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CONSERVATION OF NORTH AMERICA'S FRESHWATER MUSSEL FAUNA (UNIONOIDEA) FROM THE THREAT POSED BY THE EXOTIC ZEBRA MUSSEL (*DREISSENA POLYMORPHA*)

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ABSTRACT

The unionoid fauna of North America includes nearly 300 species, distributed primarily in the Mississippi River Basin and Coastal Plain drainages of the southeastern United States. The zebra mussel (*Dreissena polymorpha*) entered the Great Lakes, presumably in 1986, and was collected first in Lake St. Clair in 1988. Since its introduction, this species has spread rapidly and eliminated the native unionoids from Lake St. Clair, portions of Lake Erie, Detroit River, and other localized water bodies in the region. Zebra mussels passed from Lake Michigan to the Illinois River in 1991, and now infest the Ohio, Mississippi, Missouri, Tennessee, Cumberland, Tombigbee, Hudson, and numerous other mainstem rivers in the eastern and central United States. Populations fluctuate widely in abundance, achieving maximum densities in the Illinois River of more than 50,000/m^2 in 1993, but declining to less than 10,000/m^2 in 1994. To protect native unionoids at greatest risk to the zebra mussel invasion, the feasibility of using ponds and headwater rivers as refugia for riverine species is being tested. Mussels collected from the Tennessee and Cumberland rivers were cleaned and quarantined for one month, and distributed to ponds for long-term monitoring. Fifteen species of unionoids are being held in plastic-screen cages with flotation collars, and in various racks and pocket nets to monitor survival. Mean survival of species has ranged from 14% to 90% after 26 months in a farm pond. More than 5000 unionoids have been collected from the lower Tennessee River and Ohio River for relocation to sites secure from the zebra mussel. Because many populations of federally protected unionoids will eventually be colonized by zebra mussels, a geographic network of refugia is being considered to minimize a spasm of extinctions in the United States unequaled in modern times.

Key words: *Dreissena polymorpha, D. bugensis*, conservation, endangered fauna, mussels, North America, Unionoidea, zebra mussel.

INTRODUCTION

The introduction and subsequent spread of the exotic zebra mussel (*Dreissena polymorpha* Pallas 1771) into North America has occurred so rapidly that scientists in the United States and Canada have been unable to adequately monitor its progress and report its ecological effects in a timely manner. Many of the 297 species and subspecies of freshwater mussels (Unionoidea) in North America were in need of conservation efforts even before *D. polymorpha* began its epizoic colonization of native fauna (Williams *et al.*, 1993). The zebra mussel and its sibling quagga mussel (*D. bugensis* Andrusov 1897) are purportedly the most undesirable aquatic organisms to enter the North American continent, and there are numerous warnings and lessons that other nations should heed to prevent this most devastating exotic from entering navigable waterways in their respective countries.

Although the colonization of unionids (Unionidae) by zebra mussels in Europe was recorded earlier this century (Sebestyen, 1938; Zhadin, 1965; Wolff, 1969), there is sparse quantification of the infestations on unionids, except for data presented by Sebestyen (1938) and Lewandowski (1976). Sebestyen (1938) reported high numbers of dead unionids on the beaches of Lake Balaton, Hungary, in 1935 and 1936, about four years after colonization by *Dreissena polymorpha*. Lewandowski (1976) observed deformed valves and slower growth rates but concluded that the zebra mussel had no major effect on unionid populations. The remainder of the anecdotal reports is inadequate to assess severity or inconsequential nature of the interactions between these bivalve taxa (Schloesser *et al.*, 1994). The North American experience with zebra mussels is seemingly unparalleled or at least previously unrecorded within the native or expanded range of this species in Europe. The purpose of this paper, therefore, is to review the brief but dramatic chronology of entry and dispersal of the zebra mussel into the United States and to summarize studies that have documented the impacts of zebra mussels on native freshwater mussels.

Invasion of Great Lakes

The first zebra mussel in North America was discovered in June 1988 in the southern end of Lake St. Clair (Hebert *et al.*, 1989) (see Fig. 1). Although the exact date and location of introduction are unknown, benthic surveys in the early and mid-1980's failed to record this species in Lake St. Clair and connecting waterways (Hudson *et al.*, 1986; Griffiths, 1987; Nalepa & Gauvin, 1988). As judged by the reproductive cycle of this species and the size classes of zebra mussels collected in August 1988, the introduction most likely occurred in 1986. The vector for introduction was presumably a trans-Atlantic ship that discharged freshwater ballast containing veliger larvae. Ballast water discharge has been implicated in many of the recently discovered exotic species now prevalent in the Laurentian Great Lakes (Mills *et al.*, 1993).

From this localized site of introduction, the zebra mussel spread rapidly into the lower St. Clair River, southern half of Lake St. Clair, and eastern end of Lake Erie by summer 1989 (Griffiths *et al.*, 1991; Hebert *et al.*, 1991). Analysis of length-frequency distributions of zebra mussels at 16 sites in Lake St. Clair and Lake Erie in 1989-1990 indicated the presence of perhaps three cohorts (Griffiths *et al.*, 1991), with sizes up to 30 mm and a maximum density of 700,000/m^2 in the intake canal of the Monroe electrical generating plant. By late 1989, zebra mussels had spread from Lake St. Clair through Lake Erie to the western basin of Lake Ontario and had established isolated populations in Lake Huron. By late 1990, zebra mussels were well established in all but Lake Superior of the Great Lakes. The occurrence of localized populations in numerous harbors throughout the Great Lakes suggests that commercial shipping, boating, and fishing activities contributed to their rapid dispersal and establishment. The first evidence of a reproducing population within the Mississippi River drainage was recorded in the Illinois River in June 1991 (Tucker *et al.*, 1993).

Invasion of Inland Rivers

The escape of *Dreissena polymorpha* from the Great Lakes and colonization of the Illinois River (Fig. 1), a major tributary of the Mississippi River, occurred through veligers leaving Lake Michigan and colonizing the canals leading to the river. It's escape was undoubtedly facilitated by the Chicago Sanitation and Barge Canal linking Lake Michigan to the Illinois River. The dynamics of this introduced population have been closely monitored by the Illinois Natural History Survey at four sites in the Illinois River (Whitney *et al*, 1995). The population density was greatest in the lower end of the river, presumably because of the time period for veligers to settle out of the water column from Lake Michigan. The proliferation of subsequent sightings downstream of dams on the river and less than 100 km from the confluence with the Missis-

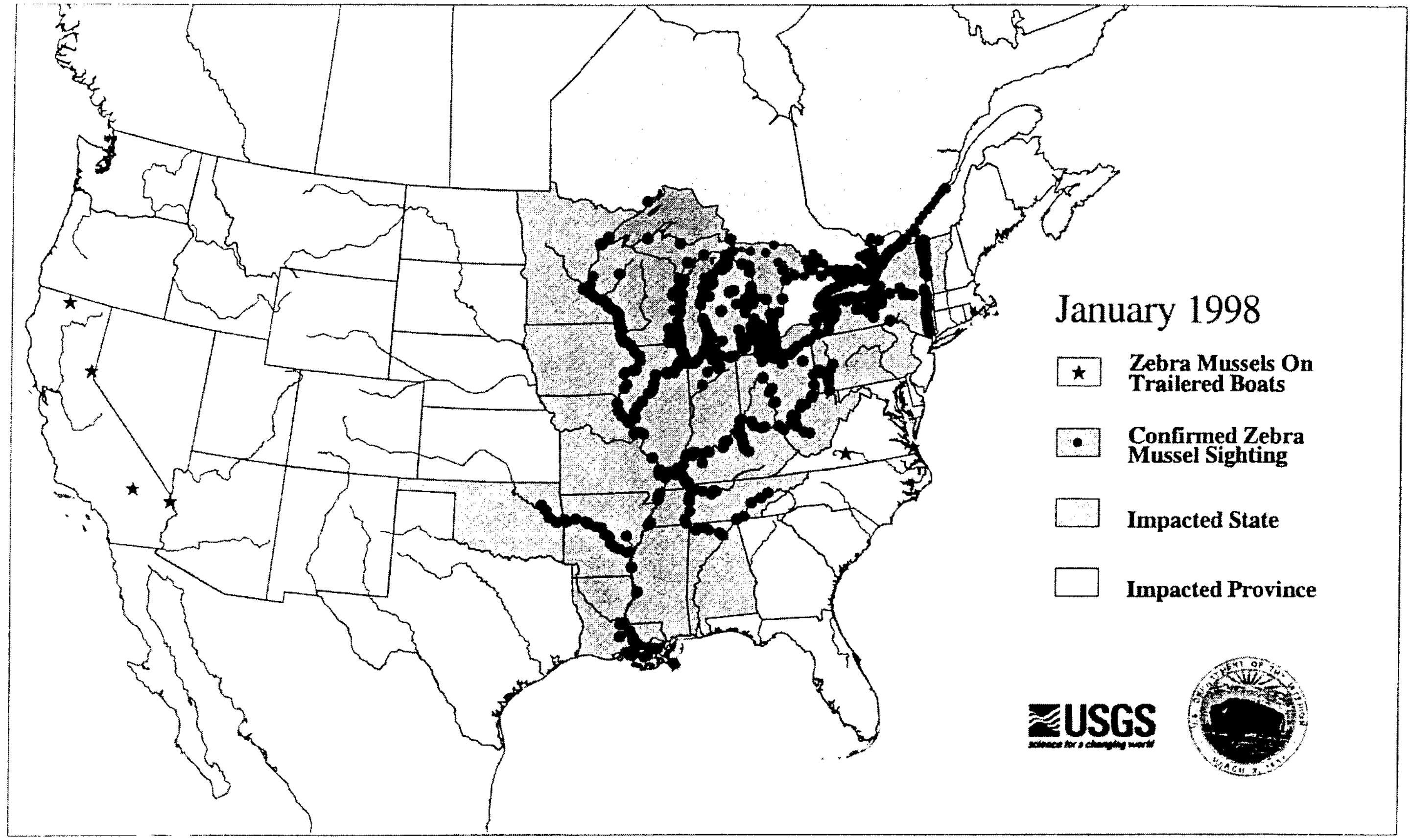

FIG. 1. Zebra mussel distribution in the United States (U.S. Geological Survey, 1998). These data are part of the U.S. Geological Survey's Nonindigenous Aquatic Species Data Base at the Florida Caribbean Science Center in Gainesville, Florida. This data base serves as a repository of distributional data for zebra mussels and other nonidigenous aquatic organisms. Information in the data base is collected from a variety of federal, state, local, and private agencies and is available to anyone upon request.

sippi River provided strong evidence that reproduction was ongoing in the river. Zebra mussel abundance exploded in summer 1993, achieving maximum densities of nearly 100,000/m^2 in the lower river. Zebra mussel densities increased in a downstream direction, and ranged from <1/m^2 at river mile 181 (Chillicothe) upstream to about 61,000/m^2 at river mile 5.5 (Grafton) downstream. At this time, downriver populations were almost entirely the 1993 cohort that settled in spring and summer 1993. Upriver populations contained age 1$^+$ (39%) and newly settled veligers (61%). The dense aggregation of zebra mussels covered all available hard substrata and carpeted expansive mud bottoms in the lower river.

By fall 1993, the population experienced high mortality, with up to 99% reduction in abundance of live zebra mussels at downriver sites (Table 1; see Whitney *et al.*, 1995). This decline in mean density continued through 1994, with no appreciable recruitment of a 1994 cohort at any of the sites. The population crash has been attributed to poor environmental conditions recorded in the summers of 1993 and 1994. Concentrations of dissolved oxygen were exceptionally low (1.7-3.0 mg/l) in the main channel, where the densest population was documented in 1993. During summer 1994, the river experienced extreme low flows, high water temperatures (>28°C) for 4-6 weeks, and low dissolved oxygen (<3 mg/l). Significant numbers of floating dead fish during July 1994 corroborates the hypothesis of density-dependent mortality from water quality degradation and stress to zebra mussels. Preliminary sampling of zebra mussels in the Illinois River in 1995 indicated a new wave of veliger settlement and a return to high population densities (S. Whitney, Illinois National History Survey, pers. comm.)

Since its introduction into the Illinois River in 1991, the zebra mussel has spread to every major river with commercial navigation in the Interior Basin (Fig. 1). The species now infests major waterways such as the Mississippi, Ohio, Tennessee, Cumberland, St. Lawrence, Hudson, Kanawha, and numerous other rivers (Tucker *et al*, 1993; Tucker, 1994; Strayer *et al*, 1994). Most of this spread has been attributed to barge traffic carrying high densities of zebra mussels, dropping adults during passage through locks and releasing veligers from barge-borne mobile populations to infest new areas. The spread in only five years in eastern North America has been phenomenal.

In addition to riverine systems, the zebra mussel has been transported to landlocked lakes in several states of the central United States (Table 2). A total of 54 inland lakes were infested in 1995; that number jumped to 116 lakes in 1998. The infestations of new lakes continue as the range and abundance of this species increase. The transport of adults attached to recreational boats, motors, and trailers, and possibly ve-

TABLE 1. Mean densities (no/m^2) of live zebra mussels recorded at five sites in the Illinois River in fall 1993 and 1994 (Whitney *et al.*, 1995).

Location (river mile)	1993	1994
Chillicothe (181.0)		
Peoria (162.3)	6998	1816
Meredosia (66.8)	12587	74
Montezuma (50.1)	8443	1630
Grafton (5.5)	34812	657

TABLE 2. Number of confirmed populations of zebra mussels in inland lakes of the United States, 1995 and 1998.

State	Lakes Infested	
	1995	1998
Michigan	29	67
New York	9	16
Indiana	3	15
Ohio	5	8
Wisconsin	4	7
Illinois	1	2
Vermont	1	1
Total	54	116

ligers in the live wells of boats, has become a major threat to most lakes with recreational fishing. Major reservoirs, particularly in the southeastern United States, attract numerous out-of-state fishers who transport their boats from zebra mussel-infested waters in northern lakes to more southerly fishing spots. Although most states have initiated a public education campaign about zebra mussels and caution boaters to treat or keep their boats out of water for several days if they have been exposed to zebra mussels, complete voluntary compliance is not possible. Thus, the zebra mussel continues its journey unabated across the United States. The continuing spread of *Dreissena polymorpha* is being monitored by the Florida Caribbean Science Center in Gainesville, Florida. New sightings are reported by agencies and individuals to the laboratory, where distribution records and a geographic information system are being used to track its dispersal across the country. Similarly, a Zebra Mussel Information Clearinghouse is being operated by New York Sea Grant Advisory Service to provide information on distribution, research, and other topics. In less than five years, the zebra mussel has spread to 19 states in the east-central United States, two provinces in Canada, and now jeopardizes some of the unionid fauna in all of these locations.

EFFECTS ON UNIONID POPULATIONS

Lake St. Clair

Infestation of native unionids was first reported in North America by Hebert *et al.* (1989) in Lake St. Clair during a preliminary survey. They reported degrees of infestation of 2-8 zebra mussels/unionid at locations with densities of 50-200 zebra mussels/m^2 of substrate. Subsequent sampling in 1989 recorded a dramatic increase in zebra mussel densities (1000's/m^2) and unionid infestations of up to 10,500 zebra mussels/unionid (Hebert *et al.*, 1991). The exposed surfaces of unionids were covered with a 4-6 cm thick layer of encrusted zebra mussels. The first evidence of lethal effects to unionids in Lake St. Clair was observed in 1990 by Hunter & Bailey (1992). The inverse relationship between zebra mussel densities and unionid densities at three sites in the lake and also the incidence of shell deformities inferred detrimental effects on native unionids. The more definitive study of Gillis & Mackie (1994) between 1990 and 1992 on the southern shore confirmed the preliminary data and worst fears of biologists (Table 3). Unionids decreased in abundance from a mean of 1.1/m^2 to 0/

m^2 at one site between 1990 and 1992, and from 1.95/m^2 to 0.43m^2 at a second site between 1991 and 1992. Unionid diversity in this section of the lake was 12 species in 1990, four species in 1991, and no species sampled in 1992 (Gillis & Mackie, 1994). They concluded that unionid density and species richness are significantly reduced within three to five years of initial infestation by zebra mussels.

Nalepa (1994) confirmed the rapid disappearance of unionids in a survey of 29 sites in 1986, 1990, and 1992 (Table 3). Mean density of unionids declined from a pre-zebra mussel density of 1.9/m^2 in 1986, to 0.7/m^2 in 1992. In the heavily infested southeastern portion of the lake, 97% of mussels were infested, and zebra mussel densities were about 400 per unionid in 1990. By 1992, no live unionids were collected in this area. In the lightly infested section of the lake (14% of unionids infested), infestations increased from <1 per unionid in 1990 to about 35 per unionid in 1992. Species richness declined from 18 unionids in 1986 to 12 in 1992. The consensus of Nalepa (1994) and Gillis & Mackie (1994) was that all unionids will be extirpated from Lake St. Clair in the next few years if current levels of zebra mussel density and infestation continue.

Lake Erie

The spread of zebra mussels throughout the western basin of Lake Erie occurred rapidly, not long after their discovery in Lake St. Clair. By 1989, densities exceeding 10,000/m^2 were reported in offshore waters (Mackie, 1993). Concurrently, zebra mussel infestations on native unionids increased from an average of 24 per unionid to 6,777 per unionid between February and August 1989. In September 1989, mean weight of epizoic zebra mussels exceeded the mean weight of infested unionid by a factor of about three (Schloesser & Nalepa, 1994). The effect of these infestations on unionid populations has been dramatic (Table 3), with no live unionids collected by fall 1990 (Schloesser & Nalepa, 1994). Maximum infestations on unionids were 11,550/live unionid and 14,393/dead unionid. Extensive clam-dredging at 17 sites that contained unionids in western Lake Erie confirmed the near-total eradication of unionids. Only four of the 191 unionids collected qualitatively were alive. Thus, the nearly complete

TABLE 3. Changes in the unionid fauna in Lake St. Clair and western Lake Erie following invasion by the zebra mussel.

Year	Mean Density (no/m^2)	Species richness	Sites with unionids
	Lake St. Clair (Nalepa, 1994)		
1986	1.9	18	25
1990	1.7	17	25
1992	0.7	12	14
	Lake St. Clair (Gillis & Mackie, 1994)		
1990	1.74	11	
1991	0.06	3	
1992	0	0	
	Western Lake Erie (Schlosser & Nalepa, 1994)		
1982	4	5	6
1991	0	0	0

disappearance of native unionids from western Lake Erie in two years post-infestation mirrors the experience in Lake St. Clair.

The continuing spread of zebra mussels into the other Great Lakes and along the St. Lawrence River provides a dire prognosis for the future of unionid populations in these water bodies. Future sampling and monitoring of inshore and offshore sites will undoubtedly record the decline and eventual extirpation of most native unionids from the Laurentian Great Lakes over the next few years.

Illinois River

The downstream trend in zebra mussel abundance in the Illinois River was also evident in infestation of native unionids. Zebra mussel densities and degrees of infestation on unionids peaked in summer 1993. Mortality of unionids was highest in the lower river, with a significant correlation (r^2=0.97) between unionid mortality in June 1994 and zebra mussel densities at the four sites in 1993 (Whitney *et al.*, 1995). Unionid mortality continued into fall 1994; recently dead animals either were heavily infested or covered with byssal threads indicative of previous infestation. The prolonged period of unionid mortality was attributed to lack of sufficient energy reserve over the winter and the environmentally stressful conditions that persisted in summer 1994. By fall 1994, infestations on unionids declined following the dramatic crash in zebra mussel abundance. At the most downriver site, mean infestation per unionid declined from about 255 zebra mussels/unionid to four zebra mussels/unionid in October 1994. However, a preliminary report on the Illinois River in 1995 indicated that zebra mussel densities were increasing again, killing native unionids that survived the initial pulse of zebra mussel abundance.

MECHANISMS OF MORTALITY

Infestations of zebra mussels are undoubtedly causing the mortality of unionids, but the exact mechanism(s) for death are unknown. Observations in field studies and laboratory analyses have identified eight factors presumed to affect unionid condition and survival (Schloesser & Kovalak, 1991): 1) impaired locomotion and burrowing behaviors, 2) prohibitive occlusion of valves, 3) prohibitive gaping of valves, 4) occluded apertures, 5) competition for food resources, 6) shell deformities, 7) exposure of unionids to toxic metabolic wastes, and 8) addition of weight to unionids promoting settlement in soft sediments. Some of these possible debilitating factors (*e.g.*, 5, 6) have been noted in European waters (Lewandowski, 1976), whereas others (*e.g.*, 7, 8) are more speculative and unsubstantiated.

Reduction in available food and loss of condition in unionids from feeding interference may be the most likely cause for mortality, as judged by available information (Gillis 1993; Haag *et al.* 1993; Gillis & Mackie, 1994). Gillis (1993) confirmed a reduced filtration rate in infested unionids by testing clearance rates at four levels of infestation and algae concentrations for the pink heelsplitter (*Potamilus alatus*). Zebra mussel infestations of up to 2000 per unionid caused total occlusion of apertures and interfered with siphoning behavior. Physiological studies by Hebert *el al.* (1991) and Haag *et al.* (1993) demonstrated a reduction in food reserves in infested vs. uninfested unionids. A decrease in lipid reserves by 50% and lower glycogen and cellulase activity was recorded in infested unionids versus unionids cleaned of infestation and monitored for four months in western Lake Erie. As noted by Schloesser *et al.* (1996), no study has resolved whether reductions in energy reserves result from reductions in available food supply or whether energy depletions are attributed to greater energy expenditures by infested unionids due to the biofouling mass of attached zebra mussels.

Physical impairment would seem to be an obvious detrimental effect of zebra mussel encrustations. Personal observations along the shore of Lake Erie indicate that live mussels with thick encrustations of zebra mussels littered the shoreline in 1992. Unionids were presumably dislodged from the substratum by wave action and carried ashore by subsequent waves. Gillis & Mackie (1994) noted many specimens of laterally compressed, thin-shelled species such as pink heelsplitters (*Potamilus alatus*) and papershells (*Leptodea fragilis*) dead on the lake bottom with large colonies of zebra mussels on their posterior ends, presumably dislodged from the excessive encrusted mass. Conversely, such thin-shelled but globose species as giant floaters (*Pyganodon grandis*) were observed less frequently dislodged and lying on the substratum. Tucker (1994) also observed encrusted unionids lying on substrata and in shoreline windrows along the banks of the Mississippi River.

Another aspect of physical impairment is the weight of colonized zebra mussels and its effect on mobility and orientation of unionids in sediments. Weight of attached colonies relative to weight of affected unionids has been reported as high as 8.5 times greater (Hebert *et al.*, 1991; Schloesser & Kovalak, 1991). Thus, unionids could be weighed down in soft sediment or expend considerable metabolic energy to maintain proper orientation or movement in the substratum. Schloesser & Kovalak (1991) speculated that mortality of infested unionids was likely due to smothering in the soft sediments of western Lake Erie. Impaired movement of infested unionids also was evident in the Mississippi River, where Tucker (1994) reported unionids living on a gravel bar, with zebra mussels on the unionids and attached to the substratum. The location where unionids were stranded in the river was attributed to their inability to burrow into the substratum.

Available studies in North America indicate that species of unionids are not equally vulnerable to infestation by zebra mussels, perhaps due to life history traits, sex, shell morphology, and other unknown factors. Preliminary studies by Haag *et al.* (1993) indicated that infested species of Lampsilinae had lower glycogen levels than infested species of Ambleminae collected at the same sites. Members of the Lampsilinae and Anodontinae have thin shells and are long-term brooders, perhaps making them more susceptible to infestations by zebra mussels. Conversely, the Ambleminae are generally thick-shelled species and are short-term brooders, providing perhaps greater tolerance or reduced vulnerability. Although several studies have documented greater mortality among thin-shelled species (Haag *et al.*, 1993; Gillis & Mackie, 1994), all species exhibit high mortality within two to three years of heavy infestation by zebra mussels. Thus, the long-term prognosis for all infested unionids is the same, namely, extirpation or near total mortality within three years of high zebra mussel densities.

Although various lakes in Europe have provided conditions for the co-existence of zebra mussels and unionids more than a century after invasion (Lewandowski & Stanczykowska, 1975), there is little evidence that co-existence will become part of the benthic dynamics in Lake St. Clair, Lake Erie, and other North American water bodies with complete overlaps in the range of dreissenids and unionids. The threshold density of zebra mussels above which unionid populations will suffer high mortalities has not been determined, although substrate densities equal to or greater than roughly 5000 zebra mussels/m^2 have been correlated with unionid mortality in Lake St. Clair (Hebert *et al.*, 1989, 1991). Similarly, maximum infestations of about 10,000 zebra mussels per unionid resulted in reduced lipid reserves in host unionids (Hebert *et al.*, 1991). However, infestation densities much lower than that for a prolonged period will undoubtedly lead to the demise of individuals and populations. The severity of decline in unionid populations affected by zebra mussel density, time period of infestation, species vulnerability, and other undefined factors is unpredictable in the short term. The prognosis for unionid populations in presently uninfested or recently infested waters of large rivers therefore is unknown at this time, but high mortality is anticipated. Small rivers without commercial navigation or reservoirs likely will be minimally affected by zebra mussels.

CONSERVATION OF ENDANGERED UNIONIDS

Until a specific pathogen is found to keep zebra mussel populations under biological control, there is no practical means of controlling the zebra mussel once it enters a river system. The options to protect and conserve native unionids therefore are limited. There are several conservation strategies being implemented to prevent the extirpation or possible extinction of unionids residing in the Mississippi, Ohio and Tennessee rivers. In the upper Ohio River, representative samples of mussels from regionally important populations are being collected, quarantined, and moved to experimental ponds at a federal research facility in West Virginia. The purpose of this project is to determine whether big-river species can survive and reproduce in ponds, with the possibility that brood stock can be established for propagation. Tributaries of the Ohio River lacking reservoirs, commercial navigation, or with limited recreational boating may not be susceptible to zebra mussel invasion or provide conditions marginally suited to the zebra mussel. The vulnerability and suitability of these habitats will be determined within the next few years to provide possible locations for the introduction of native unionids at risk in the main stem Ohio River.

To anticipate the threat posed by the zebra mussel to unionid beds in the Mississippi River, an experimental relocation project is underway in the upper Mississippi River to obtain information on growth and survival of seven unionid species removed from Pool 9 of the river and placed in a holding pond at the National Fish Hatchery in Genoa, Wisconsin (Welke *et al.*, 1995). Unionids are being held using different methods (treatments): suspended substrate-filled trays, buried substrate-filled trays, corrals, and suspended pocket nets. The unionids were collected in May 1995, scrubbed to remove zebra mussels, and transported to a small pond for a 35-day quarantine period. These unionids were divided into two groups and placed into the four treatments in the hatchery pond and into Pool 9 of Mississippi River. Preliminary results indicate >80% survival after quarantine for five species, and lower survival rates of 35% for deertoe (*Truncilla truncata*) and 48% for fragile papershell (*Leptodea fragilis*). The experiment will continue for at least two years, with bi-annual evaluations of survival and growth.

In the Tennessee River, the zebra mussel has spread to the upstream extent of commercial navigation in eastern Tennessee. The Tennessee River system had the highest diversity of unionids globally, and the threat of extinction to this endemic fauna is great. Although zebra mussel densities are low at this time, an increase in abundance is likely. In anticipation of a worst case scenario, the North Fork of the Holston River in Tennessee and Virginia has been targeted as a natural refugium for unionid species at greatest risk in the mainstem Tennessee River. Because the North Fork of the Holston River has no reservoir, no motorized craft, and limited access to possible vectors of zebra mussels, it has been selected for an experimental relocation program. The river historically contained more than 30 species of unionids that were eliminated by mercury contamination (Ortmann, 1918). The river has been in recovery for the last 25 years, and recent water quality monitoring and experimental transplants of unionids indicate that restoration of unionids can succeed. Species from the lower Tennessee River have been moved to this tributary for the purpose of establishing reproducing populations, should these species be eliminated from the mainstem Tennessee River by the epizoic zebra mussel.

As judged by the dramatic impact of zebra mussels on unionids in the North American Great Lakes, the establishment of natural or created refugia for highly vulnerable unionid species offers some hope to preventing a spasm of extinctions that is unprecedented in modern times. These proactive efforts, supported by affected states, the U.S. Fish and Wildlife Service, and the Biological Resources Division of the U.S. Geological Survey, will provide not only hope for jeopardized species but research results that will be used in the recovery of 69 federally endangered mussel species in the United States. Until the tools and techniques for propagation are perfected and made available to the U.S. Fish and Wildlife Service and the state fish and wildlife agencies, there is limited prospect for conserving the globally significant unionid fauna that resides in the United States.

CONCLUSION

The invasion and infestation of zebra mussels on native unionids, and subsequent mortalities of the latter in North America, are unprecedented. Studies in the Great Lakes seem to indicate that substratum densities of zebra mussels exceeding several thousand per 1 m^2 result in infestations of unionids that are lethal within two to three years. Thus, the entire cycle of zebra mussel appearance to unionid disappearance typically occurs within a four year period. With such an exponential increase in abundance, wide tolerance of environmental conditions, and a penchant for attachment to native unionids, the zebra mussel now threatens unionid populations in all large rivers of the Interior Basin of the United States and of many navigable waterways in eastern Canada (Clarke, 1992). Management options are few and mostly impractical (Schloesser *et al.*, 1996).

Federal regulatory agencies, responsible for navigation, interstate commerce, and the conservation of national biodiversity have been ineffective to coordinate efforts to contain the spread of this exotic mollusk. Commercial navigation and recreational boating continue to expand the zebra mussel's range, and educational campaigns aimed at these vectors of transport have largely been inconsequential. The Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990 was passed by the U.S. Congress to control the spread of zebra mussels, prevent further introductions of such species into the United States, and address the problem of ballast water discharges into freshwater. Under the Act, voluntary guidelines implemented in May 1991 request ships to exchange ballast water in the open ocean before entering the Great Lakes. In May 1993, these guidelines became mandatory under federal law. All ships operating outside the waters of the United States and Canada must exchange ballast water on the high seas (>2000 m depth) before entering the Great Lakes and the Hudson River, an aquatic corridor to the Great Lakes (Mills *et al*,. 1994). In spite of this significant law, there is no clear national policy on non-indigenous species introductions in the United States (Office of Technology Assessment, 1993). Prevention of the introduction of harmful species is the first and best line of defense. Without a comprehensive law or strict policy, introductions of exotic mollusks into the United States will continue to wreak havoc on native species, and jeopardize the fate of our globally significant molluscan diversity.

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