015). This allows for several possible control strategies. First, some marshes can be aerated to stabilize native predators. Second, migratory routes can be exploited to remove adults that move to marshes or block juveniles that migrate from marshes to lakes. New autonomous transport systems developed for salmonids in the western United States are currently being developed at MAISRC to remove carp. Perhaps even more exciting is the possibility that cognitive aspects of common carp's foraging behavior could also be exploited to develop selective toxin delivery systems. Common carp are known to consume grain-based products, such as corn, that are not consumed by most species native to North America. They can be conditioned to aggregate in specific areas of lakes by systematic application of such baits (Bajer et al., 2011). There is an opportunity to condition (train) common carp to consume baits that are selective to them and then switch the baits with ones that contain a toxin (such as Antimycin A; Marking, 1992). This effort is also currently being pursued at MAISRC. Finally, new genetic technologies are being developed to make male common carp sterile (P. Bajer, personal communication). Integrated strategies that employ various tools that target specific weaknesses in life history and behavior offer the most promises, and their effectiveness has already been demonstrated in model systems of lakes.

Novel opportunities for AIS management

Most of the current approaches for the management of the invasive vertebrate species like the common carp include physical removal and whole lake poisoning. These approaches are nonspecific, impacting both the invasive and the native fish, and are also relatively inefficient in regions with low density of invading individuals (e.g., the invasion front; ACRCC, 2014). Approaches including pheromones, environmental DNA, or eDNA, and sound application are highly species-specific, and will greatly enhance the chances of early detection of few individuals at the invasion front.

Early detection research-pheromones

Measuring the presence/absence of a species in a natural environment is a key factor in assessing the spread of invasive species (ACRCC, 2014), and therefore, our ability to target prevention and control efforts. This is particularly important in regions where the invaders occur at low densities. Recent studies have recognized the potential of measuring chemical signals, like pheromones, that can be used to detect the presence of a species in a natural environment (Xi et al., 2011; Stewart and Sorensen, 2015; Sorensen and Johnson, 2016). Released by animals, pheromones are chemical signals which readily disperse in the natural environment (Wyatt, 2014). Fish heavily rely on pheromones for the purpose of shoaling with conspecifics, upstream migration, and to select mates during the spawning period (Sorensen and Johnson, 2016). Several techniques are being developed to measure fish pheromones and proof-of-concept studies have had some success (Fine and Sorensen, 2005; Xi et al., 2011). However, measuring pheromones in natural environments has been mostly limited to the invasive sea lampreys (*Petromyzon marinus*; Xi et al., 2011). Nonetheless, with the progress being made in this field, i.e., identification of sex pheromones in different fish species, measurements in natural waters could become a reliable tool to inform the presence and sexual maturity of species of interest.

Most of the traditional methods (netting and electrofishing) used in locating the invasive fish are non-species specific (Sorensen and Johnson, 2016), expensive, (Bajer et al., 2011), and less efficient in low-density areas (ACRCC, 2014). Recent trends to measure biochemical and molecular markers in natural environments are appealing due to the species-specific nature of these markers and the relative ease in collecting water samples. For instance, eDNA that is released by fishes, can now be measured with extreme sensitivity (Jerde et al., 2011; Eichmiller et al., 2014; Gingera et al., 2016) and has been widely used to detect the presence of invasive carp (Jerde et al., 2013). Like eDNA, measuring pheromone concentrations could provide valuable information on the presence or absence of fish while adding new information on reproductive condition. It is important to note, however, that multiple pheromone candidates and eDNA markers need to be targeted to detect multi-species assemblages.

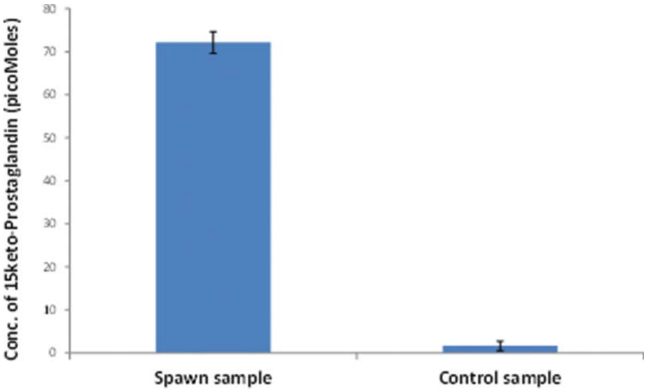

Figure 8. Concentration of 15-Keto-ProstaglandinF2α measured in lake water samples. Samples collected for hormone measurements from spawning aggregation (spawn sample) and 100 meters away from the aggregation (control) in Wasserman Lake, Minnesota. Spawning aggregations typically consisted of 3–4 males and 1–2 females. Source: Modified from Sorensen and Johnson (2016).

Of special interest to analysis is prostaglandin F2α (PGF2α) and its metabolite, 15-keto PGF2α (Figure 8), which drive ovulation and sexual behavior in all female carp and serve as female pherormone in both common and bigheaded carp (*Hypophthalmichthys nobilis*) (Stacey, 2003). These species release PGF2α and its metabolites, but in species-specific ratios (Sorensen and Johnson, 2016). Thus, measuring a combination of products will help determine the presence of a particular species. Further, to develop pheromone measurements as a biomarker to indicate the distribution and abundance of invasive fish, research should be directed towards determining the degradation rates and dilution effects of these compounds in natural environments.

Prevention research-bubble curtains

Abundance of common carp in Midwestern North America appears to be attributable to the tendency of adults to leave lakes and use wetland habitats for spawning, where predator densities are low, and of juveniles to return to the lakes (Bajer and Sorensen, 2010). Disrupting this bi-directional movement could provide significant gains towards long-term carp control. Although upstream movement of adults can be prevented by temporary physical screens (Chizinski et al., 2016) or electrical barriers (Verrill and Berry, 1995), such technologies are ill-suited to stop small downstream-moving juveniles because fine screens clog and fish can drift past an electric field. Behavioral deterrents (i.e. light and sound) could provide a safe and inexpensive solution for such applications (Noatch and Suski, 2012). In

Figure 9. Bubble curtain. Upstream view of bubble curtain tested in Zielinski and Sorensen, (2015) in Kohlman Creek, Minnesota (45°01′36″ N 93°02′48″ W). Upstream of the bubble curtain is a wetland used by carp for spawning; a chain of lakes is downstream. The bubble curtain blocked up to 60% of juvenile common carp moving downstream.

particular, sound has special promises since common carp have well-developed hearing abilities (Ladich and Fay, 2013) that are superior to many native fish in the Great Lakes region.

A bubble curtain is one behavioral deterrent that produces acoustic and hydrodynamic stimuli which could be deployed inexpensively in small streams that connect lakes and wetlands, which are common in the Great Lakes region. In the laboratory, juvenile common carp movement through a circular channel was reduced by 75–80% with a bubble curtain when air flow and bubble size were optimized for sound production (Zielinski et al., 2014). The same system blocked up to 60% of downstream swimming juvenile carp in a stream connecting a wetland and a lake (Zielinski and Sorensen, 2015; Figure 9). Avoidance responses to bubble curtains appear to be species specific as both walleye and muskellunge were shown to be minimally deterred by bubble curtain systems (Flammang et al., 2014; Stewart et al., 2014). Ultimately, bubble curtains are an inexpensive tool for sites where reductions in common carp movement, not total elimination, is the goal.

Bubble curtain efficacy could be improved by combining them with additional stimuli like sound from underwater speakers or strobe lights (Perry et al., 2014). Using bubble curtains to deflect rather than block movement can reduce air flow requirements (Zielinski and Sorensen, 2016) or facilitate the use of traps to remove carp. A similar electric deflection screen and trap system was found to be effective in sea lamprey control (Johnson et al., 2016). Future studies should continue to examine nontarget species responses and how moderate reductions in passage could be integrated into common carp management schemes.

AIS control research-human-dimensions

The social aspects of invasive species management are receiving renewed attention (Tassin and Kull, 2015). Although social aspects of invasive species are classically thought of in terms of how humans mediate the spread of invaders and how that can be reduced (Clout and Williams, 2009), there is a growing realization of the importance of values-based judgments within many different aspects of invasive species management. Many invasive species management decisions contain values-based judgments and have the potential for conflict, from defining what species are invasive, to determining when a particular management action is worth the required resources and what degree of nontarget effects of management actions are acceptable (Carballo-Cardenas, 2015). For example, although scientific studies can identify how an invasive species may impact native species, it is fundamentally a values-based choice to determine when inconsequential change becomes significant harm and what resources should be expended to address or prevent that harm (Sagoff, 2009). There have been calls to more explicitly identify and reflect upon the values-based nature of invasive species management (Larson and Kueffer, 2013).

Two key ways to address the values-laden nature of invasive species management are ecological risk assessment and qualitative inquiry into problematic invasive species management issues. First, ecological risk assessment provides a way to inform management priorities by characterizing risk in a way that synthesizes existing scientific knowledge with transparent values-based judgments about the management context (U.S. EPA, 1998). For example, risk assessment makes explicit key values-based judgments, such as what ecological entities are most valued and important to assess, what is considered harmful to those entities, and what spatial and temporal scale is being considered. Risk assessment for invasive species can take place at a variety of scales, degrees of formality, and levels of participation, but it is generally concerned with determining the likelihood of introduction, establishment, or spread of a species, and the resulting probability and severity of economic, ecological, or human health consequences (Anderson et al., 2004). Risk assessments for AIS have been conducted at national and regional scales to help inform invasive species management (Kolar et al., 2007; Cudmore et al., 2012). To support efforts to inclusively and reflexively arrive at necessary values-based judgments within invasive species risk assessment, the risk assessment process can be opened to a deliberative process with a broad range of participants (e.g., academic and agency researchers, state and federal managers, and stakeholders; Stern and Fineberg, 1996). Focus groups, surveys, and expert workshops can all be used during a risk assessment process to arrive at key values-based judgments informing risk assessment and to characterize the risk itself. A participatory risk assessment that drew upon these methods was used to help better understand the impacts from, and prioritize management for silver (*Hypophthalmichthys molitrix*) and bighead carps in the Great Lakes region (Kokotovich and Andow, 2017).

Another way to address the values-laden nature of AIS management, and the conflicts that may result, is to study conflicting case studies using qualitative methods (Carballo-Cardenas, 2015). In-depth interviews or focus groups with people involved with a particular management issue can help identify, reflect upon, and address key conflicts that hamper management. For example, in-depth interviews were used to study the tensions and conflicts impacting carp (*H. molitrix, H. nobilis, Ctenopharyngodon idelle, Mylopharyngodon piceus*) management in Minnesota (Kokotovich and Andow, 2017). These interviews revealed how scientific uncertainty (concerning the effects of carp and the efficacy and collateral damage of management actions) and social uncertainty (concerning the lack of societal agreement on how to respond to carp and the need to avoid acting out of apathy and/or fear) combine to complicate efforts to determine the desired path for carp research and management. These findings emphasized the need to reflect on questions such as: what level of certainty is required to act, what is the acceptable level of collateral damage from potential management actions, and how can we avoid apathy- and fear- based responses to Asian carp? Qualitative research like this is well-suited to explore the values-related challenges facing invasive species management with the necessary detail and nuance.

The need to deal with the values-laden nature of invasive species management will grow with the emergence of complex and conflictual invasive species issues. The need to incorporate social science expertise in invasive species management is apparent (Larson and Kueffer, 2013) from designing and conducting risk assessments that deal with values-based judgments to helping disentangle conflict-ridden management issues. Although the door has opened for this type of work, there is a need for it to grow and to be recognized as essential to productive AIS management.

AIS control research-microbe-mediated approaches

Interactions between AIS and microbes are potential targets for biological control and management strategies. Microbes, such as bacteria and fungi, could interact with AIS via several mechanisms, which could be pathogenic or mutualistic in nature (Kowalski et al., 2015). For example, the introduced AIS might initially encounter fewer pathogens in its new habitat, although it is likely that the number of novel pathogens would increase over time. In addition, the AIS might colonize a new habitat with or without their native mutualist, or with a novel mutualist that could enhance its competitive ability and invasiveness.

Several steps have been proposed to develop microbe-mediated AIS management approaches (Kowalski et al, 2015). The first step is characterizing the microbial communities associated with AIS and native species, across time and space. The advent of high-throughput sequencing technologies has enabled an in-depth understanding of host-associated microbial communities when compared to traditional culture-based methods. Recently, several studies utilized this approach to elucidate microbes associated with invasive carp species, including common carp, bighead carp, silver carp, and grass carp (*Ctenopharyngodon idella*; van Kessel et al., 2011; Wu et al., 2012; Li et al., 2014, 2015; Ni et al., 2014; Ye et al., 2014; Eichmiller et al., 2016). Similar studies must be performed on other high priority AIS such as Eurasian watermilfoil, curly-leaf pondweed, hydrilla (*Hydrilla verticillata*), zebra mussels, and quagga mussels (*Dreissena bugensis*). Second, elucidating the functional contribution of specific microbes towards the fitness and competitive ability of AIS. Third, targeting key AIS–microbe interactions for control or enhancement. Finally, evaluating the efficacy and feasibility of each control method under field conditions. These studies would help to better inform the use of microorganisms for AIS control, reducing our current dependency on chemicals and manual removal.

Final remarks

The Great Lakes region of the United States is of great ecological and economic importance. Unfortunately, these sometimes-fragile ecosystems have a high vulnerability to aquatic invasive species, which can result in both expensive and irreversible damages. Invasive species that pose threats to this region range from enormous fish such as bighead carp to microscopic pathogens such as VHSv. This vast diversity of species and taxa among AIS that are present in the Great Lakes region adds great complexity to control and management issues. Therefore, a dedicated response to these issues across many levels – from research to implementation – is crucial. Finding solutions to AIS will require not only scientific advancement, but also personal responsibility, adaptation of norms, informed policy, and effective agency management. Additional research from partners across the region and the globe will be critical. As illustrated, there are numerous ongoing studies to address AIS. By developing an in-depth understanding of the biology and ecology of AIS, we can discover weaknesses in their life cycles that can be targeted for control. Indeed, targeting the vulnerability of an invader's biology has worked (e.g., sea lamprey in the Great Lakes; http://www.seagrant.umn.edunfo/aisnfo/sealamprey_battle), and it can work for other AIS as well. Aquatic invasive species are a vexing problem and managers must be equipped with robust information and effective tools to mobilize citizens who care about the quality and integrity of inland waters.

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