Request for Funding

Lessard-Sams Outdoor Heritage Council
Fiscal Year 2015 / ML 2014

Program or Project Title: Statewide AIS Facilities and Equipment

Funds Requested: $25,182,900

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County Locations: No Counties Listed

Ecological Planning Regions:

- Northern Forest
- Forest / Prairie Transition
- Southeast Forest
- Prairie
- Metro / Urban

Activity Type:

- Protect in Fee
- AIS inspection and decontamination for Publically Protected Aquatic Habitat

Priority Resources Addressed by Activity:

- Habitat

Abstract:

This proposal would provide grants to local and tribal government units and the MN DNR for AIS inspection/decontamination facilities and equipment enabling their efforts to stop the spread of AIS, thereby protecting fish habitat and waterfowl from the AIS threat.

Design and Scope of Work:

AIS pose the biggest threat to Minnesota's waters. Our proposal focuses primarily on zebra/quagga mussels due to their damaging ecological impacts on the fish habitat, while our proposed solutions address zebra/quagga mussels plus other AIS transported by humans.

AIS scientists view “transport by people” as the primary vector for the spread of zebra mussels and many other AIS; not waterfowl as per popular myth. [Attachment#105]

The problems…

Problem #1: Long-term impact to fish habitat from zebra/quagga mussels

Zebra/quagga mussels "have the ability to change aquatic ecosystems including native plant and animal populations. The amount of food the mussels eat and the waste they produce has negative effects on the ecosystem and can harm fisheries. As filter feeders, these species remove large amounts of microscopic plants and animals that form the base of the food chain, reducing available food for native aquatic species. Zebra mussels attach to and encrust native organisms, essentially smothering them and removing more animals from the food chain." [Attachment#100]

"Most of the impacts of zebra mussels in freshwater systems are a direct result of their functioning as ecosystem engineers (Karayayev, *et al*. 2002). An individual zebra mussel can filter one to two liters of water each day; as a result high densities of zebra may cause major shifts in the plankton communities of lakes and rivers. Reductions in phytoplankton numbers and biomass also limit food to fish larvae and other consumers further up the food chain (Birnbaum 2006)". [Attachment#130]

The Great Lakes has suffered from zebra and quagga mussels for over 20 years and may be a predictor of our future if we are unable to stop the spread of AIS. Research has found that the "biodiversity of the Great Lakes ecosystem has been devastated by zebra mussel colonization as evidenced by declines in native clam populations and the loss of spawning habitat for some native fish species." [Attachment#120]

Problem #2: Likely secondary effects on waterfowl

Scientists with the U.S. Geological Survey think a complex interplay of invasive species may be the cause of the mass die-offs. "The researchers suspect invasive zebra and quagga mussels create ideal conditions in Lake Michigan for the bacteria that produces botulism toxin. The mussels filter the water so it's incredibly clear, allowing an algae called cladophora to grow in huge amounts. Storms churn up the algae, which settle to the lake bottom and rot. That creates an environment without any oxygen, an ideal home for bacteria that produce botulism. The toxin is ingested by tiny worms and freshwater shrimp, which are eaten by fish, including the invasive round goby, which are then eaten by diving birds -- including loons". [Attachment#110] [Attachment#115]

Problem #3: Unavailability of decontamination capability

While education, with emphasis on personal responsibility is essential, the means for residents and visitors to decontaminate must be made reasonably convenient and available. Unfortunately, it is not and most people who want to do the right things simply cannot, harming our efforts to stop the spread.

The strategies to address the problems…

Strategy #1: Stop or at least slow the spread of AIS.

Inspection and decontamination has the greatest short-term potential for stopping the spread of AIS. While not ideal, slowing the spread would still bring positive benefits; buying time for research and keeping the problem constrained awaiting more-effective solutions.

Strict controls on boat launches in other states have been effective in halting new AIS introduction into valued water resources in western states and in particular at Lake Tahoe.

Strategy #2: Deploy cost-effective inspection and decontamination models.

Inspecting and decontaminating at 2,000 public landings is cost prohibitive, however current AIS statutes allow for more cost-effective shared services models (regional inspection) serving multiple lake or accesses. Our proposal will use a combination of dedicated "at the access" and shared "regional" inspection and decontamination stations.

Strategy #3: Widely deploy decontamination capabilities.

Commissioner Landwehr's focus on personal responsibility becomes a reality with available and convenient decontamination stations. Our proposal would increase decontamination units from 20 today to over 177 statewide.

Strategy #4: Leverage and enable local efforts.

Many local groups are ready to act, but virtually all are hampered by a lack of facilities and equipment. The following local groups can be leveraged through this proposal:

- Local and Tribal Units of Government
- Volunteers
- Commercial interests

Our proposed solution…

Solution Component #1: Grant funds for up to 127 shared AIS inspection and decontamination stations.

This would enable local and tribal units of government, and the DNR to acquire the land, build-out, and equip regional AIS stations for inspections and decontamination. Deployment support would ensure consistency and success.

Solution Component #2: Grant funds for equipping up to 50 dedicated AIS stations with decontamination equipment.

These higher volume facilities already exist and many are owned by the DNR, but the majority does not have available decontamination units.

Expected Opposition

Opposition to inspection/decontamination procedures exists today and will grow with wider deployment. The opposition should fade in time.

Immediate attention is needed…

Over 17 new lakes and hundreds of river miles were designated infested in 2012 and 2013.

Over 100 waters have zebra mussels, including some premier fisheries and recreational lakes.

Quagga mussels are more harmful than zebra mussels, and are in the Mississippi River in Lake Pepin and the Lake Superior Harbor, but not yet in inland lakes.

Up to 36.8% of random boaters were caught violating Minnesota's AIS laws in 2012.

Most AIS, and zebra mussels in particular, spread downstream naturally. Connected lakes and streams are routinely infested within a few years, e.g. Le Homme Dieu Chain of Lakes.

A zebra mussel infestation typically begins 3 years before the DNR finds adult zebra mussels and declares the water "infested." Waters now being declared "infested" were in fact infested with veligers up to 3 years ago. This 3-year lag complicates knowing which lakes are at risk of damaging other lakes.

With infestations in Itasca County one has to ask: "are the Boundary Waters next?" Big Sand Lake now has zebra mussels and is connected with the Rainy River.

While there is no clear guide to how and when zebra and quagga mussels will affect any given lake, the science is clear that habitat damage will occur. Avoiding the damage can only come from avoiding infestation.

Planning

MN State-wide Conservation Plan Priorities:

- H4 Restore and protect shallow lakes
- H6 Protect and restore critical in-water habitat of lakes and streams

Plans Addressed:

- 100th Meridian Initiative

LSOHC Statewide Priorities:

- Address Minnesota landscapes that have historical value to fish and wildlife, wildlife species of greatest conservation need, Minnesota County Biological Survey data, and rare, threatened and endangered species inventories in land and water decisions, as well as long-term or permanent solutions to aquatic invasive species
- Are ongoing, successful, transparent and accountable programs addressing actions and targets of one or more of the ecological sections
- Attempts to ensure conservation benefits are broadly distributed across the LSOHC sections
- Ensures activities for "protecting, restoring and enhancing" are coordinated among agencies, non profits and others while doing this important work; provides the most cost-effective use of financial resources; and where possible takes into consideration the value of local outreach, education, and community engagement to sustain project outcomes
- Leverage effort and/or other funds to supplement any OHF appropriation
- Produce multiple enduring conservation benefits
- Use a science-based strategic planning and evaluation model to guide protection, restoration and enhancement, similar to the United States Fish and Wildlife Service's Strategic Habitat Conservation model

LSOHC Prairie Section Priorities:

- No Prairie Section Priorities Listed

LSOHC Forest Prairie Transition Section Priorities:

- No Forest Prairie Transition Priorities Listed

LSOHC Northern Forest Section Priorities:

- No Northern Forest Priorities Listed

LSOHC Metro Urban Section Priorities:

- No Metro Urban Priorities Listed

LSOHC Southeast Forest Section Priorities:

- No Southeast Forest Priorities Listed

Relationship to Other Constitutional Funds:

- No Relationships Listed

Accelerates or Supplements Current Efforts:

Grass-roots efforts are pushing LGU's to help stop the spread of AIS. The occasional finger-in-the-dike approach is no longer acceptable and complete AIS programs are being demanded.

AIS statutes now make it possible for LGU's to help stop the spread. However, LGU's have not dealt with AIS issues until recently and few have budgets for control and containment.

This proposal would accelerate inspection and decontamination activities at the local level, but those programs would still require supplemental funding sources.

Today, volunteers and volunteer organizations are giving their time and money to inspect watercraft at accesses to stop the spread. [Attachment#180] These efforts will continue as long as the state makes progress towards more complete and cost-effective solutions for stopping the spread of AIS.

DNR staff doesn't plan significant expansion of their AIS program; instead they look to local government partners to help protect our public waters. DNR AIS budgets don't include additional decontamination units, so this request is not a substitution.

We expect that DNR, Federal and other grant programs will continue. This proposed one-time funding would remove a significant barrier to a more complete program that protects our public waters for future generations.

Sustainability and Maintenance:

The two uses of these proposed funds have different sustainability and maintenance needs, as detailed below:

The grant recipients intending to acquire land and establish regional AIS inspection stations would be responsible for maintaining these AIS stations. Clearly defined maintenance approaches for a minimum of 5 years would be a requirement of their grant request. In case of default, we suggest the land be ceded to the State.

The decontamination assets are pieces of capital equipment with useful lives of 10-15 years. An equipment maintenance plan would be a requirement of their grant request. Depending on the AIS programs in effect, these assets might need to be replaced after their useful lives. In case of default, we suggest the equipment be repurposed or resold with proceeds going to the State.

The LGU's need time to find funds for AIS and this 3-year deployment provides time to establish their funding sources.

As to on-going reliance on volunteers and volunteer organizations for time and money, we know that Minnesotans care about our environment and our heritage, and will continue to fund efforts that are successful and cost-effective. The vote to enact the Legacy Fund is demonstrable proof of our collective commitment.

Government Approval:

Will local government approval be sought prior to acquisition? - **Yes**

Permanent Protection:

Is the land you plan to acquire free of any other permanent protection? - **Yes**

Hunting and Fishing Plan:

Is this land open for hunting and fishing? - **No**

Other Activity:

AIS inspection and decontamination for Publically Protected Aquatic Habitat

The primary thrusts of this proposal are to:

1. Provide grants to local government units, tribal government units, and the MN DNR for the establishment of Regional AIS inspection stations with decontamination units
2. Provide grants to local government units, tribal government units, and the MN DNR for decontamination units at Dedicated AIS inspection stations.

Any acquired land will be specifically requested in the grant process for use as Regional AIS inspection stations. As these lands will have a defined purpose they are inappropriate for hunting and fishing.

Deployment management help will be provided to ensure consistency and success in the establishment of the Regional AIS inspection stations.

Accomplishment Timeline

Activity	Approximate Date Completed
Establish the grant program	9/30/2014
Establish Regional AIS inspection station deployment BMPs	9/30/2014
Call for Funding Requests	10/1/2014
Consider funding requests quarterly	Each quarter, ending on 6/30/17
Report on grant activity quarterly	Each quarter, ending on 6/30/17
Deployment Phase 1 (Approx. 6%)	12/31/2014
Deployment Phase 2 (Approx. 34%)	12/31/2015
Deployment Phase 3 (Approx 64%)	12/31/2016
Deployment Phase 4 (Approx. 100%)	6/30/2017

Outcomes

Programs in the northern forest region:

- Our intended outcome is that we stop or at least slow the spread of man's actions in transferring AIS to uninfested waters. Our conclusive data, however, would lag the term of this proposal.

  All AIS infestations are unknown until they manifest themselves and/or are discernible through testing. For example, zebra mussels undergo a 3-year gestation period, thus it means that it will be another year to determine effectiveness in stopping their spread from 2011 efforts, 2 more years for 2012 actions, and 3 years for 2013 actions.

  As local AIS protection programs are designed, it is vital to recognize that due to the flow of water between lakes, unprotected upstream waters compromise the intended outcomes of any downstream protected waters.

  Nonetheless, once this more comprehensive AIS prevention program is implemented for connected bodies of water, we would expect that no more than 10-15% of those water bodies will have a human transferred species of AIS introduced. There is some level of inherent error in every element of our proposed solution, but this more comprehensive solution of inspections and decontamination will dramatically reduce the risk of man's unintended spread of AIS.

We recommend that the MN DNR begin tracking effectiveness of the local AIS programs, and specifically linking infestations to the completeness of the local AIS programs or lack thereof. Once the DNR has established a comprehensive reporting program, AIS prevention solutions implemented across the state can be better assessed.

Programs in forest-prairie transition region:

- As our proposal is for statewide impact, the proposed program outcomes are the same for each region. Please refer to the "Other" program outcomes detailed in the northern forest region.

Programs in metropolitan urbanizing region:

- As our proposal is for statewide impact, the proposed program outcomes are the same for each region. Please refer to the "Other" program outcomes detailed in the northern forest region.

Programs in southeast forest region:

- As our proposal is for statewide impact, the proposed program outcomes are the same for each region. Please refer to the "Other" program outcomes detailed in the northern forest region.

Programs in prairie region:

- As our proposal is for statewide impact, the proposed program outcomes are the same for each region. Please refer to the "Other" program outcomes detailed in the northern forest region.

Budget Spreadsheet

Total Amount of Request: $25,182,900

Budget and Cash Leverage

Budget Name	LSOHC Request	Anticipated Leverage	Leverage Source	Total
Personnel	$470,600	$0		$470,600
Contracts	$5,537,300	$0		$5,537,300
Fee Acquisition w/ PILT	$0	$0		$0
Fee Acquisition w/o PILT	$4,433,300	$0		$4,433,300
Easement Acquisition	$0	$0		$0
Easement Stewardship	$0	$0		$0
Travel	$68,400	$0		$68,400
Professional Services	$0	$0		$0
Direct Support Services	$0	$0		$0
DNR Land Acquisition Costs	$0	$0		$0
Capital Equipment	$14,673,300	$0		$14,673,300
Other Equipment/Tools	$0	$0		$0
Supplies/Materials	$0	$0		$0
DNR IDP	$0	$0		$0
Total	$25,182,900	$0	-	$25,182,900

Personnel

Position	FTE	Over # of years	LSOHC Request	Anticipated Leverage	Leverage Source	Total
DNR Grant Supervisor	1.00	3.00	$211,800	$0		$211,800
DNR Grant Staff	2.00	3.00	$258,800	$0		$258,800
Total	3.00	6.00	$470,600	$0	-	$470,600

Capital Equipment

Item Name	LSOHC Request	Anticipated Leverage	Leverage Source	Total
Decontamination units for Regional AIS Inspection Stations	$11,000,000	$0		$11,000,000
Decontamination units for Dedicated AIS Inspection Stations	$3,673,300	$0		$3,673,300
Total	$14,673,300	$0	-	$14,673,300

Output Tables

Table 1. Acres by Resource Type

Type	Wetlands	Prairies	Forest	Habitats	Total
Restore	0	0	0	0	0
Protect in Fee with State PILT Liability	0	0	0	0	0
Protect in Fee W/O State PILT Liability	0	0	0	1,267	1,267
Protect in Easement	0	0	0	0	0
Enhance	0	0	0	0	0
Total	0	0	0	1,267	1,267

Table 2. Total Requested Funding by Resource Type

Type	Wetlands	Prairies	Forest	Habitats	Total
Restore	$0	$0	$0	$0	$0
Protect in Fee with State PILT Liability	$0	$0	$0	$0	$0
Protect in Fee W/O State PILT Liability	$0	$0	$0	$25,182,900	$25,182,900
Protect in Easement	$0	$0	$0	$0	$0
Enhance	$0	$0	$0	$0	$0
Total	$0	$0	$0	$25,182,900	$25,182,900

Table 3. Acres within each Ecological Section

Type	Metro/Urban	Forest/Prairie	SE Forest	Prairie	Northern Forest	Total
Restore	0	0	0	0	0	0
Protect in Fee with State PILT Liability	0	0	0	0	0	0
Protect in Fee W/O State PILT Liability	103	178	21	186	779	1,267
Protect in Easement	0	0	0	0	0	0
Enhance	0	0	0	0	0	0
Total	103	178	21	186	779	1,267

Table 4. Total Requested Funding within each Ecological Section

Type	Metro/Urban	Forest/Prairie	SE Forest	Prairie	Northern Forest	Total
Restore	$0	$0	$0	$0	$0	$0
Protect in Fee with State PILT Liability	$0	$0	$0	$0	$0	$0
Protect in Fee W/O State PILT Liability	$2,052,200	$3,534,600	$413,100	$3,705,400	$15,477,600	$25,182,900
Protect in Easement	$0	$0	$0	$0	$0	$0
Enhance	$0	$0	$0	$0	$0	$0
Total	$2,052,200	$3,534,600	$413,100	$3,705,400	$15,477,600	$25,182,900

Table 5. Target Lake/Stream/River Miles

0 miles

Parcel List

Section 1 - Restore / Enhance Parcel List

No parcels with an activity type restore or enhance.

Section 2 - Protect Parcel List

No parcels with an activity type protect.

Section 2a - Protect Parcel with Bldgs

No parcels with an activity type protect and has buildings.

Section 3 - Other Parcel Activity

No parcels with an other activity type.

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GEOGRAPHIC SPREAD OF EXOTIC SPECIES: ECOLOGICAL LESSONS AND OPPORTUNITIES FROM THE INVASION OF THE ZEBRA MUSSEL Dreissena polymorpha

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Abstract
The spatial and temporal dynamics of the recent invasion of North American fresh waters by the zebra mussel Dreissena polymorpha are reviewed in terms of the mechanistic bases behind the dispersal and colonization processes. The planktonic phase of the life cycle (the veliger), the ability of the benthic stage to attach to submerged objects, and the prominence of human activities as vectors for dispersal has promoted rapid spread of this aquatic pest to 18 states in the USA and two provinces in Canada within the first seven years of its introduction into the Laurentian Great Lakes. So far, the majority of range expansion has occurred within commercially navigable waters, and thus commercial shipping appears to be the most important vector of spread within connected bodies of water, especially to areas upstream of established populations. In contrast, overland spread to isolated inland waters appears to occur more slowly, and by early 1994 adult mussels had only been found in eight inland lakes. Although there are many potential vectors of overland spread, transient recreational boating activity is suspected of being the primary means of overland dispersal, and several mechanisms associated with boating have been shown to be capable of transporting mussels in large numbers. Studies on waterfowl indicate that although

Keywords: biological invasions, dispersal, human vectors, invading species, recreational boating.

INTRODUCTION

The impact of an exotic species on native ecosystems or human activities is not only a function of its local abundance but also the spatial extent of its range. The eventual distribution of an invading species can, at times, be predicted on the basis of its ecological requirements. However, a focus on the 'inevitable' or 'eventual' outcome of an invasion (i.e. the maximal geographic range of an invader) misses a rich area of investigation, namely the temporal and spatial patterns of geographic spread on a more local or regional basis and the underlying mechanistic bases of dispersal and population establishment. Typically, an invasion begins with the establishment of a founding population after which the invader's geographic range is expanded by local and regional dispersal and the subsequent colonization of uninhabited areas. The geographic trajectory of both the initial and subsequent stages of an invasion are influenced by a combination of the ecological conditions required by the invader and the dynamics of

ducks are capable of transporting zebra mussels, the rate of transport is quite small relative to boating activity. Other methods of inferring the relative importance of dispersal vectors are outlined, and an example of predicting the spread on the basis of regional patterns of recreational boating trafific is given. Finally, studies on the demographic conditions necessary for the establishment of new populations are suggested as a rewarding area of further research.

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its dispersal (Carey, this issue). In many ways, these issues of invading species are similar to those considered by epidemiologists studying the spread of disease (Mollison et al., 1994).

A better understanding of the process of invasion offers many potential benefits. First, we will be better able to predict the rates and directions of spread. Second, such knowledge is critical for the selection and evaluation of interventions aimed to slow or stem the spread of invading species. Finally, exotic species can act as 'biological tracers' from which we can extract valuable information on the dispersal of established species or future invaders. Although introduced species generally have characteristics that enhance dispersal

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and colonization, knowledge of dynamics of their geographic spread can at least identify the pathways and vectors of dispersal of similar species if not the quantitative rates of spread.

Of the large number of exotic species that have invaded natural habitats around the world, the dynamics of invasion have rarely been examined, and instead attention has usually focused on the local ecological impacts (but see Johnstone et al., 1985; Carey, this issue). In most cases, only the large-scale range expansion of the species has been determined (Andow et ul., 1990; Hengeveld, 1992; Rowell et al., 1992; Liehhold et al., 1992; and several examples in Grosholz & Ruiz, this issue). In spite of the potential gains to our understanding of the invasion process, the spatial and temporal dynamics of particular invasions have, in the past, been difficult or nearly impossible to predict (Hengeveld, 1989, 1992; Lawton, 1993; Mollison er al., 1994). Predictions are particularly hindered by a lack of knowledge of the rates of local population growth and an ignorance of the vectors and dynamics of dispersal. In some cases, after the initial stages of range expansion, estimates of the rates and directions of spread can be made and possible vectors of dispersal identified. Unfortunately, these predictions are usually made with unreliable data collected from incidental discoveries or biased sampling (Hengeveld, 1989). This level of resolution may be adequate for examining large-scale (e.g. continental) range expansion but is inadequate for a more detailed determination of the pattern and pace of geographic spread.

populations in the hopes that the necessary experimental approaches might be condoned and adopted as recommended by Levinton (1994).

BACKGROUND

The discovery of zebra mussels in North America occurred in 1988 in Lake St Clair near Detroit, Michigan (Hebert et al., 1989). Based on the population size-frequency distribution, it was estimated that the initial introduction took place in 1986. The mussels were most likely introduced as larval stages in ballast water discharged from an international freighter originating from an unknown Eurasian freshwater port (Hebert er al., 1989; Carlton, 1993). Since their initial establishment, the mussels have spread rapidly to the waters of 18 states in the USA and two provinces in Canada, and have caused major economic problems and environmental perturbations in areas where populations have reached high levels, primarily in the Great Lakes (see Nalepa & Schloesser, 1993 for examples). The impact of the mussel has been caused by two features that make it unique among the North American freshwater fauna. First, it is a biofouling organism capable of attaching to solid or stable surfaces in very high densities. This can hinder the performance of equipment exposed directly to lake or river water, e.g. intake pipes, cooling systems, boat hulls (Ludyanskiy et al., 1993), and smother some aquatic organisms, e.g. unionid clams (Tucker et al., 1993). Second, it is an abundant benthic filter feeder and is capable of remov-

The recent invasion of North America fresh waters by the Eurasian zebra mussel Dreissena polymorpha offers a rare opportunity for examining the dynamics of geographic spread. The invasion has been widely publicized for both the incredible speed of range expansion and the large economic and ecological effects (see various chapters in Nalepa & Schloesser, 1993), and substantial funding has been provided for both research and education. The eventual distribution of zebra mussels within North America is, of course, an important concern, and several models have been developed to predict the potential geographic range of the zebra mussel based on broad climatological tolerance (Strayer, 1991), tolerance to low pH (Neary & Leach, 1992), and the physicochemical properties of lakes where zebra mussels are known to have invaded in Europe (Ramcharan el al., 1992). In this paper, we examine the dynamics of the zebra mussel invasion and its potential for producing information on the underlying mechanisms governing the geographic spread of this exotic species. In particular, we contrast dispersal within and between bodies of water to discern the relative importance of the many potential vectors involved. We also discuss possible approaches to studying the local and regional spread of introduced species. Finally, we emphasize the need for understanding the initial demographic conditions necessary for establishing new ing planktonic organisms and particulates from the water column. Its ability actively to pump water makes it an especially effective filter feeder in the calmer conditions of lake environments. Mussels remove particles from water that they filter, some portion of which they consume. The remainder is bound in mucus as pseudofeces which are expelled and deposited on the benthos. The great filtering capacity (Sprung & Rose, 1988), of large populations of zebra mussels thus gives the potential to affect planktonic communities (Padilla et al., 1996a). Initial studies have documented marked increases in water clarity and decreases in phytoplankton (e.g. Reeders et al., 1989; Reeders & Bij De Vaate, 1990; Leach, 1993; but see Wu & Culver, 1992) as the mussel alters the paths of energy flow through the aquatic food web. Concomitant changes in zooplankton abundance and pelagic fish species may result as the planktonic resource base is diminished (but see Padilla et al., 1996a). The combination of the dramatic economic impacts and the rapid population growth and spread of the zebra mussel has led to federal legislative action to control 'aquatic non-indigenous nuisance species' and prevent their establishment and spread. Specifically, an act of Congress has produced dedicated funds for zebra mussel research and directed several federal agencies to develop research and policy programs on non-indigenous aquatic species.

DISPERSAL

The rapid spread of the zebra mussel across eastern North America has been due largely to its phenomenal rate of population growth and the presence of effective vectors of dispersal. Carlton (1993) has detailed the possible dispersal vectors available to zebra mussels and has identified several important distinctions among vectors: (1) ability to transport mussels upstream, downstream, or overland, (2) natural or human-mediated, and (3) the potential to disperse various life history stages (i.e. larval stages vs adults). The life cycle of this mussel is unlike other freshwater bivalves and instead parallels the marine mussels. Sexes are separate and the sedentary adults release gametes directly into the water. After fertilization, the resulting larva (termed a 'veliger' once the larval shell is developed) is an obligatory planktotrophic stage which must remain watersheds and have increased the number of connections and amount of water exchange in others. Thus, many of the present-day connections among water bodies in the Great Lakes region are human-created canals (e.g. the Erie Canal). Dispersal through such waterways may occur 'naturally' in the sense that no active human participation is necessary, but such dispersal must be considered human-mediated in the sense that it could not have occurred without human interventions at some point in time. This type of human activity will greatly aid the natural ability of aquatic species to spread.

The importance of any particular vector will depend on the life cycle stage that is transported, number of surviving mussels transported per dispersal event, the frequency of such events, and the spatial patterns of vector movement. The key to our predictive abilities will lie in knowing the relative importance of both human-caused and natural vectors of dispersal.

for approximately 2-4 weeks in the plankton while feeding and growing. Although larvae are capable of limited locomotion, dispersal during the planktonic period primarily depends on currents and other hydrographic movements. Juveniles and adults are capable of some movement by unattaching and reattaching byssal threads, effecting a slow crawl. Unattached mussels or mussels attached to drifting substrata (e.g. wood, dislodged macrophytes) will be subject to downstream advective movement. Thus natural mechanisms of dispersal are capable of spreading zebra mussels rapidly to areas downstream or within a lake. Indeed, the unidirectional nature of large freshwater systems probably limits natural populations of zebra mussels to lake environments and the portions of rivers and streams downstream of established lake populations.

The natural spread to areas upstream and the maintenance of populations in fast moving lotic systems are more problematic. The larvae of zebra mussels do not possess the adaptations of the larvae some other freshwater bivalves (e.g. unionids Corbicula) use to attach to larger organisms that might swim or fly upstream. Unintentional attachment or entanglement of zebra mussels on more mobile animals can occur, e.g. ducks (Johnson & Carlton 1996), but this passive mechanism of transport is unlikely to lead to rapid or consistent dispersal. Moreover, mortality rates are likely to be high during transit because neither the larval or adult stages of the zebra mussel have physiological adaptations (e.g. resting stages) for persisting for extended periods out of water.

Potential human-mediated dispersal mechanisms are almost limitless (Carlton, 1993). Essentially, any activities that can move water (which can contain veligers) or submerged objects (which can have adult or juvenile mussels attached) within or between bodies of water has the potential to accelerate the spread of this species, especially upstream or overland. It is also worth noting that humans have created many connections between otherwise isolated water bodies and

The importance of scale

The time scale of spread, the types of dispersal vectors, and the appropriate types of models will differ depending on the geographic scale of concern (i.e. local spread within connected water bodies, regional and direct pathways of spread among watersheds, or the ultimate timing and extent on a continental area; Table 1). For example, local spread will be a function of both larval and adult transport, natural and human vectors (although human vectors alone will be responsible for upstream or counter current movement). Thus the rates of local population increases and population size will have a large impact on spread, and diffusion-reaction and or telegraph type models would be important (Kareiva & Odell, 1987; Holmes, 1993). At a continental scale, human-aided dispersal would greatly expedite spread, and the level of resolution of spatial extent that is necessary is coarse (e.g. 10s or 100s of km year‘). Diffusion models, Advection—Ditfusion models, or Interacting Particle models may be adequate for describing the broad patterns of the moving fronts of invasion (Okubo, 1980; Lubina & Levin, 1988; Levin et al., l993; Grosholz & Ruiz, this issue; Hastings, this issue). However, at the regional scale, the scale at which slowing or preventing local invasion is possible, we have the least amount of experience, models, and predictive power. Here, knowing: (I) the most likely dispersal vectors, their direction and rate of movement of propagules, and (2) the overlap between dispersal and acceptable habitat patches (i.e. water bodies with physicochemical conditions necessary for zebra mussels reproduction and population growth; Ramcharan et al., 1992, Koutnik & Padilla, 1994) is critical. The intersection of these two will tell us the most likely paths of invasion.

With such knowledge the rate and direction of spread can be estimated, the bodies of water that are most at-risk can be identified, and the pathways of expansion disrupted if deemed feasible, necessary, or cost-effective. Unfortunately, there have been no previous

Table 1. The importance of scale on dispersal mechanisms and patterns of geographic spread

	Local spread	Regional spread	Large scale spread
Geographic scale	Within a water body or	Among watersheds,	Across a continent

	connected water bodies	within and among states	
Likely vectors	Passive diffusion and advection of larvae downstream and human mediated	Human mediated	Human mediated
Time scale	Rapid	?	Slow
Pattern of spread	From initial invasion to downstream areas and, if navigable, upstream areas	?	Wave fronts of invasion
Models of invasion dynamics	Telegraph, Difi"usion-Reaction	?	Advection—Diffusion, Interacting particles

studies on the long-range dispersal vectors of this mussel, and policy makers and water managers have instead had to rely on their own intuition or that of scientific experts.

Identification of dispersal vectors

There are four ways in which dispersal mechanisms can be verified and possibly quantified.

Direct observations

When the presence of the target organism can be detected on or associated with the dispersal vector as it moves from one place to another, direct observations can provide valuable information on the potential of the vector to expand the range of the invading species. If the frequency of vector movement, the number of individuals transported, and their survival during transit can all be documented, absolute estimates of dispersal rates, potential pathways, and geographic scales can be made and compared among the various dispersal mechanisms. In practice, the opportunities to determine all these aspects of dispersal are rare (but see Johnstone et al., 1985). However, the documentation of the ability of a potential vector actually to transport the target organism and estimations of the numbers transported per dispersal event are important first steps in comparing the relative importance of a suspected subset of dispersal vectors (Johnson & Carlton, 1996).

Correlates of invaded waters

This indirect, observational approach compares the characteristics of invaded and uninvaded waters to discern features that would be correlated with particular vectors and the ability of taxa to invade suitable habitats (Johnstone et al., 1985; Ramcharan et al., 1992; Koutnik & Padilla, 1994). For example, the initial spread of zebra mussels to major ports in the Great Lakes suggests that shipping or boating were the primary vectors of spread. Unfortunately, the strength of any such conclusion is compromised by a lack of standardized sampling, and alternative explanations could include a lack of sampling in areas outside of ports or differences in ecological conditions between areas inside and outside of ports. It is often difficult to determine whether the absence of a species from a location is due to true absence or to a lack of detection. If it is truly absent, we can distinguish between unsuitable habitat (where, if introduced, a species could not live or reproduce) and suitable habitat (able to establish a viable population) to determine the potential for invasion. And, as always, it must be kept in mind that correlation is not always the same as causation.

Predictions of range expansion

Patterns of range expansion can be compared to those predicted by the patterns of vector movements (Padilla et al., 1996b). Measurements of vector movements can even be made after the spread has occurred if movement patterns are assumed not to have changed. If the predicted pattern of invasion matches that of the actual invasion, then there is strong evidence that the vector of interest has the dominant effect on dispersal.

Experiments

By manipulating the vector (e.g. the agent or its pathway is removed), experimental areas can be compared with appropriate control areas. Obviously, this is the most difficult approach, but it would provide the most convincing evidence.

The use of any of these approaches for a large variety of dispersal mechanisms would probably be impossible, but a combination of approaches directed at subsets of likely dispersal mechanisms may be effective in discerning the relative importance of several vectors.

Dispersal **within** a **body** of water vs dispersal between **bodies** of water

An important, yet often overlooked, dichotomy in the process of range expansion of freshwater organisms is the distinction between dispersal within a body of water or connected bodies of water and dispersal between hydrographically isolated bodies of water. As described above, the life cycle of the zebra mussel places unusual constraints on its natural ability to disperse upstream and overland. Some introduced marine species do have a life cycle similar to that of the zebra mussel, but the more well-connected nature of marine environments permits more rapid dissemination of propagules to suitable habitats. In contrast, overland dispersal between unconnected bodies of fresh water is a particularly difiicult challenge for the zebra mussel. Lakes and rivers are effectively discrete habitat patches which, in some senses, are analogous to anthropogenically fragmented habitats of terrestrial environments (e.g. forests). However, habitat fragmentation in terrestrial environments is less likely to affect survival during dispersal than it will affect the post-dispersal stages of establishment such as habitat choice, reproduction, or survival. For zebra mussels and many other aquatic organisms, the terrestrial environmental conditions that separate aquatic habitats are simply lethal. This condition and the dependence on vectors for transportation make these barriers to natural dispersal more effective than for terrestrial species that can actively move among habitat patches (e.g. insects, birds). Of course, some freshwater organisms (e.g. aquatic insects with aerial adult stages) have obvious adaptations for overland dispersal, and for them this distinction is probably not as critical. However, for organisms like the zebra mussel, this dual nature of the dispersal process must always be kept in mind. Range expansion in this species is essentially a two-stage process in which the pattern of range expansion is likely to be a series of overland 'jumps' followed by dispersal within the newly colonized watershed. As described below, this first step appears to be the rate-limiting step in the further spread of the zebra mussel because the rate of overland spread seems to be far slower than the spread within connected bodies of water.

Dispersal within connected bodies of water

The range expansion of the zebra mussel has been larvae downstream, transport of adults as fouling organisms on boats, barges. and ships may account for the 'jumps' in distributions that occurred ahead of the main population (eg. the initial populations in the Erie Canal and the St Lawrence River.) Because reproductive output in zebra mussels increases exponentially with body mass, the movement of adults will allow newly colonized populations to grow more rapidly, and increase the likelihood that they will serve as sources for propagules for colonization further downstream. Again, without some type of standardized sampling or monitoring programs being conducted throughout the area of range expansion, it is difficult to explain gaps in the distribution of an invading species, or predict where the next area of colonization will occur.

During this same period, substantial upstream dispersal was also occurring. As early as 1990, populations of adult mussels were found in ports of all three of the upper Great Lakes, and by 1991 the adults had dispersed through the Chicago Sanitary and Ship Canal into the Illinois and Mississippi Rivers. The mussel then spread quickly both up and down all the major rivers of this system, and by the end of 1993 they could be found from Minnesota to Louisiana and Oklahoma to West Virginia.

The most likely mechanisms of dispersal during this range expansion are the natural drifting of the larvae (but see above comments on canals) and the human-mediated transport of adults through shipping and boating activities. Anecdotal observations have documented the presence of adult mussels on a commercial barge that had previous traveled 15,000 km of these waterways (Keevin & Miller, 1993), and the observation that the present range of the zebra mussel almost perfectly coincides with that of the commercially navigable waters of the Great Lakes and the Mississippi watershed is strong evidence that commercial shipping and not recreational boating is primarily accountable for the within-basin transportation of the zebra mussel (McMahon, 1992). Overall, the dispersal of the zebra mussel within connected bodies of water or watersheds appears rather straightforward although surprisingly fast. Indeed, the linear spread of zebra mussels along from Lake St Clair to Québec and Louisiana (approximately 300-500 km/year) greatly exceeds that observed for most marine and terrestrial invasions (see Grosholz & Ruiz, this issue, for estimates of rates in terrestrial tracked for the past five years (Ludyanskiy et al., 1993; O'Neill & Dextrase, 1994). Unfortunately, this record relies primarily on incidental discoveries and non-standardized sampling. However, we can still detect some coarse-scale patterns and attempt to infer the relative importance of various dispersal mechanisms. After the initial detection in Lake St Clair, mussels were soon found downstream in Lake Erie (1988), Lake Ontario (1990), the Erie Canal (1990), the St Lawrence River (1990), and the Hudson River (1991). Although much of this spread was probably due to the dispersal of

and marine habitats). Remaining questions concern the relative importance of human-mediated and natural vectors of downstream spread, the maintenance of lotic populations, and the rates of spread in smaller rivers and streams, especially those that are not navigable. It is also of considerable conceptual interest to know the metapopulation structure (Goldwasser er al., 1994) of this species in these connected waters. Given the para]-lels between the life history of the zebra mussel and many marine species, there are also many questions of concern to marine ecologists about the role of sources

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and sinks of reproduction in determining the structure of adult populations (i.e. 'supply-side ecology'; Roughgarden et al., 1987). These types of questions might be fruitfully addressed by the study of zebra mussels. The maintenance of lotic populations by upstream populations in lakes or impoundments would be of particular interest.

Dispersal between isolated bodies of water

In sharp contrast to the above patterns of spread, the spread of the zebra mussel into inland waters (i.e. those lakes, rivers, and streams that are hydrographically isolated from invaded waters or are upstream of navigable waters) has been quite slow. By the end of 1993, 5 years after their initial discovery in Lake St Clair, isolated populations of adult mussels had only been found in eight inland lakes or lake systems. Three explanations could account for this pattern.

Overland dispersal is indeed slow: In spite of the multitude of potential vectors and pathways, it may be that mussels are not easily transported, have poor survival rates during transportation, are transported primarily to lakes in which they have low survival or do not achieve the demographic conditions needed for a self-sustaining population.

Sampling is biased towards larger bodies of water: Smaller inland waters are more numerous and probably receive much less attention from biologists than do the larger aquatic systems. In Wisconsin alone there are more than 3600 inland lakes over 8 ha in size. This bias is certainly true for studies investigating the zebra mussel and is probably true for biological investigations in general. Indeed, most of the findings of zebra mussels in inland lakes have been by the educated public rather than of these lakes. Thus the initial adult populations are difficult to detect and may persist for years before becoming readily detectable.

In the same vein, it may be possible that some populations do not persist and thus are never detected. In several lakes of the above study in which only veligers were found, the animals appeared to be in poor condition or only empty shells were found. This suggests that conditions in the planktonic environment of some lakes might be unsuitable for this stage of the life cycle. Several other studies have found veligers in inland waters without subsequently finding adults (C. O'Neill, pers. comm.). While the possibilities of misidentification (e.g. ostracods are very similar to veligers) or cross-contamination of samples cannot be totally excluded in all these cases, the evidence is mounting that small populations of adult zebra mussels might be unable to replace themselves if unfavorable conditions for the larval phase persist. (The alternative possibility exists that the veligers were not the result of local reproduction of introduced adults but were instead introduced themselves. However, it is exceedingly unlikely that veligers could be introduced in high enough numbers, e.g. millions, to be detected by sampling programs.) Such local extinctions of undetected populations can confound any inter- pretation of the mechanisms of dispersal if it is assumed that a lack of range expansion is due to slow rates of transport instead of low survival rates or inadequate reproduction of founding populations.

Mechanisms of overland dispersal

At present, we still know very little about the vectors and pathways by which zebra mussels are dispersed by scientists. In a study specifically funded to sample inland waters for zebra mussels (Johnson & Carlton, unpublished data), zebra mussels were detected in seven of the 27 inland lakes in Michigan that were considered at highest risk of invasion due to the high degree of public access, their large size, and their proximity to infested waters (the three other lakes in which mussels were found were connected by navigable connections to infested waters). Thus, zebra mussels can be found if we look, at least in the most likely places.

Inland populations take longer to develop: In the demographically open systems of larger waters, the fast growth of incipient populations is probably supported by immigrations from older populations, i.e. population growth of adults near the margins of the distribution is not due to local reproduction but instead is supported by larval production elsewhere. In the closed systems of smaller lakes and rivers, newly established populations may take some time to develop to levels that are easily detectable. In the above mentioned sampling of inland lakes in Michigan, populations of zebra mussels were first detected by finding veligers in very low densities in the plankton (< 0-01/litre). In subsequent benthic sampling, adults were found in only one

overland and even less about the demographic conditions necessary to establish self-sustaining populations. Intuition has unfortunately been substituted for scientific information and, in some cases, has led to the widespread belief in 'mussel myths' (Johnson & Carlton, 1993). For example, it is widely believed that waterfowl will eventually disperse zebra mussels to all habitable waters, and this belief is often used to justify a lack of action to prevent additional spread. Additionally, public advisories have warned that it 'only takes two mussels' to establish a new population (the 'Noah Fallacy'), a statement that is demographically unlikely. Given this type of misinformation and the plethora of potential vectors, any type of quantitative (or even qualitative) ranking of the importance of potential vectors would be valuable. By combining the above-mentioned approaches, a preliminary understanding is beginning to emerge.

Direct observations of transport

A number of the potential overland dispersal vectors identified by Carlton (1993) have now been examined for their ability to transport either the larval or adult stages. Recreational boating and fishing activities appear capable of transporting zebra mussels in a variety

of ways (Johnson & Carlton 1995, unpubl. data) including as adults attached to the exterior hull or to aquatic macrophytes entangled on the trailer or boat exterior and as larvae in live wells, bilges, bait buckets, and cooling systems. Adult mussels were also taken occasionally by boaters as souvenirs. Based on the frequency and numbers of mussels transported by these mechanisms, entangled vegetation and live wells appear to have the most potential for transporting substantial numbers of mussel overland to uninfested waters (Johnson & Carlton, 1995). Surprisingly, boat hulls fouled by mussels were rarely observed (<0.1%). Apparently, boats that reside in infested waters long enough to become fouled are rarely transported overland. However, their potential to move large numbers of adult mussels suggests that this mechanism of dispersal, although rare, may be an important component of the geographic spread of zebra mussel.

The transport of zebra mussels by waterfowl has been examined experimentally, and although waterfowl

Given the small number of overland zebra mussel invasions that have been documented so far (approximately 25 by the end of 1994 with either adults or veligers detected). it is premature to draw many conclusions. Invaded waters include both large (> 500 ha) and small (< 100 ha) lakes as well as lakes with and without public access. Considerably more examples, especially from systematic surveys, will be needed before any strong conclusions can be made using this approach.

Predictions based on vector activity

If the movement patterns of a particular vector among a group of inland waters is known. then predictions can be made as to the spatial and temporal dynamics of the invasion of the area. If the pattern of invasion matches the predicted pattern, then the vector of interest is likely to be responsible for the dispersal. We have attempted to document the patterns of transient boating activity in a system of eight popular recreational inland lakes in southeastern Michigan. These lakes are

are capable of transporting small numbers of larval and juvenile stages (<1 zebra mussel/bird), the numbers appear insignificant relative to those of other vectors (Johnson & Carlton 1995, unpubl. data). Larval stages can also be transported on the wetsuits of divers (K. D. Blodgett, pers. comm.).

Successful dispersal also requires survival of the mussels during transit. For most of these documented vectors, there is no information on the survival during transit between infested and uninfested waters. Larval stages can survive at least 8 days in water collected from the live wells of recreational fishing boats (Johnson, unpubl. data), and similar data will be needed to assess further the relative importance of these dispersal vectors.

Correlates of vectors

If a particular vector can be correlated with patterns of range expansion, the importance of the vector can be inferred. For example, if the first lakes invaded all have public access, then transient boating activity could be implicated as the likely vector. However, many factors may be intercorrelated, making it difficult to separate the important factors. For example, lake size per se might influence the susceptibility of a lake to invasion, but lake size will also influence the likely volume of boater activity, the availability or diversity of stable substrata for zebra mussel settlement, or some other variable important to the establishment of a population (e.g. dispersion of introduced larvae; see below).

Buchan and Padilla (unpubl. data) are using this approach to examine the dynamics of the invasion of Eurasian watermilfoil M yriophyllum spieatum, an aquatic weed readily transported by recreational boat trailers. As zebra mussels are often found attached to milfoil on boat trailers (Johnson & Carlton, 1996), understanding the invasion pathways of one exotic (milfoil) may aid in our understanding of the invasion of another (zebra mussels).

located in Oakland County approximately 50 km from an established population of zebra mussels in Lake St Clair. Boat movement was assessed through interviews with boaters at public boat ramps at each lake (Johnson & Carlton, unpubl. data). Among other questions, boaters were asked where they had last used their boats (although information on all lakes used within an appropriate time frame would be ideal, preliminary attempts to do so suggested that reliable data would be difficult to obtain). From these data, a matrix was constructed of the probability of a boat coming from the other lakes. A schematic diagram of the larger probabilities (Fig. 1) suggests that if certain lakes are invaded (e.g. Lake C), they may act as foci for rapid subsequent secondary spread of the invading organism to nearby lakes. Surprisingly, such ‘gateway’ lakes may not be as important for the spread to other subsets of lakes (e.g. boats arriving at Lakes R-S-L are more likely to be from Lake P or 0, instead of Lake C). For this particular set of lakes, secondary spread may not be as important as spread from the primary source (i.e. the Great Lakes): the probability of a boat being used most recently in the waters of the Great Lakes was equivalent to that of all the system lakes and was over half the probability of a boat being used in any other inland lake [mean (SD): Great Lakes -0206 (0-074), system inland lake —0-215 (0-053), other inland lakes —0~l5 (0047); the remaining boats were returning to the same lake].

In another study dealing with a larger spatial scale, Padilla et al. (1996b) have used a boater use survey conducted by the Wisconsin Department of Natural Resources to formulate similar connectedness between inland Wisconsin lakes and infested Great Lakes as well as connectedness among inland lakes. Boaters were selected randomly from the register of all licensed boats in the state of Wisconsin. Surveys were distributed every two weeks, and inquired, among other

‘natural experiments’, it may be the best and perhaps only opportunity available.) The most promising situation in this regard is the water supply system of New York City (NYC) which includes 19 reservoirs and lakes. Due to the perceived risk of a zebra mussel infestation, boats used on other bodies of water are now not allowed on these waters. Five of these bodies of

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Fig. 1. Map of eight popular recreational lakes in Oakland County, Michigan with arrows showing probabilities of a boat arriving at one lake originating from the other (only probabilities > 0-04 are shown for clarity; C I Cass, L I Lakeville. M I Maceday, O I Orchard, R I Orion, P I Pontiac, **S** I Stony Creek Impoundment, U I Union).

things, which lakes were used by a boater, and which counties were used most often during the previous two-week period. Of all boaters surveyed, 21% reported that they had used both a Great Lake and an inland lake during the two-week survey period. Of those, 89% had used an inland lake in a county bordering a Great Lake, primarily Lake Michigan. Two of the inland lakes identified by this study to be most at risk for invasion of zebra mussels were found to contain veligers and small adults in the summer of 1994. No other inland lakes in Wisconsin have been found to contain zebra mussels.

Experimental manipulation of vectors

Given that (1) many of the vectors of dispersal involve human activities and (2) the process of dispersal occurs over a large spatial scale, it is dificiult to manipulate vectors experimentally, even though this would be the most convincing approach towards determining the relative importance of particular vectors. If access to an isolated body of water is controlled by a single party, it may be possible to use it as a control for the likely invasion due to different vectors. For example, some lakes may have no recreational boat use, and therefore boaters cannot be vectors of transport of zebra mussels to those lakes. In response to the threat of zebra mussel infestations, several municipalities and industries have applied restrictions to the use of reservoirs or lakes under their control. If comparable waters exist in adjacent areas, then such situations can be used to examine the role of certain vectors of spread. (Although this reliance on outside agents to determine the assignment of treatments has the problems long associated with water have good environmental conditions for zebra mussels and are located within an area that includes another seven that are not under the control of NYC and therefore experience transient boating activity. Unfortunately, NYC is only monitoring its own lakes for zebra mussels (S. Neuman, pers. comm.) in spite of the knowledge that could be gained from monitoring the ‘control’ lakes as well. Similar data might be obtained from comparing lakes with and without public access sites, but even on lakes without public access sites, there is often substantial transient boat use by lakeshore residents or through private (‘for fee’) ramps associated with marinas.

Previous freshwater invasions and possible parallel systems

Zebra mussels are not the first exotic species to invade fresh water in North America, and are not likely to be the last. Knowledge of the invasion pathways and dynamics of previous invaders, particularly those that may have the same dispersal vectors, would be of critical value. The freshwater clam Corbicula fluminea was first discovered in North America in 1924 and then again in 1938 (McMahon, 1983). The documentation of the progress of the spread of this species is sporadic and poor, and gives us little insight into the spread of zebra mussels. Also, as Corbicula has a life history and growth habit that is quite different from the zebra mussel, understanding the spread of this species may not help us understand the zebra mussel invasion.

Another important invader in fresh water has been Eurasian watermilfoil Myriophyllum spicatam, which, like the zebra mussel, has large impacts on the lakes in which it lives. Also, like the zebra mussel, the activity of boaters is likely to be the major vector of overland spread for this species, and the movement of milfoil may in fact facilitate the spread of zebra mussels. Its spread among inland lakes has been followed throughout the Great Lakes region since the 1960s. An examination of the geographic distribution of its progress across Wisconsin appears to be similar to a moving front, with the rate of increase in the number of counties invaded by milfoil increasing with time. In the 1960s there were two counties with Eurasian watermilfoil, in the 1970s there were ll, in the 1980s there were 25, and now in the 1990s there are 43 (Buchan & Padilla, unpubl. data). However, this pattern of range expansion can be misleading regarding the actual spread of milfoil among individual lakes and watersheds. Within a county, not all of the lakes have been infested with Eurasian watermilfoil. In fact, lakes without

Eurasian watermilfoil can be nearest neighbors of lakes containing Eurasian watermilfoil (Buchan & Padilla, unpubl. data). Understanding the role and movement of dispersal vectors will help us determine the causes of the patterns of geographic spread that we observe.

Demographic conditions for establishment

A major shortcoming in our understanding of how aquatic species spread overland is the lack of knowledge of the demographic conditions (i.e. the size and life stage of the founding populations) needed for the establishment of a self-sustaining population. However, questions have been raised about the role of local population size or density on rates of range expansion (Hengeveld, 1992; Lawton, 1993). Several features of the zebra mussel life cycle make it difficult to imagine that new populations can be founded by a few individuals. The sessile nature of adult zebra mussels combined with external fertilization suggests that founding populations must be either very large or else spatially aggregated. Otherwise, dilution of gametes after spawning may lead to inefficient rates of fertilization. Studies in marine environments have provided both empirical and theoretical results that suggest fertilization rates drop off exponentially with increasing distance between spawning individuals and with higher levels of water motion (Levitan et al., 1992, and references therein; but see Babcock & Mundy, 1992). Even at distances of less than 1 m, fertilization rates can approach zero. The calmer hydrodynamic conditions of the freshwater habitats of the zebra mussel and the ability to spawn synchronously (Haag & Garton, 1992; Nichols, I993) will probably counteract these effects to some degree, but the extent of this increase remains unknown. Experiments in which the densities and spatial distribution of spawning adults were manipulated would provide much needed data.

Similar logic also argues against the ability of introduced veligers to establish new populations. Even late-stage veligers will undoubtedly be dispersed within a body of water after their introduction, and by the time they settle they are likely to be too far from other mussels for effective external fertilization (see above). With this is mind, introductions of veligers are less likely to establish populations in larger lakes because, all else being equal, the veligers will be spread out over a greater area. Indeed, the initial establishment of the zebra mussel in Lake St Clair, the smallest of the Great Lakes, may reflect this constraint. Although the gregarious settlement observed in zebra mussels might counteract that introduction (probably millions of liters) far exceeds the capability of any overland vector of dispersal. Repeated inoculations could increase the number of larvae introduced into a system, but we have no estimate of what threshold density is needed to overcome problems associated with gamete dilution.

Thus, unlike some invasive zooplankton that can reproduce parthenogenetically (e.g. Bythorrephes), or other invading bivalves that can be hermaphroditic and brood their young (e.g. Corbicula), introductions of either small numbers of adult zebra mussels or moderately large numbers (e.g. 1000s) of veligers have a poor chance of establishing new populations in isolated waters. Unfortunately, we have little chance of ever observing and quantifying the actual numbers of either adults or larvae introduced into an uninfested body of water. Thus, experimental introductions will be necessary for determining the demographic requirements for establishing new populations, but the politically sensitive nature of this approach gives it few proponents. Indeed, experimental introductions were explicitly excluded from a recent request-for-proposals to study the zebra mussel invasion (National Sea Grant College Program, 1993), and researchers interested in such approaches will face an uphill battle. Clearly the careless spread of exotic species must be avoided for both ethical and political reasons, but the information that might be gained by carefully controlled experiments should justify the risks (Levinton, l994). Furthermore, it seems rather contradictory for public officials to state on the one hand that the spread of zebra mussels is inevitable (and thus preventive measures are not appropriate) while claiming on the other hand that all experimental introductions are inappropriate. In the future, the effects of zebra mussels might be demonstrated to be either minor or perhaps even beneficial in some aquatic environments (Reeders et al., 1989; Reeders & Bij De Vaate, 1990; Padilla et al., 1996a), thereby making controlled introductions easier for others to condone. Another option is the use of experimental ponds in geographic areas already infested with zebra mussels although it is unclear how well the conditions of small ponds will mimic the environment of larger natural bodies of water.

CONCLUSIONS

The spatial and temporal dynamics of geographic spread are an important, but often overlooked, aspect of biological invasions. Difficulties in determining the

the effects of post-introduction dispersion of veligers, the likelihood of finding other settlers will be extremely small if densities are low.

Because the initial population of zebra mussels in Lake St Clair is thought to have been established by veligers discharged in ballast water, the larval stage is widely perceived as having great potential to start new populations. However, the volume of water involved in relative importance of suspected vectors of dispersal and in documenting the true changes in the distribution of an invading species will continue to hamper the collection of the information necessary to develop and test predictive models of biological invasions, especially at a regional level. The invasion of North America by the zebra mussel provides a rare opportunity to examine the regional dynamics of an invasion. At this point, the

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invasion of the zebra mussel must be considered in terms of both the dispersal within and among bodies of waters. Whereas our understanding of the spread within connected bodies of water is fairly complete, the rates and directions of overland spread and the underlying mechanistic bases remain poorly known. Based on limited information, human activities appear most important especially those transporting adult mussels to uninfested waters. However, the characteristics of uninfested waters (e.g. size, public use) that may make them more susceptible to invasion remain unclear. Further investigations into this area should provide valuable information for predicting and possibly preventing the range expansion of this and other similar aquatic species. Moreover, we may obtain a better understanding of the dispersal of propagules within a species range, thereby learning more about the genetic and demographic structure of metapopulations.

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Table of Contents

They have significant ecological impacts

Invasive species have the ability to change aquatic ecosystems including native plant and animal populations. The amount of food the mussels eat and the waste they produce has negative effects on the ecosystem and can harm fisheries. As filter feeders, these species remove large amounts of microscopic plants and animals that form the base of the food chain, reducing available food for native aquatic species. Zebra mussels attach to and encrust native organisms, essentially smothering them and removing more animals from the food chain.

PHOTO BY BRAD HENLEY

PHOTO BY GREAT LAKES ENVIRONMENTAL RESEARCH LABORATORY

They have water recreation impacts

These mussels encrust docks and boats and attached mussels can increase drag on boats. Small mussels can get into engine cooling systems causing overheating and damage. Increased hull and motor fouling will result in increased maintenance costs on vessels moored for long periods of time. The weight of attached mussels can sink navigational buoys. Zebra and quagga mussels also impact fish populations and reduce sport-fishing opportunities. Their sharp shells can cut the feet of swimmers, beach goers, and dogs.

PHOTO BY MNDNR

900 loons die in migration; invasive species suspected


An adult loon escorts one of its chicks through the waters of Little Birch Lake near Melrose, Minn. (Pioneer Press file photo)

DULUTH, Minn. -- Nearly 900 loons and probably more died while migrating south across Lake Michigan last fall, and scientists suspect invasive species may be to blame.

With the iconic birds of the North Country beginning their migration back from the Atlantic and Gulf coasts in less than a month, Minnesota Public Radio reported Monday that scientists with the U.S. Geological Survey think a complex interplay of invasive species may be the cause of the mass die-offs.

The researchers suspect invasive zebra and quagga mussels create ideal conditions in Lake Michigan for the bacteria that produces botulism toxin. The mussels filter the water so it's incredibly clear, allowing an algae called cladophora to grow in huge amounts. Storms churn up the algae, which settle to the lake bottom and rot. That creates an environment without any oxygen, an ideal home for bacteria that produce botulism. The toxin is ingested by tiny worms and freshwater shrimp, which are eaten by fish, including the invasive round goby, which are then eaten by diving birds -- including loons.

"What happens is they can't move their muscles, and, eventually, they usually die because they can't breathe or they can't hold their head up out of the water," said Stephen Riley, a fisheries biologist with the U.S. Geological Survey in Ann Arbor, Mich.

Scientists to figure out a way to break a link in that chain before it can kill more loons.

Lynette Grimes

saw the problem last October as she was hiking toward Lake Michigan at Sleeping Bear Dunes National Lakeshore, outside Traverse City, Mich., where nearly 600 loons washed ashore. She and her husband worked until sunset burying them in 3-foot-deep trenches.

"The beach was just pockmarked with birds everywhere you looked," Grimes said. "This one little peninsula had over 100 dead birds."

Kevin Kenow, a USGS wildlife biologist in LaCrosse, Wis., tracks loons with radio transmitters. His work has shown that some Minnesota loons spend nearly a month on Lake Michigan fattening up before their long flight south.

"They're diving up to 40, 45 meters in some of these areas," Kenow said, "and the pattern of dives suggests that they aren't stopping in the water column anywhere, but they're continuing all the way down to the bottom, feeding on the bottom substrates and then returning to the surface."

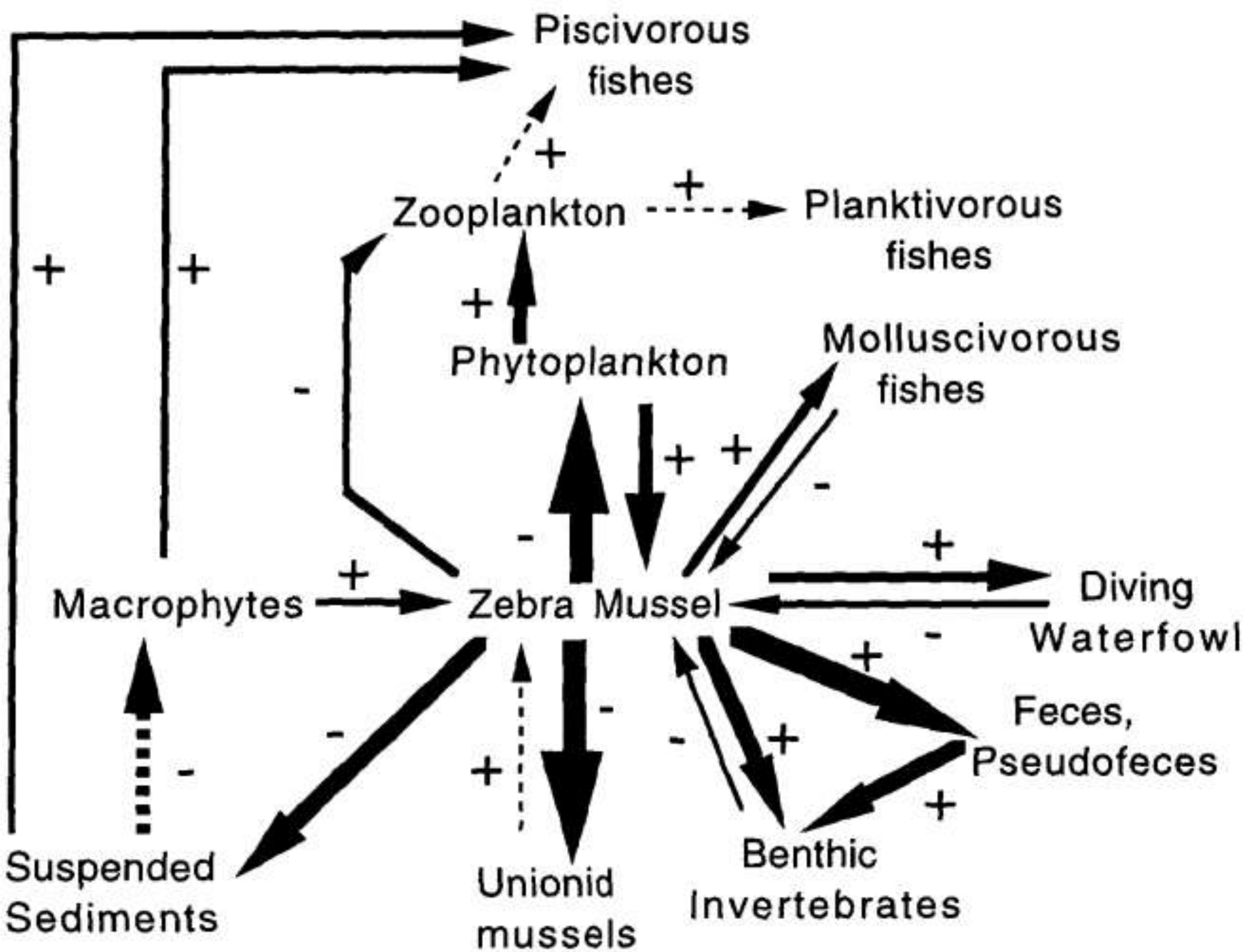
It's at the lake bottom where scientists believe fish such as the round gobies pick up botulism before they're eaten by loons.

Before last fall, it had been five years since the last large botulism outbreak. National Park Service ecologist Brenda Lafrancois of Ashland, Wis., said the outbreaks seem to be tied not just to invasive species but also to warmer weather.

So far the outbreaks don't seem to have affected Minnesota's loon population, said Carrol Henderson, Nongame Wildlife Program supervisor at the Minnesota Department of Natural Resources. Henderson said the population appears stable at more than 10,000 adult loons, so it's still unclear how many of the loons dying in Lake Michigan spend their summers in Minnesota.

Last October, Damon McCormick, a wildlife biologist with Common Coast Research and Conservation in Houghton, Mich., found 300 dead loons in just a seven-mile stretch of Lake Michigan beach near the Upper Peninsula town of Gulliver.

"If the die-off continues, to any extent like it has, then I think it's a genuine concern for the long term viability of loons," McCormick said.


Piscivorous fishes
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Phytoplankton
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Macrophytes
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Zebra Mussel
Diving Waterfowl
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Feces, Pseudofeces
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+
Suspended Sediments
Unionid mussels
Benthic Invertebrates

An illustration of water discharge from a maritime vessel. Photo courtesy Marine Invasions Laboratory, Smithsonian Environmental Research Center.

Future Directions of AIS Management in the Great Lakes

» Public education: Specific user groups are being targeted with outreach methods such as regulation booklets, signs at water accesses and advertising for recreational boaters. National voluntary guidelines help to deliver consistent messages on AIS prevention and control.

» Policy, regulations and enforcement: Mechanisms are being created to ensure compliance with AIS prevention and control measures at a state, tribal and federal level. Examples include prohibition of the possession, sale or transport of live aquatic invasive species.

» Watercraft inspection: Educational programs conducted by agency inspectors and volunteers provide a valuable resource reaching potentially thousands of boaters and anglers with prevention messages.

» Early detection, monitoring and rapid response: Innovative management strategies enhance the capacity to anticipate, prevent and respond to new aquatic invasions before they become established as reproducing populations.

» Predictive modeling: Use of life history analysis and computer modeling helps to identify potential new invaders and forecast their possible range of infestation.

» Pathway and vector analysis: Research is providing valuable information on the relative risk of geographic routes of introduction or spread and mechanisms of spread, such as ballast water.

» Risk assessment: Analysis on a quantitative basis is helping managers determine the "invasiveness" of verified new species and identify their potential impacts on local industry, ecosystem and human health.

Vector

Maritime Commerce

Transoceanic shipping has operated in the Great Lakes since the opening of the St. Lawrence Seaway in 1959. Ship ballast has been recognized as a leading vector of AIS introductions since the discovery of zebra mussels in Lake St. Clair in 1988. The zebra mussel and a host of other species introduced by ballast have quickly spread throughout the Great Lakes via intrabasin ballast exchange and other vectors. As of 2007, Canada has implemented mandatory ballast water control and management regulations for both ballast and No Ballast on Board (NOBOB) vessels. The U.S. has instituted mandatory ballast water requirements for ballast vessels and voluntary management guidelines for NOBOBs. The development of a ballast water management discharge standard to define the maximum permissible concentration of organisms at all life stages per volume of ballast water has been a regional priority. New innovations for ship design are also being investigated to diminish the potential for AIS transport through ballast water and the ship itself, such as surface fouling.

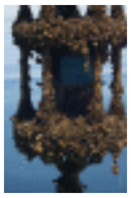
Photo courtesy Michigan Sea Grant.

Case Study: Zebra Mussel

(*Dreissena polymorpha*)

The zebra mussel, native to eastern Europe, was most likely discharged into the Great Lakes from the ballast water of ships while in their free-swimming larval stage of their life, called veligers. Rapidly spread by a variety of vectors, this non-native mollusk attaches to hard surfaces, including pipes and other submerged structures. Maintenance to clean infested pipes costs industry millions of dollars each year. Biodiversity of the Great Lakes ecosystem has been devastated by zebra mussel colonization as evidenced by declines in native clam populations and the loss of spawning habitat for some native fish species. Zebra mussels are efficient filter feeders and are linked to contaminant cycling and the collapse of forage populations, such as the shrimp-like amphipod *Diporeia*. By depleting the base of the food web, zebra mussels can impact important fish species such as trout and salmon. Costly recreational impacts associated with zebra mussels include the sharp shells littering Great Lakes beaches and the proliferation of the often toxic blooms of the blue-green algae *Microcystis*.

issg Database: Ecology of Dreissena polymorpha

Taxonomic name: *Dreissena polymorpha* (Pallas, 1771)

Synonyms: *Mytilus hagenii*, *Mytilus polymorpha* Pallas 1771, *Mytilus polymorphus* (Pallas), *Tichogonia chemnitzii* (Rossm.)

Common names: Dreiecksmuschel (German-Germany), Dreikantmuschel (German-Germany), dreisena (Lithuanian-Lithuania), Eurasian zebra mussel (English), moule zebra (French), racicznica zmienna (Poland), Schafklaumuschel (German-Germany), svitraina gliemene (Latvian-Latvia), tavaline ehk muutlik rändkarp (Estonian-Estonia), vaeltajasimpukka (Finnish-Finland), vandremusling (Danish-Denmark), vandringsmussla (Swedish-Sweden), wandering mussel (English), Wandermuschel (German-Germany, Austria), zebra mussel (English), zebra mussel (Swedish-Sweden), Zebramuschel (German-Germany), Zebra-Muschel (German)

Organism type: mollusc

Description

The shell of *D. polymorpha* is triangular (height makes 40-60 % of length) or triagonal with a sharply pointed shell hinge end (umbo). The maximum size of *D. polymorpha* can be 5 centimetres, though individuals rarely exceed 4 cm (Mackie *et al*. 1989). The prominent dark and light banding pattern on the shell is the most obvious characteristic of *D. polymorpha*. The outer covering of the shell (the periostracum) is generally well polished, a light tan in colour with a distinct series of broad, dark, transverse colour bands which may be either smooth or zigzag in shape.

The mussel attaches itself to hard surfaces by byssal threads which are secreted from a byssal gland just posterior to the foot. The byssal threads emerge from the between the valves through a byssal notch along the posterior margin. This byssal hold-fast distinguishes the zebra mussel from all other similar-sized or larger North American freshwater bivalves (McMahon 1990; GSMFC 2005).

Occurs in:

estuarine habitats, lakes, urban areas, water courses

Habitat description

Zebra mussel larvae are planktonic for 2-4 weeks, prior to beginning their juvenile phase by attaching themselves to substrates by means of byssal threads. Although the juveniles prefer a hard or rocky substrate, they have been known to attach to vegetation (Benson & Raikow 2008). In areas where hard substrates are lacking, such as a mud or sand, zebra mussels cluster on any hard surface available (Benson & Raikow 2008). Given a choice of hard substrates, zebra mussels do not show a preference. Zebra mussels attach to any stable substrate in the water column or benthos including rock, macrophytes, artificial surfaces (cement, steel, rope, etc.), crayfish, unionid clams and each other, forming dense colonies called *druses* (Benson & Raikow 2008). As adults, they have a difficult time staying attached when water velocities exceed two meters per second (Benson & Raikow 2008). Long-term stability of substrate affects population density and age distributions on those substrates. Within Polish lakes, perennial plants maintained larger populations than did annuals (Stanczykowska & Lewandowski 1993, in Benson & Raikow 2008). Populations on plants also were dominated by mussels less than a year old, as compared with benthic populations; as the mussel colonies grow they sink the macrophytes to which they are attached.

In their native region zebra mussels will colonise surface standing waters, surface running waters, the littoral zone of inland surface waterbodies, estuaries, brackish coastal lagoons, large estuaries and inland waters, and hard and soft bottom habitats (DAISIE 2006). In their occupied invaded range they will colonise similar habitats with the most typical habitats colonised being lakes, rivers, and estuaries, particularly places where there are firm surfaces suitable for attachment (DAISIE 2006). Zebra mussels tolerate temperatures from -20°C to 40°C; the best growth is observed at 18-20°C (DAISIE 2006). They tolerate brackish waters with salinity up to 7 ppt (DAISIE 2006). They are, however, extremely sensitive to rapid fluctuations in salinity; in the northern Gulf of Mexico, where tidal fluctuations are not great, zebra mussels are found to invade areas with salinities up to 12 ppt, however, they appear unable to tolerate salinities above 12 ppt for any extended period (GSMFC 2005). Zebra mussels prefer moderately productive (mesotrophic) temperate water bodies and occur from the lower shore to depths of 12 m in brackish parts of seas and to 60 m in lakes (DAISIE 2006). They are able to tolerate low oxygen content in water for several days and to survive out of water under cool damp conditions for up to three weeks (DAISIE 2006). Zebra mussel are most abundant in hard waters (30-50 mg Ca L-1) but occur in water with Ca concentrations as low as 12 mg Ca L-1 (Cohen and Weinstein 2001).

General impacts
For a detailed account of the environmental impacts of *Dreissena polymorpha* please read: *Dreissena polymorpha* Impacts Information. The information in this document is summarised below.

To date (2002) *D. polymorpha* has been the most aggressive freshwater invader worldwide (Karayayev *et al*. 2002). Once introduced, populations of zebra mussel can grow rapidly and the total biomass of a population can exceed 10 times that of all other native benthic invertebrates (Sokolova *et al*. 1980a; Karatayev *et al*. 1994a; Sinitsyna & Protasov 1994, in Karayayev *et al*. 2002)

Ecosystem Change: Most of the impacts of zebra mussels in freshwater systems are a direct result of their functioning as ecosystem engineers (Karayayev, *et al*. 2002). An individual zebra mussel can filter one to two liters of water each day; as a result high densities of zebra may cause major shifts in the plankton communities of lakes and rivers. Reductions in phytoplankton numbers and biomass also limit food to fish larvae and other consumers further up the food chain (Birnbaum 2006).

Modification of Natural Benthic Communities: The introduction of *Dreissena* is generally associated with increased benthic macroinvertebrate density and taxonomic richness (Ward & Ricciardi 2007). Biodeposition of organic wastes and dense colonization of the benthos by zebra mussels has also substantially altered benthic communities; many invertebrates benefit from the increased food resources and complex habitat, while benthic spawning and foraging fishes may be negatively impacted. Overall gastropod densities increased in the presence of *Dreissena*, but large-bodied snail taxa tended to decline (Ward & Ricciardi 2007).

Habitat Alteration: The high consumption of phytoplankton by zebra mussels results in increased water clarity, changing habitat characteristics and ecosystem functions (DAISIE 2006). The dense colonization of soft substrates can impede fish foraging (Beekey *et al*. 2004), and colonization of hard substrates affects spawning fishes (Marsden & Chotkowski 2001).

Predation: Zebra mussel populations significantly deplete plankton densities as a result of filter feeding.

Competition: Suspension-feeding species may experience increased competition for resources in the presence of high zebra mussel densities, as was reflected in the declines of sphaeriid clams in the Hudson River

(Strayer, *et al*. 1998).

Modification of Nutrient Regime: Zebra mussels may influence ecosystem processes such as nitrogen (N) cycling by increasing denitrification rates (Bruesewitz *et al*. 2006).

Threat to Endangered Species: Freshwater mussels (Order Unionoida) are the most imperiled faunal group in North America with 60% of the species considered endangered or threatened (Ricciardi *et al*. 1998). The zebra mussel represents a new stress to populations of these native mussels as it is a biofouling organism that smothers the shells of other molluscs and competes with suspension feeders for food (Ricciardi, *et al*. 1998).

Biofouling: Other mussels serve as substrate for settlement by *Dreissena*, and are energetically stressed and eventually starve as filter feeding is disrupted (Böhmer *et al*. 2001, in Birnbaum 2006)

Economic Impact: Negative economic impacts caused by *D. polymorpha* include those caused by fouling of intake pipes, ship hulls, navigational constructions and aquaculture cages; the zebra mussel may also reduce angling catches (Gollasch & Leppäkoski 1999; Minchin *et al*. 2002, in Birnbaum 2006)

Bioaccumulation: Zebra mussels may bioaccumulate pollutants which may poison animals further up the food chain (DAISIE 2006).

Uses
Bioindicator: Due to its sensitivity to anthropogenic influences *Dreissena* is important as a bioindicator and biomonitoring organism (Franz 1992, in Birnbaum 2006), and quantitative assessments have been conducted regularly since the 1960s in the context of water quality surveys (e.g. in the Rhine) (Schiller 1990, in Birnbaum 2006).

Products: Crushed shells of the zebra mussel can be used as fertiliser and poultry feed (Birnbaum 2006). Zebra mussels have been used as fishing bait and for fish meal production (DAISIE 2006).

Notes
The rapid expansion of the zebra mussel has been linked to its possession of planktonic veliger larvae, byssal threads (for attachment to hard surfaces) and high rates of growth and recruitment (Stanczykowska 1977; Carlton 1993, in Ricciardi Serrouya & Whoriskey 1995b).

The specific name *polymorpha* derives from the many variations in shell colour, pattern and shape (Birnbaum 2006).

Geographical range
Native range: Native to the drainage basins of the Black, Caspian, Aral and Azov seas (DAISIE 2006; Stanczykowska 1977 in Birnbaum 2006).
Introduced range: Introduced to north-west Russia, central and western Europe, Scandinavia, Britain, Ireland and North America (DAISIE 2006). During the 19th century the zebra mussel occupied most of inner water systems of western and central Europe, in the 1920s it appeared in Sweden, in the 1960s it was found in alpine lakes around the Alps and reached Italy in 1977, Ireland by 1994 and Spain by 2001 (DAISIE 2006). In 1988 it first appeared in Lake St. Clair and rapidly spread throughout the Great Lakes and large river drainages of North America (DAISIE 2006); it appeared on the west coast in California in 2008 Further range expansions are expected in temperate latitudes of the Northern Hemisphere (DAISIE 2006). Future expansion to South America, South Africa, Australia and New Zealand is possible (DAISIE 2006).

Introduction pathways to new locations

Floating vegetation/debris: Zebra mussels attach to floating material and may readily be transported on vegetation or flotsam.
Pet/aquarium trade: The zebra mussel is possibly introduced into the wild by aquarium dumping.
Ship ballast water: The main pathways of the expansion in the range of *D. polymorpha* are through oceanic shipping, in ballast water, and inland navigation, through solid ballast and other cargoes. Inland navigation transport increased since the opening of new waterways between eastern and central Europe at the beginning of the 1800s (Martens 1865, Rebhan 1984, Kinzelbach 1992, Dreyer 1995, Reinhold & Tittizer 1997, Nehring & Leuchs 1999, Gollasch 1996, Orlova 2002, Nehring 2002, in Birnbaum 2006), and within North America (e.g., Marsden & Hauser 2009).
Ship/boat hull fouling: Zebra mussel adults routinely attach to boat hulls and floating objects and are thus anthropogenically transported to new locations (Benson & Raikow 2008). Humans may spread zebra mussels considerable distances upstream on the hulls of commercial barges (Keevin *et al*. 1992, in Ricciardi Serrouya & Whoriskey 1995b) and to isolated lakes and rivers through fishing and boating activity (Carlton 1993, McNabb 1993, in Ricciardi Serrouya & Whoriskey 1995b).
Translocation of machinery/equipment: Results of a study by Ricciardi Serrouya & Whoriskey (1995b) suggest that, given temperate summer conditions, adult *Dreissena* may survive overland transport (e.g., small trailered boats) to any location within three to five days drive of infested waterbodies.
Transportation of habitat material: D. polymorpha could be transported with timber or river gravel and overland transport (DAISIE 2006).

Local dispersal methods
Aquaculture (local): Larvae may be transported during fish stocking and in bait buckets.
Boat: The zebra mussel's rapid dispersal throughout the Great Lakes, USA, and major river systems was due to its ability to attach to boats navigating these lakes and rivers (Benson & Raikow 2008).
Natural dispersal (local): During the pelagic state veligers and post-veligers are transported by currents (DAISIE 2006). Secondary dispersal occurs by the drifting of post-larvae and young adults using byssal and/or mucous threads (Martel 1993, DAISIE 2006).
On animals: Byssal threads have been an important adapatation for the zebra mussel's success in invading North America (Benson & Raikow 2008). Byssal threads develop in the larvae of some non-dresissenid endemic bivalves and are used to attach to fish gills, there are no endemic freshwater bivalves with byssal adult stages. Speculation exists that waterfowl can disperse zebra mussels, but this has yet to be conclusively demonstrated (Benson & Raikow 2008).
Other (local): Zebra mussel larvae may be transported on scuba divers' wetsuits, in felt soles of wading boots ,or in scientific sampling equipment.
Transportation of habitat material (local): Zebra mussel adults attach to aquatic floating plants and may disperse great distances this way (Horvath & Lamberti 1997).
Water currents: Its rapid dispersal throughout the Great Lakes was also due to the passive drifting of the larval stage (Benson & Raikow 2008).

Management information
The following control methods for zebra mussel are potentially useful in certain circumstances (Benson and Raikow 2008):

- Chemical Molluscicides: Oxidizing (chlorine, chlorine dioxide) and non-oxidizing
- Manual removal (pigging, high pressure wash)
- Dewatering/desiccation (freezing, heated air)
- Thermal (steam injection, hot water 32oC)
- Acoustical vibration
- Electrical current

- Filters/screens
- Coatings: toxic (copper, zinc) and non-toxic (silicone-based)
- Toxic constructed piping (copper, brass, galvanized metals)
- CO2 injection
- Ultraviolet light
- Anoxia/hypoxia
- Flushing
- Biological (predators, parasites, diseases)

Preventative measures: Preventing overseas transfer can only be achieved by mid-ocean exchange or by suitable disinfection of ballast water (DAISIE 2006). Certain guidelines and regulatory instruments may be applied in areas where the species does not yet occur (Gollasch 2006). For further details see the Ballast Water Management Convention of the International Maritime Organization (www.imo.org) and the Code of Practice for the Introduction and Transfer of Marine organisms of the International Council for the Exploration of the Sea (www.ices.dk).
Appropriate control measures (inspection, removal of attached mussels, drying, etc.) should be taken to minimise risk of inoculation by transfer of boats, fishing gears, etc (DAISIE 2006). Applying copper based anti-foulant coatings in new facilities may offer protection from *Dreissena polymorpha*. The use of retrofitted screens can be effective but such screens are difficult to apply to existing pipelines (Aldridge *et al*. 2006).

Physical: Physical removal using high-pressure water jets is feasible on easily accessed industrial facilities (Aldridge *et al*. 2006). Larvae suffer total mortality after exposure to ultrasonic vibration (22 to 800 kHz) for 3 minutes (Schalekamp 1971, in Birnbaum 2006), but the technical effort involved is prohibitive.

Chemical: Many chemicals will kill zebra mussels but the suitability of a particular chemical is determined by considerations of effect on water quality, residual concentrations, byproducts, cost and practicality. Chemicals which have proven moderately successful include molluscicides (such as Bayer 73; Birnbaum 2006), chloramines, chlorine dioxide, ozone, hydrogen peroxide, potassium permanganate, pH adjustment, and inorganic salts. Chlorination remains the only widespread method used. It must be dosed continuously for up to 3 weeks to achieve complete elimination, though dosing for 2-3 days is sufficient to remove the majority of attached mussels.
Microencapsulation of toxins in particles that are edible to zebra mussels has the potential to overcome the rejection and valve-closing response generally seen when zebra mussels are exposed to toxic substances. The active ingredient used is potassium chloride, which is not lethal to most organisms, including fish, at low doses but which is particularly toxic to freshwater bivalves (Aldridge *et al*. 2006). Another emerging control for *D. polymorpha* is the use of endocannabinoids, anandamide and other compounds which have been tested to inhibit zebra mussel byssal attachment. These naturally occurring and synthetic cannabinoids can serve as non-toxic efficacious zebra mussel anti-foulants (Angarano *et al*. 2009).

Biological control: Large-bodied molluscivores such as common carp, freshwater drum, and channel catfish can limit zebra mussel numbers in coastal wetlands. Densities of other molluscs were not affected, suggesting that fish can have a greater impact on numbers of attached zebra mussels than other benthic molluscs (Bowers & DeSzalay, 2007). Known predators also include roach, eel, sturgeon, diving ducks, crayfish and muskrats (Molloy *et al*., 1997).

Nutrition
Zebra mussels filter a wide range of size particles, but select only algae and zooplankton between 15 and 400 microns. Larval stages of the mussel feed on bacteria.

Reproduction
Zebra mussels have separate sexes, usually with a 1:1 ratio; fertilisation takes place externally (DAISIE 2006). Synchronised spawning occurs once mussels are greater than 8 mm (or females in their second year) and is influenced by water temperatures (DAISIE 2006). A mature female may produce one million eggs per year (DAISIE 2006). Spawning begins at 12 to 15ºC and is optimal at 14 to 16ºC or 18 to 20ºC (depending on sources) and may take place over a period of three to five months (DAISIE 2006; Benson & Raikow 2008). In natural ecosystems oogenesis occurs in autumn, with eggs developing until release and fertilization in spring; in areas of warm water or where the thermal regime has been altered, reproduction can occur continually throughout the year (Benson & Raikow 2008). Eggs are expelled by the females and fertilized outside the body by the males; over 40 000 eggs can be spawned in a reproductive cycle and up to one million in a spawning season (Benson & Raikow 2008).

Lifecycle stages
Fertilised eggs hatch into trocophores (40-60 microns, 1 to 2 days), which develop within a day into a free-swimming planktonic *veliger*. Veligers develop from a d-shaped to umbonal morphology, and remain planktonic for up to 4 weeks. Optimal temperature for larval development is 20 to 22oC (Benson & Raikow 2008). Larvae normally disperse by being passively carried downstream with water flow (Benson & Raikow 2008). The larvae develop into their juvenile stage once they have reached about 350 microns in size by settling to the bottom where they crawl about by means of a foot, searching for suitable substratum (Benson & Raikow 2008). They then attach themselves to substrates by means of a byssus, a cluster of threads produced by an external organ near their foot (Benson & Raikow 2008). They may mature within the first year of life under optimal conditions; maturity in the second year is more usual. Once attached, the life span of *D. polymorpha* is variable, but can range from 3 to 9 years (Benson & Raikow 2008). Adult mussels can voluntarily detach and move around the substrate to seek alternate locations.

This species has been nominated as among 100 of the "World's Worst" invaders

Reviewed by: J. Ellen Marsden, Rubenstein School of Environment and Natural Resources, University of Vermont,Burlington, USA.

Principal sources: Birnbaum, C. 2006. NOBANIS – Invasive Alien Species Fact Sheet – *Dreissena polymorpha*
Delivering Alien Invasive Species Inventories for Europe (DAISIE), 2006. *Dreissena polymorpha*

Compiled by: Profile revision: National Biological Information Infrastructure (NBII) & IUCN/SSC Invasive Species Specialist Group (ISSG)

To contribute information, please contact Shyama Pagad.

Last Modified: Tuesday, 22 September 2009

2012 Open Water Season

LAW COMPLIANCE CONTACTS	EDUCATIONAL CONTACTS	CRIMINAL CITATIONS	CIVIL CITATIONS	WRITTEN WARNINGS	VERBAL WARNINGS
16079	18060	302	615	1447	281

- These numbers reflect statewide work crew information from March – September (open water season), and do not represent individual enforcement officer efforts.
- Total years violation rate is currently at 14.7%
- August violation rate was 8.9%
- September (to date) 10% violation rate

Statewide Enforcement AIS Check Station Summary.

- To date the Division of Enforcement has conducted 12 check stations statewide.
- Resulting in 60 hours of operation.
- A total of 219 various water related items have been inspected.
- The average delay time is 4.3 minutes within the check station for no violation and 8.48 minutes with a violation.
- The average violation rate for these check stations combined is: 36.8%.

We are pleased that the violation rate is trending down but acknowledge the fact that we still have work that needs to be done. We continue to analyze our data and refine our work to provide the best protection we can for our natural resources. Our AIS enforcement work fits very well into our mission statement. " We are committed to serve the people of Minnesota by protecting natural resources, the environment and public safety through quality education and law enforcement."

Major Phil Meier
Operation Manager
MN DNR Enforcement
651-259-5045

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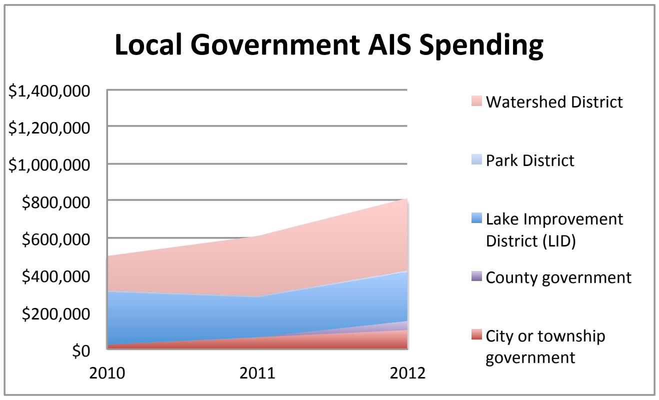
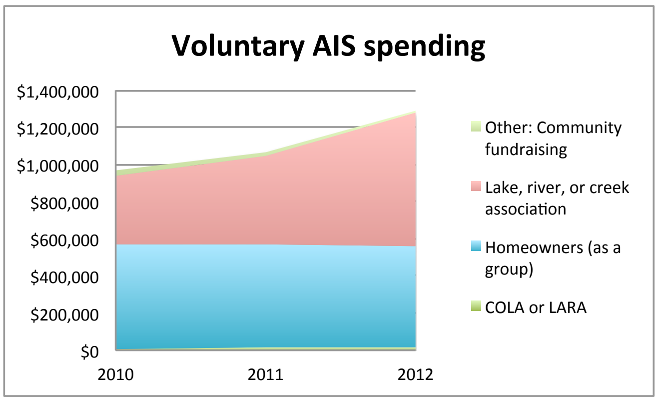
2010-2012 Minnesota AIS Spending by Local Government and Voluntary Sources[1,2]



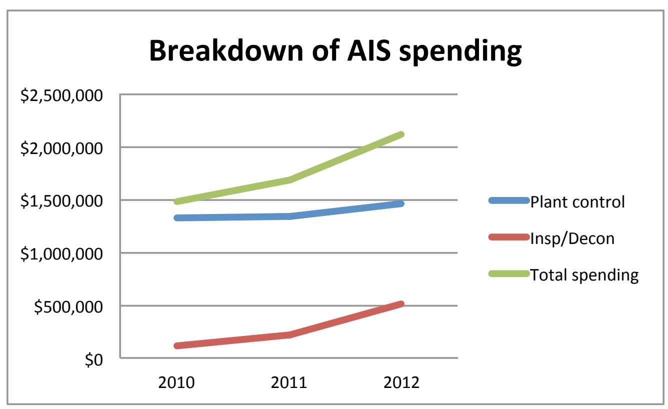


In the last 3 years…

- Local government units (LGU) and volunteer sources spent over $5M on AIS prevention and management
- Local AIS spending grew by 40%
- LGU spending increased by over 50% with significant increases planned for 2013. Watershed districts are leading the charge
- Volunteer spending increased by more than 35% with a doubling of lake and river association spending

In 2012 alone…

- LGU and volunteer sources spent over $2M on AIS prevention and management
- Over $1M was spent on Lake Minnetonka and select metro area waters
- Spending to control AIS plants was approximately 70% of the total
- Spending for AIS inspections and decontamination reached nearly 25% and is growing rapidly



[1] This data specifically excludes all MN-DNR expenditures and all state-funded grants.
[2] This data underestimates the AIS spending as not all lake and river organizations have supplied their spending data. In addition, the data collected from MN COLA organizations conservatively reports the actual spending.

MN COLA - Statewide AIS Facilities and Equipment Proposal

Economic comparisons of "Proposed" versus "At access" AIS inspection models

This material is provided as an attachment to our proposal to substantiate the cost effectiveness of the shared or "regional" model for AIS inspections and decontamination versus the more generally understood "at access" models.

This data comes from a 2012 proposal for a similar solution prepared by the Coalition of Minnehaha Creek Waters for 70 accesses on the accessible lakes in the Minnehaha Creek Watershed District. The data is for a complete new solution, including the one-time costs as well as the operating costs. It includes a mix of dedicated and regional inspection stations, similar to our LSOHC proposal.

This data compares this mixed dedicated and regional AIS inspection approach versus the current model of "at access" inspections coupled with occasional decontamination provided by the DNR.

In summary:

- The 5-year costs to deploy and operate the regional AIS inspection model are approximately 38% less than providing all accesses with staff to inspect.

- Ignoring the one-time costs, the operating costs are approximately 54% less on an annual basis.

Cost element	**Basis**	**2013**	**2014**	**2015**	**2016**	**2017**	**5 yr total**
Operating costs							
Inspection labor for Dedicated AIS inspection sites		414,206	426,632	439,431	452,614	466,192	2,199,074
Inspection labor for Regional AIS inspection sites		469,131	604,007	622,127	640,791	660,014	2,996,070
Inspector training for Dedicated AIS inspection sites	12 hours per inspector	5,040	5,191	5,347	5,507	5,673	26,758
Inspector training for Regional AIS inspection sites	12 hours per inspector	5,760	7,416	7,638	7,868	8,104	36,786
Call center costs		15,000	15,450	15,914	16,391	16,883	79,637
Educational handouts	For regional insp stations	8,000	10,000	10,000	10,000	10,000	48,000
Communications	Heavy in 1st 2 years	20,000	10,000	5,000	5,000	5,000	45,000
Regional AIS insp. station maintenance	$5,000	20,000	25,000	25,000	25,000	25,000	120,000
Maintenance for Dedicated site decontamination equipment	10%	8,000	8,000	8,000	8,000	8,000	40,000
Maintenance for Regional site decontamination equipment	10%	8,000	8,000	8,000	8,000	8,000	40,000
Program management		100,000	103,000	106,090	109,273	112,551	530,914
Total operating costs		1,073,137	1,222,696	1,252,547	1,288,443	1,325,416	6,162,239
One-time costs							
Acquire land for Regional AIS inspection stations	$50,000	200,000	50,000	0	0	0	250,000
Establish Regional AIS inspection stations	$30,000	120,000	30,000	0	0	0	150,000
Acquire decontamination equipment for Dedicated sites	$20,000	80,000	0	0	0	0	80,000
Acquire decontamination equipment for Regional sites	$20,000	80,000	20,000	0	0	0	100,000
Implement communications program		50,000					50,000
Program Manager		150,000	50,000				200,000
Total one-time costs		680,000	150,000	0	0	0	830,000
Total costs		1,753,137	1,372,696	1,252,547	1,288,443	1,325,416	6,992,239

For Comparison to an on-site model

Cost element	**Basis**	**2013**	**2014**	**2015**	**2016**	**2017**	**5 yr total**
Operating costs							
Annual inspector training	255 inspectors, 10 hours of training, $15/hr	38,250	39,398	40,579	41,797	43,051	203,074
Inspection labor	112 hrs/wk, 15 weeks, $15/hr, 70 insp. stations	1,764,000	1,816,920	1,871,428	1,927,570	1,985,398	9,365,316
Educational handouts	80% in 2012	8,000	10,000	10,000	10,000	10,000	48,000
Communications	Heavy in 1st 2 years	20,000	10,000	5,000	5,000	5,000	45,000
Total operating costs		1,830,250	1,876,318	1,927,007	1,984,367	2,043,448	9,661,390
Differential		-77,113	-503,622	-674,460	-695,924	-718,032	-2,669,151
Percent change		-4%	-37%	-54%	-54%	-54%	-38%

MN COLA - Statewide AIS Facilities and Equipment Proposal
Financial and operational assumptions

Access mix assumptions	
Public accesses addressed	2000
Percent of accesses with Dedicated inspection stations	5%
Number of Dedicated inspection stations	100
Percent of accesses with Regional inspection stations	95%
Accesses sharing each Regional inspection station	15
Number of Regional inspection stations	127

Decontamination mix assumptions	
Percent of Dedicated I/S with decontamination units	100%
Percent of Dedicated I/S with high-end decon units	50%
Percent of Dedicated I/S with low-end decon units	50%
Percent of Regional I/S with decontamination units	100%
Percent of Regional I/S with high-end decon units	5%
Percent of Regional I/S with low-end decon units	95%

Cost assumptions	
Land cost for each Regional inspection station	$35,000
Cost to establish (build-out) each Regional I/S	$40,000
Cost of high-end decontamination unit	$200,000
Cost of low-end decontamination unit	$20,000

Other assumptions	
Acres of land needed for each Regional I/S	10

MN COLA

Minnesota Coalition of Lake Associations

June 13, 2013

Lessard-Sams Outdoor Heritage Council
100 Rev. Dr. Martin Luther King Jr. Blvd.
State Office Building, Room 95
St. Paul, MN 55155

Dear Council Members,

We are very pleased to submit this request for funding to the Lessard-Sams Outdoor Heritage Council for fiscal year 2015.

The Minnesota Coalition of Lake Associations (MN COLA) represents 11 coalitions of lake, river, and creek associations throughout the state. Collectively we represent over 47% of the square miles of water in the state of Minnesota.

Our proposal would provide one-time funding for local and tribal government units and the MN DNR to accelerate their work on protecting our "publically protected aquatic habitat" from the further spread of aquatic invasive species (AIS). Your mission to "restore, protect, and enhance Minnesota's wetlands, prairies, forests, and habitat for fish, game, and wildlife" aligns perfectly with the intent of our efforts to stop the spread of AIS.

We already know the outcome of doing nothing, or too little: this is a crisis that we are only now beginning to recognize. The march of AIS infestation across our state is relentless. AIS have already damaged the fish habitat in Minnesota, and while research works on potential restoration opportunities, it is incumbent on Minnesota to avoid further damaging ecological impact.

A more comprehensive solution to stop the spread of AIS is necessary to avoid more lakes from becoming infested with one or more new species, including species that will be new to Minnesota.

This one-time funding request is only part of the solution, but a critically important early step. Local grass roots efforts are moving into the mainstream as local governments are pushed action to stop the spread of AIS.

As the Commissioner of the DNR reminds us, long-term funding is critical for these AIS programs. We couldn't agree more and will continue to work for new funding streams to support the operations of local AIS programs.

We look forward to hearing back from you on our proposal and working together to help protect Minnesota's outdoor heritage.

Sincerely,

Thomas K. Nelson

Thomas K. Nelson
President, MN COLA

Minnesota Coalition of Lake Associations (MN COLA) ● P.O. Box 1802 ● Detroit Lakes, MN 56502

MinnesotaCOLA@gmail.com

Minnesota Coalition of Lake Associations (MN COLA) is a statewide citizen network of County Lake and River Associations, representing the interests of over 40,000 lakeshore property owners, organized to protect and improve the waters and shorelands of the State of Minnesota.